

Cryptomarasmius* gen. nov. established in the Physalacriaceae to accommodate members of *Marasmius* section *Hygrometrici

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Abstract: Phylogenetic placement of the infrageneric section *Hygrometrici* (genus *Marasmius* sensu stricto) in prior molecular phylogenetic studies have been unresolved and problematical. Molecular analyses based on newly generated ribosomal nuc-LSU and 5.8S sequences resolve members of section *Hygrometrici* to the family Physalacriaceae. The new genus *Cryptomarasmius* is proposed to accommodate members of *Marasmius* section *Hygrometrici*. Fourteen species belonging to section *Hygrometrici* whose available type specimens bear morphological features corresponding to the new genus are formally combined in *Cryptomarasmius*. Taxonomic transfers are made only for taxa in which type specimens have been studied and/or representative material sequenced. Although other species placed in section *Hygrometrici* may belong in *Cryptomarasmius*, further transfers are not proposed until additional studies on type material are conducted.

Key words: Agaricales, Marasmiaceae, phylogenetics, systematics, taxonomy

INTRODUCTION

Marasmius section *Hygrometrici* initially was established by Kühner (1933) as the infrageneric group “*Hygrometricae*”, to accommodate small species of *Marasmius* with a wiry, dark insititious stipe, non-collariate lamellae and a dark pileus composed of a hymeniform layer of broom cells (“éléments en brosse”). It was based on *M. hygrometricus* (V. Brig.) Sacc. and included *M. buxi* Fr., *M. hudsonii*

(Pers.:Fr.) Fr. and *M. capillipes* Sacc. (= *M. minutus* Peck). Kühner distinguished the *Hygrometricae* from his group *Epiphylleae* (= sect. *Epiphylli*) mainly on the presence of brown pigments in the pileus of the former, localized as membrane pigments of the thick-walled pileipellis broom cells. Singer (1958) accepted the group’s circumscription and added a few erroneous species (e.g. *M. leveilleanus* [Berk.] Pat., *M. rotalis* Berk. & Broome, *M. aciculiformis* Berk. & M.A. Curtis, *M. ventalloi* Singer), which later were removed and inserted into other sections of *Marasmius* (Singer 1962). Currently sect. *Hygrometrici* is circumscribed for species with these features: small basidiomes with convex, mostly darkly pigmented pilei less than 5 mm diam; non-collariate, pallid, adnate lamellae; wiry, darkly pigmented, insititious stipes; a hymeniform pileipellis composed of *Rotalis*-type broom cells, with or without fusoid, unornamented pileocystidia; cheilocystidia similar to the pileipellis elements; a cutis-type stipitipellis composed of darkly pigmented hyphae that are roughened, verrucose or diverticulate; inamyloid and non-dextrinoid, clamped hyphae; and basidiome formation on leafy debris. No fewer than 28 species have been accepted by various authors as belonging to the section (TABLE I). The greatest diversity of members of section *Hygrometrici* occur in tropical habitats, but because of their small size they are rarely collected and only a few European species are well known (e.g. *M. buxi*, *M. corbariensis* [Roum.] Singer, *M. hudsonii*, *M. minutus*).

The first phylogenetic analysis to include a member of section *Hygrometrici* was that of Tan et al. (2009) based on ITS sequences, in which four specimens of *M. micraster* Petch from Malaysia were included. The four sequences formed a monophyletic group on a long branch embedded among members of *Marasmius* sect. *Marasmius* subsections *Marasmius* and *Sicciformes* but without statistical support for this placement. During our ongoing study to clarify the infrageneric taxonomy in *Marasmius* based on nuclear large subunit (nuc-LSU), nuclear 5.8S and internal transcribed spacer (ITS) sequences datasets, the placement of five species of sect. *Hygrometrici* in *Marasmius* sensu stricto was revealed as problematical. Data presented herein support the recognition of a new genus in family Physalacriaceae to accommodate species

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TABLE I. Species accepted in *Marasmius* section *Hygrometrici*

Epithet	References
<i>aucubae</i> Neda	Neda and Doi 1998
<i>buxi</i> Fr.	Antonín and Noordeloos 1993
<i>celtibericus</i> G. Moreno & Raitviir	Moreno and Raitviir 1998
<i>corbariensis</i> (Roum.) Singer (= <i>hygrometricus</i> [V. Brig.] Sacc.)	Antonín and Noordeloos 1993 Kühner 1933
<i>crescentiae</i> Murrill	Singer 1976, Desjardin and Horak 1997a
<i>dicandinus</i> Desjardin, Retn. & E. Horak	Desjardin et al. 2000
<i>exustoides</i> Desjardin & E. Horak	Desjardin and Horak 1997b
<i>exustus</i> Berk. & M.A. Curtis	Desjardin and Horak 1997b
<i>fishii</i> G. Stev. & G.M. Taylor	Desjardin and Horak 1997b
<i>hudsonii</i> (Pers.: Fr.) Fr.	Antonín and Noordeloos 1993
<i>ilicis</i> Singer	Singer 1976
<i>kroumirensis</i> (Pat.) Sacc. & P. Syd.	Singer 1976
<i>magnoliae</i> Singer	Singer 1976
<i>micraster</i> Petch	Pegler 1986, Desjardin and Horak 1997b, Desjardin et al. 2000, Tan et al. 2009
<i>micraster</i> var. <i>brevipes</i> Corner	Corner 1996
<i>minutoides</i> Antonín	Antonín 2003, Antonín 2007
<i>minutoides</i> var. <i>angustisporus</i> Antonín	Antonín 2003, Antonín 2007
<i>minutus</i> Peck	Gilliam 1976, Antonín and Noordeloos 1993
<i>mulanjensis</i> Antonín	Antonín 2003, Antonín 2007
<i>nyikae</i> Antonín	Antonín 2003, Antonín 2007
<i>parviconicus</i> Pegler	Pegler 1982, Antonín 2007
<i>paucilamellatus</i> Desjardin & E. Horak	Desjardin and Horak 1997a
<i>pichinchensis</i> Singer	Singer 1989
<i>pseudominutus</i> Singer	Singer 1989
<i>sphaerodermatoides</i> Singer	Singer 1989
<i>sphaerodermus</i> Speg.	Singer 1976, Desjardin et al. 1992
<i>subalbidulus</i> Antonín	Antonín 2004
<i>thwaitesii</i> Berk. & Broome (= <i>echinosphaerus</i> Singer)	Pegler 1986, Antonín 2007 Singer 1964, 1976; Pegler 1969
<i>unilamellatus</i> Desjardin & E. Horak	Desjardin and Horak 1997b

currently accepted in *Marasmius* section *Hygrometrici* of family Marasmiaceae.

MATERIALS AND METHODS

For newly generated sequences, genomic DNA was extracted from approximately 1–5 mg fungal tissue excised from dried herbarium specimens. DNA extractions were performed with the E.Z.N.A.[®] Forensic DNA Extraction Kit according to the manufacturer's instructions with slight modifications (Omega Bio-tek Inc., Norcross, Georgia). The ITS rDNA region was amplified and cycle sequenced with the primers ITS1-F paired with either ITS4-B or ITS4-m (Gardes and Bruns 1993, Wannathes et al. 2009). The 5' region of the nuclear LSU rDNA (nuc-LSU) gene was amplified with primers LR0R paired with LR5 and cycle sequenced with LR0R, LR5 and LR21 as an internal primer (Vilgalys and Hester 1990).

Polymerase chain reactions (PCR) and cycle sequencing reactions were performed with either a GeneAmp PCR System 9600 (Applied Biosystems, Perkin-Elmer Corp., Norwalk, Connecticut) or a PCT100 (MJ Research Inc., Watertown, Massachusetts). Successful amplification was

verified by electrophoresis on a 1% agarose gel. PCR products were purified with ExoSAPIT (USB Corp., Cleveland, Ohio). Purified PCR products were cycle sequenced using dye-terminator reagents (Applied Biosystems Inc., Foster City, California). Cycle-sequence reaction products were precipitated with sodium acetate in ethanol and run on an ABI 3100 Genetic Analyzer System (Applied Biosystems Inc., Foster City, California). Sequence fragments were edited and assembled into contiguous sequences with Sequencher 4.2 (Gene Codes Corp., Ann Arbor, Michigan).

Preliminary analyses within a broad dataset of Agaricales.—To assess the phylogenetic placement of the putative segregate taxa belonging to section *Hygrometrici*, initial phylogenetic analyses were conducted by aligning newly generated nuc-LSU and 5.8S sequences of *Hygrometrici* taxa including the type species of section *Hygrometrici*, *Marasmius corbariensis* (TABLE II) and a sequence of the segregate marasmioid taxon *Marasmius epiphyllus* (GenBank AY207237) with the nuc-LSU/5.8S dataset of Matheny et al. (2006). Sequences were aligned manually in MacClade 4.04 (Maddison and Maddison 2001). The original 288-taxon dataset of Matheny et al. (2006) represents an

TABLE II. *Marasmius* section *Hygrometrici* taxon sampling, voucher data and GenBank accession numbers to nucleotide sequences generated for this study

Taxon	Voucher ID, (herbarium)	Collection locality	GenBank no.	
			nuc-LSU	ITS
<i>M. corbariensis</i> ^a	Nguyen 11.12.09 (SFSU)	California, USA	JN585128	JN601433
<i>M. exustoides</i>	DED 6249 (SFSU)	Hawaii, USA	JN585129	JN601434
<i>M. hudsonii</i>	Griffin 1209 (BRNM 658229)	England, UK	JN585130	JN601435
<i>M. micraster</i>	DED 7647 (SFSU)	Malaysia	JN585131	JN601436
<i>M. thwaitesii</i>	DED 5918 (SFSU)	Hawaii, USA	JN585132	JN601437

^a Indicates type species of section *Hygrometrici*. Voucher collections deposited at San Francisco State University Herbarium, USA (SFSU), and Moravian Museum Herbarium, Czech Republic (BRNM).

extensive sampling of the Agaricales including the type species of the genus *Marasmius* sensu stricto, *M. rotula*, and was provided by Dr P. Brandon Matheny (University of Tennessee at Knoxville). This alignment and all others used for this study have been submitted to TreeBASE and are available from the following URL: <http://purl.org/phylo/treebase/phylovs/study/TB2:S14142>.

Parsimony analyses were conducted in PAUP* 4.0b10 (Swofford 2002), using a two-step search protocol similar to the one described by Hibbett and Donoghue (1995). Heuristic searches were conducted with all characters weighted equally, gaps treated as missing data, branch swapping with tree bisection reconnection (TBR). The first step of the analysis consisted of 1000 random sequence addition replicates, saving no more than five trees per replicate, with MAXTREES set to auto increase. The most parsimonious trees from the first step were used as starting trees for the second parsimony search, with MAXTREES set to 15 000.

Maximum-likelihood (ML) analysis of the above dataset was performed in RaxML 3.0 (Stamatakis et al. 2005), employing a general time reversible model with gamma-distributed rate heterogeneity parameters (GTR+G). Maximum-likelihood bootstrap support (BS) was estimated using RaxML, with 1000 rapid bootstrap replicates under the same model as above. All likelihood parameter values for bootstrapping were estimated by the program with the default-run termination settings. Trees resulting from the bootstrap 1000 replicates were used to construct a 50% majority-rule consensus tree in PAUP* 4.10 to assess clade support in the ML estimations.

Analysis of section Hygrometrici in a focused Physalacriad dataset.—As a result of the initial analyses of the wider Agaricales dataset, a focused dataset of nuc-LSU sequences from taxa in the Marasmioid clade sensu Matheny et al. (2006) was constructed with emphasis on the family Physalacriaceae. This “Physalacriad” dataset consisted of 79 published sequences obtained from NCBI GenBank (<http://www.ncbi.nlm.nih.gov>) and our newly generated nuc-LSU sequences of *Hygrometrici*.

Parsimony analysis of the Physalacriad dataset was performed as described above. ModelTest 3.06 (Posada and Crandall 1998) was used to identify the likelihood model of sequence substitution that best reflects the new dataset. Maximum-likelihood analysis was conducted in PAUP* 4.0b10 (Swofford 2002) with the GTR+I+ Γ model

of nucleotide substitution. ML searches were iterative processes initiated by constructing a neighbor-joining (NJ) tree under the Jukes-Cantor (JC) distance model. The initial NJ tree was used to estimate six model parameters under maximum likelihood criterion, base frequency for each of the four base nucleotides, among site rate variation and gamma distribution parameters. These estimated model parameters are fixed, and the first of three ML searches was conducted. After this first ML search was completed the six model parameters were re-estimated from the resulting ML tree(s), fixed and the next ML search was initiated with starting trees obtained via NJ. This step was completed a third and final time, resulting in a total of three independent ML searches. On completion of the iterative searches, trees resulting from all three searches were compared to ensure that they had converged on equally likely topologies. Maximum likelihood bootstrap support (BS) was estimated with 300 bootstrap replicates under the GTR+I+ Γ model of sequence substitution. Calculation of majority-rule consensus tree to assess clade support was performed as described above.

Estimation of Bayesian posterior probability of clade support was performed with MrBayes 3.1.2 (Ronquist and Huelsenbeck 2003) under a GTR+I+ Γ model of nucleotide substitution as determined by prior nucleotide substitution model testing. This analysis consisted of two parallel searches run with eight Metropolis-coupled Markov chains with Monte Carlo simulation (MCMCMC) for 5 000 000 generations with random starting trees. Chain convergence and stationarity was assessed with Tracer 1.5 (Rambaut and Drummond 2009) by plotting $-\ln L$ and estimated parameter values against number of analysis generations. Once stationarity was achieved, chains were sampled every 500 generations. Bayesian posterior probabilities (BPP) to assess clade support in the ML estimations were calculated by constructing majority-rule consensus tree in PAUP* using trees remaining after the burn-in.

To test the monophyly of *Marasmius* sensu lato as sampled in our dataset, including the taxa currently recognized in section *Hygrometrici*, a constraint tree enforcing the monophyly of these taxa was constructed in MacClade 4.04 and used in ML analyses in PAUP* with the same search procedure and model of nucleotide substitution as above. All resulting most likely constrained topologies were compared with the unconstrained ML

topology with the Shimodaira-Hasegawa test (Shimodaira and Hasegawa 1999) as implemented in PAUP* 4.10 with REL test distribution as generated by 1000 bootstrap replicates.

RESULTS

Preliminary analyses within a broad dataset of Agaricales.—MP analyses of the nuc-LSU/5.8S sequences of the members of *Hygrometrici* and a downloaded sequence of *Marasmius epiphyllus* (GenBank accession number AY207237), aligned to the Agaricales nuc-LSU/5.8S dataset of Matheny et al. (2006), recovered 15 000 most parsimonious trees (7653 steps, CI = 0.136, RI = 0.538). The strict consensus tree places the representative members of *Hygrometrici* within the family Physalacriaceae (data not shown). The represented members of *Hygrometrici* are not resolved as monophyletic in the MP analysis. Four of the represented *Hygrometrici* taxa (*M. corbariensis*, *M. exustoides*, *M. micraster*, *M. thwaitesii*) are resolved as a monophyletic clade in the strict consensus of 15 000 most parsimonious trees. The European collection of *M. hudsonii* is resolved as a sister taxon to a member of genus *Cyptotrama*. This group is resolved as a sister clade to members of the genus *Xerula* and embedded within the lineage containing *Marasmius epiphyllus*, the type species of *Marasmius* section *Epiphylli*. Also resolved within this lineage are representatives of the genera *Mycaureola* and *Gloiocephala*.

The ML analysis of the nuc-LSU/5.8S sequences of the members of *Hygrometrici* with the Agaricales nuc-LSU/5.8S dataset of Matheny et al. (2006) resulted in a single most likely topology (SUPPLEMENTARY FIG. 1). The ML analysis also resolves the representative members of *Hygrometrici* within the family Physalacriaceae with maximum-likelihood bootstrap (BS) support of 99%. Again, the represented members of *Hygrometrici* are not resolved as monophyletic in this analysis. Four of the represented *Hygrometrici* taxa (*M. corbariensis*, *M. exustoides*, *M. micraster*, *M. thwaitesii*) are resolved as a monophyletic clade (BS 94%). This core *Hygrometrici* clade, containing the type species of section *Hygrometrici* (*M. corbariensis* = *M. hygrometricus*), is not resolved with the type species of *Marasmius* but is placed sister to a clade containing representatives of the genera *Flammulina*, *Cylindrobasidium*, *Physalacria*, *Gloiocephala*, *Xerula* and others (BS 97%). As in the MP analysis, the European collection of *M. hudsonii* is resolved as a sister taxon of *Marasmius epiphyllus* (BS < 50%). The *M. hudsonii/epiphyllus* lineage is resolved as sister to a clade containing members of the genera *Xerula* and *Cyptotrama* (BS < 50%).

Analysis of section Hygrometrici in a focused Physalacriad dataset.—MP analyses of the nuc-LSU sequences of the Physalacriad dataset with members of *Hygrometrici* recovered 15 000 most parsimonious trees (963 steps, CI = 0.388, RI = 0.7888). The strict tree also places the representative members of *Hygrometrici* within the family Physalacriaceae (data not shown). The represented members of *Hygrometrici* again are not resolved as monophyletic in this MP analysis. As in the wider Agaricales analyses, four of the represented *Hygrometrici* taxa (*M. corbariensis*, *M. exustoides*, *M. micraster*, *M. thwaitesii*) are resolved as a monophyletic clade in the strict consensus of 15 000 most parsimonious trees. *Marasmius hudsonii* is resolved as a sister taxon to a clade consisting of several representatives of *M. epiphyllus*.

Each of the ML analysis iterations of the nuc-LSU sequences of the members of *Hygrometrici* with the Physalacriad dataset converged on two most likely topologies, one of which is illustrated (FIG. 1, $-\ln L = 6126.99106$). Bootstrap support above 50% for nodes as calculated from 300 bootstrap replicates are presented. Bayesian analyses reached an average standard deviation of split frequencies below 0.03 after 1 236 000 generations, and the initial 2472 trees recovered were excluded as the burn-in. The remaining 7528 trees were used to calculate Bayesian posterior probabilities.

The ML analysis of the focused Physalacriad dataset also resolves the representative members of *Hygrometrici* within the family Physalacriaceae (BPP 0.81, BS 61%). The represented members of *Hygrometrici* are not resolved as monophyletic in this analysis as well. Again, four of the represented *Hygrometrici* taxa (*M. corbariensis*, *M. exustoides*, *M. micraster*, *M. thwaitesii*) are resolved as a monophyletic clade (BPP 0.82, BS 63%). This core *Hygrometrici* clade containing the type species of section *Hygrometrici* (*M. corbariensis* = *M. hygrometricus*) is resolved as a sister lineage of a clade containing representatives of the genera *Rhodotus*, *Physalacria* and *Cylindrobasidium*. The core *Hygrometrici* + *Rhodotus* + *Physalacria* + *Cylindrobasidium* clade is resolved as sister lineage of the genus *Flammulina* in a weakly supported monophyletic lineage (BPP 0.76, BS < 50%).

The European collection of *M. hudsonii* is resolved as a sister taxon of the *Marasmius epiphyllus* clade with BPP 0.58, BS < 50% support. The core *Hygrometrici* clade and the core *Epiphylli* clade are resolved in a wider unsupported monophyletic lineage within the Physalacriaceae that includes *Strobilurus*, *Rhodotus*, *Physalacria*, *Cylindrobasidium* and *Flammulina*.

Constrained ML analyses for the Shimodaira-Hasegawa test recovered two most likely topologies

TABLE III. Shimodaira-Hasegawa (1999) likelihood test values comparing topologies resulting from unconstrained and constrained maximum likelihood analyses

Topology	$-\ln L$	Diff. $-\ln L$	P
Unconstrained maximum likelihood analysis (FIG. 1)	6126.99016	(best)	—
Monophyly <i>Marasmius</i> s.s. + sect. <i>Hygrometrici</i> Most likely constraint topology	6397.99518	271.00502	< 0.001
Monophyly <i>Marasmius</i> s.s. + sect. <i>Hygrometrici</i> Second most likely constraint topology	6398.66537	271.67521	< 0.001

The most likely trees according to likelihood score are provided for each analysis. All constrained trees enforcing the monophyly of *Marasmius sensu stricto* + *Hygrometrici* taxa sampled can be rejected based on the results of the S-H test ($P < 0.01$).

differing only in branch lengths and placement of terminal, non-Marasmiod taxa. The two constrained topologies did not differ significantly in their likelihood scores. All topologies resulting from the constraint analysis enforcing the monophyly of *Marasmius sensu stricto* and *Hygrometrici* taxa were rejected as significantly ($P < 0.001$) less likely than the unconstrained ML topology (TABLE III), supporting the recognition of *Hygrometrici* taxa as distinct from those currently treated in *Marasmius sensu stricto*.

TAXONOMY

Cryptomarasmius T.S. Jenkinson & Desjardin, gen. nov.

Mycobank MB561776

Synonym: *Marasmius* Sect. *Hygrometrici* Kühner, Botaniste 25:95. 1933 (ut *Hygrometricaceae*)

Basidiomes tiny, marcescent. Pileus less than 5 mm diam, convex, smooth to rugulose, rarely spinulose, even or striate, dry, usually darkly pigmented (yellowish brown, orangish brown, grayish brown, brown, dark brown), rarely pallid (yellowish white to tan). Lamellae vein-like to well developed, rarely absent and with smooth hymenophore, free to adnate, never collariate, remote to subdistant, pallid. Stipe central, rarely absent, wiry-filiform, tough, insititious, glabrous or pruinose, darkly pigmented at maturity (brown to dark brown or black); rhizomorphs usually absent, rarely present. Basidiospores ellipsoid to fusoid or lacrymoid, smooth, hyaline, inamyloid, thin-walled; white in deposit. Basidioles fusoid. Basidia four-spored. Pleurocystidia absent or present, lageniform to fusoid, unornamented. Cheilocystidia present, of *Rotalis*-type broom cells or lageniform to fusoid and

nonornamented, often dimorphic. Pileipellis a hymeniform layer of *Rotalis*-type broom cells, rarely some cells lacking setulae, with or without scattered pileocystidia, rarely composed of chains of *Rotalis*-type cells. Pileocystidia (when present) lageniform to fusoid, nonornamented or rarely with a few setulae centrally. Stipitipellis a cutis of roughened to verrucose or diverticulate (rarely smooth), thick-walled, darkly pigmented hyphae. Caulocystidia absent or present, as small outgrowths or terminal cells, cylindrical to fusoid, nonornamented. Setae absent. Hyphae inamyloid, with clamp connections. Solitary to scattered, usually on leafy debris or rarely on bark.

Etymology: *Crypto-* hidden, referring to the historical placement of sect. *Hygrometrici* hidden within the genus *Marasmius*, as well as to the tiny, often hidden basidiomes of representative species.

Type species: *Marasmius hygrometricus* (V. Brig.) Sacc., Syll. Fung. 5:543. 1887. Basionym: *Agaricus androsaceus* var. *hygrometricus* V. Brig., in F. Brig., Hist. Fung. Reg. Neapol.: 87.1852. Currently accepted name: *Marasmius corbariensis* (Roum.) Sacc., Syll. Fung. 20:14. 1911.

Cryptomarasmius corbariensis (Roum.) T.S. Jenkinson & Desjardin, comb. nov.

Mycobank MB561778

Basionym: *Agaricus corbariensis* Roum., Revue Mycol. 2:198. 1880. Type specimen: France, Quillan, 1879, C. Roumeguere, in Roumeguere – Fungi Gallici exsiccati, No. 801 (Lectotype, BP 18081; Isolectotypes, BR, K).

Taxonomic transfers.—Formal transfers are made herein for those taxa that we have studied the type specimens and/or sequenced representative material.

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Armillaria. Numbers associated with branches in boldface to the left of / are Bayesian posterior probabilities, numbers to the right are maximum likelihood bootstrap values > 50% (300 replicates). Sequences obtained from GenBank are indicated by accession number.

Although we recognize that other species in sect. *Hygrometrici* (TABLE I) might belong in *Cryptomarasmius*, we do not propose their formal transfer until additional studies of type material are conducted.

Cryptomarasmius aucubae (Neda) T.S. Jenkinson & Desjardin, comb. nov.
Mycobank MB561779

Basionym: *Marasmius aucubae* Neda, Mem. Nat. Sci. Mus., Tokyo 31:92. 1998 [ut *Marasmius aukubae*]. Type specimen: Japan, Kumamoto Pref., Kumamoto City, 23 June 1998, *S 615* (TNS) – representative material sequenced by Neda and Doi 1998.

Cryptomarasmius crescentiae (Murrill) T.S. Jenkinson & Desjardin, comb. nov.
Mycobank MB561780

Basionym: *Marasmius crescentiae* Murrill, N. Amer. Fl. (New York) 9(4):259. 1915. Type specimen: Cuba, 5 mi east of Santiago de las Vegas, 11 Sept. 1904, *F.S. Earle 184* (NY) – type specimen examined by DED.

Cryptomarasmius dicandinus (Desjardin, Retn. & E. Horak) T.S. Jenkinson & Desjardin, comb. nov.
Mycobank MB561781

Basionym: *Marasmius dicandinus* Desjardin, Retn. & E. Horak, Sydowia 52(1):140. 2000. Type specimen: Indonesia, Bali, Desa Belimbing, temple south of Sanda, 16 Jan. 1999, *A. Retnowati 135* (SFSU) – type specimen examined by DED.

Cryptomarasmius exustoides (Desjardin & E. Horak) T.S. Jenkinson & Desjardin, comb. nov.
Mycobank MB561782

Basionym: *Marasmius exustoides* Desjardin & E. Horak, Bibliotheca Mycol. 168:114. 1997. Type specimen: New Zealand, South Island, Prov. Canterbury, Springfield, Mt. Grey, Kowai Bush, 28 Sept. 1967, *Horak 67-140* (PDD) – type specimen examined by DED.

Cryptomarasmius fishii (G. Stev. & G.M. Taylor) T.S. Jenkinson & Desjardin, comb. nov.
Mycobank MB561783

Basionym: *Marasmius fishii* G. Stev. & G.M. Taylor, Kew Bull. 19(1):36. 1964. Type specimen: New Zealand, North Island, Rotorua, Lake Ngapouri, 3 Sept. 1960, *Fish in Taylor 39* (K) – type specimen examined by DED.

Cryptomarasmius ilicis (Singer) T.S. Jenkinson & Desjardin, comb. nov.
Mycobank MB561784

Basionym: *Marasmius ilicis* Singer, Lilloa 26:142. 1953. Type specimen: Brazil, ad folia dejecta *Ilicis microdontae*, *Singer B88* (Holotype LIL; Isotype MICH) – isotype specimen examined by DED.

Cryptomarasmius kroumirensis (Pat.) T.S. Jenkinson & Desjardin, comb. nov.
Mycobank MB561785

Basionym: *Androsaceus kroumirensis* Pat., Cat. Rais. Pl. Cellul. Tunisie (Paris): 32. 1897. Type specimen: Tunisia, Aïn Darham, July 1895, *N. Patouillard* (FH) – type specimen examined by DED.

Cryptomarasmius magnoliae (Singer) T.S. Jenkinson & Desjardin, comb. nov.
Mycobank MB561786

Basionym: *Marasmius magnoliae* Singer, Mycologia 37(4):435. 1945. Type specimen: USA, Florida, Gainesville, Experimental Station Grounds, 16 May 1943, *Singer FI4110* (FLAS) – type specimen examined by DED.

Cryptomarasmius micraster (Petch) T.S. Jenkinson & Desjardin, comb. nov.
Mycobank MB561787

Basionym: *Marasmius micraster* Petch, Trans. British Mycol. Soc. 31:42. 1948. Type specimen: Sri Lanka, Central Prov., Kandy District, Peradeniya, 21 Oct. 1914, *Petch 4195* (K) – type specimen examined by DED.

Cryptomarasmius minutus (Peck) T.S. Jenkinson & Desjardin, comb. nov.
Mycobank MB561788

Basionym: *Marasmius minutus* Peck, Ann. Rep. N. Y. St. Mus. Nat. Hist. 27:97. 1875 [1874]. Type specimen: USA, New York, Catskill Mts., Sandlake, July 1873, *C.H. Peck* (NYS) – type specimen examined by DED.

Cryptomarasmius paucilamellatus (Desjardin & E. Horak) T.S. Jenkinson & Desjardin, comb. nov.
Mycobank MB561789

Basionym: *Marasmius paucilamellatus* Desjardin & E. Horak, Bibliotheca Mycol. 168:53. 1997. Type specimen: Papua New Guinea, Morobe District, Bulolo, Nauwatabanda, 25 Nov. 1971, *Horak 71-342* (Holotype ZT; Isotype SFSU) – type specimen examined by DED.

Cryptomarasmius sphaerodermus (Speg.) T.S. Jenkinson & Desjardin, comb. nov.
Mycobank MB561790

Basionym: *Marasmius sphaerodermus* Speg., Anal. Soc. Cient. Argent. 9:163. 1881. Type specimen:

Argentina, Buenos Aires, La Plata River (LPS) – material no longer extant.

Cryptomarasmius thwaitesii (Berk. & Broome) T.S. Jenkinson & Desjardin, comb. nov.

Mycobank MB561791

Basionym: *Marasmius thwaitesii* Berk. & Broome, J. Linn. Soc., Bot. 14:39. 1873. Type specimen: Sri Lanka, Central Prov., Kandy District, Peradeniya, Oct. 1868, Thwaites 827 (K) – type specimen examined by DED.

DISCUSSION

In the limited phylogenetic studies of *Marasmius* that have included members of section *Hygrometrici*, members of this section always are resolved on an exceptionally long branch indicating considerable genetic divergence from all other members of the genus (Tan et al. 2009). Our Shimodaira-Hasegawa test in which members of *Hygrometrici* were constrained within the genus *Marasmius* sensu stricto rejects the monophyly of the genus *Marasmius* containing section *Hygrometrici* (TABLE III). The problems of limited taxon sampling of members of *Hygrometrici*, coupled with the a priori assumption that these species fall within the genus *Marasmius*, have hindered their phylogenetic placement. The results of analyses conducted for this study demonstrate that members of *Hygrometrici* do not share most recent common ancestry with members of *Marasmius* sensu stricto.

The putative segregate section *Hygrometrici* is polyphyletic with *M. hudsonii* resolved apart from a core *Hygrometrici* clade (FIG. 1, SUPPLEMENTARY FIG. 1). All members of section *Hygrometrici* examined however are resolved within the family Physalacriaceae (Dentinger and McLaughlin 2006) in each of our analyses conducted to address their placement. The core *Hygrometrici* clade, which includes the type species of section *M. corbariensis* (= *M. hygrometricus*), is consistently resolved as a monophyletic lineage and has phylogenetic affinity to the genera *Cylindrobasidium*, *Physalacria*, *Rhodotus* and *Flammulina* in the best estimate of their phylogenetic placement, the ML analysis of the focused Physalacriad dataset (FIG. 1).

The ML analyses of the focused Physalacriad LSU dataset (FIG. 1) place *M. hudsonii* sister of the clade made up of representatives of *M. epiphyllus*. *Marasmius epiphyllus*, type species of *Marasmius* section *Epiphylli*, has been shown as closely allied with *Strobilurus* and *Rhizomarasmius* (Owings 1997, Owings and Desjardin 1997), two genera currently

accepted in family Physalacriaceae. The core *Hygrometrici* clade is phylogenetically distinct from members of the segregate marasmioid section *Epiphylli*, which also awaits segregation from *Marasmius* sensu stricto and formal recognition as a distinct lineage in the Physalacriaceae. Closer examination of the macro- and micromorphology of *M. hudsonii* reveal many similarities to *M. epiphyllodes* of section *Epiphylli* (Antonín and Noordeloos 1993) and might be indicative of evolutionary homology. For example, both form pale (white to cream) pilei, often with poorly developed, anastomosing lamellae, and have a pileipellis formed of *Rotalis*-type broom cells in addition to unique exudative, lageniform cells. In combination with the molecular data presented here, *M. hudsonii* appears more closely related to *M. epiphyllus* than to members of section *Hygrometrici* and is excluded from the core *Hygrometrici* lineage. Establishment of a new genus for the traditional *Marasmius* sect. *Epiphylli*, including *M. hudsonii* will be proposed by other researchers (Antonín et al. in prep).

These data support the elevation of the core *Hygrometrici* clade to generic rank. Section *Hygrometrici* was the only exclusively non-dextrinoid section of *Marasmius* sensu Wilson and Desjardin (2005) and Antonín and Noordeloos (1993). The segregation of *Hygrometrici* from *Marasmius* sensu stricto to *Cryptomarasmius* gen. nov. proposed here would result in all of the remaining sections of *Marasmius* sensu stricto displaying a dextrinoid reaction in Melzer's reagent as a unifying character.

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