A synopsis of the genus *Scleromitrula* (= *Verpatinia*) (Ascomycotina: Helotiales: Sclerotiniaceae)

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The systematics of *Scleromitrula* and *Verpatinia* of the family Sclerotiniaceae is reevaluated on the basis of morphological, cultural and molecular criteria. *Scleromitrula shiraiana, Verpatinia* species and *Ciborinia candolleana* share gross morphological, microanatomical and cultural features which clearly distinguish them from the closely related *Ciborinia* and *Rutstroemia* species. Phylogenetic analyses of sequences from the internal transcribed spacer region (ITS1, ITS2, and the 5.8S gene) of nuclear ribosomal DNA demonstrate that the stipitate-capitate specimens of *Scleromitrula* and *Verpatinia* species plus the stipitate-cupulate *Ciborinia candolleana* constitute a monophyletic clade separate from a clade including the type species of *Ciborinia*. *Scleromitrula* is emended to include *S. shiraiana*, the new species *S. rubicola*, *C. candolleana*, and specimens formerly assigned to *Verpatinia*. A key to the accepted species of *Scleromitrula* is provided.

Key Words——discomycetes; ITS rDNA phylogeny; morphology; taxonomy.

Scleromitrula, typified by Microglossum shiraianum Henn., was introduced by Imai (1941) to accommodate a group of inoperculate discomycetes previously referred to Microglossum Gill. and Mitrula Fr., producing stipitatecapitate apothecia emanating from sclerotia or stromatized fruits of its hosts. Apparently unaware of Imai's study, Whetzel (1945) four years later erected another genus of stipitate-capitate, stromatic discomycetes, Verpatinia Whetzel & Drayton, to include the putatively new species Verpatinia calthicola Whetzel (type species) and V. duchesnayensis Whetzel. Verpatinia was referred to his new family Sclerotiniaceae of the Helotiales (Whetzel, 1945). Batra and Korf (1959) emended the genus Ciborinia Whetzel to include Verpatinia, stating that the sclerotia of the latter are of a rather similar type to those in Ciborinia, and differing mainly in that the apothecial margin becomes strongly recurved ("verpoid") at maturity. Kohn and Nagasawa (1984) revised the genus Scleromitrula to include Scleromitrula shiraiana (Henn.) S. Imai as the only species. According to them Scleromitrula and Verpatinia are closely related. However, in Scleromitrula the sclerotia are hollowspheroid and ascocarps are produced on stromatized fruits (Morus alba L.), the ascus pore channel wall is J-, and the ectal excipulum of the fertile head is composed of chains of inflated prismatic to angular cells (Kohn and Nagasawa, 1984), while in Verpatinia the sclerotia are pulvinate and ascocarps are produced on stromatized leaves and stems, the ascus pore channel wall is J+, and the ectal excipulum of the fertile head is composed of globose cells.

The habit of producing stipitate-capitate ascocarps arising from a substratal or sclerotial stroma are features shared by other discomycete genera as well, e.g., *Episclerotium* L. M. Kohn, *Mitrulinia* Spooner, and *Sclerocrana* Samuels & L. M. Kohn, representing different lineages and families within the Helotiales (Kohn and Nagasawa, 1984; Samuels and Kohn, 1986; Spooner, 1987).

Over the past few years we have had the opportunity to compare a number of freshly collected specimens, herbarium specimens, axenic culture isolates, and nuclear ribosomal DNA sequences of specimens from a variety of hosts and geographic locations, representing closely related species of *Verpatinia*, *Scleromitrula*, and *Ciborinia*. In this work we report the results of examinations of teleomorphs, cultural isolates and phylogenetic analyses of nuclear Internal Transcribed Spacer (ITS) rDNA sequences of specimens and reconsider the systematics in this complex of closely related species of the family Sclerotiniaceae.

Materials and Methods

Axenic culture isolates were obtained from freshly collected apothecia by shooting ascospores onto water agar (1.5% agar). Single or mass ascospore isolates were transferred to potato-dextrose agar (PDA; Difco) and incubated in the dark at 20°C. Culture characteristics and morphology were scored during the first 4 wk after inoculation. The material was supplemented with an axenic

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culture isolate from the Institute for Fermentation, Osaka (IFO; Japan) and specimens from the university herbaria of Oslo (O) and Cornell (CUP).

Microscopic investigations were carried out on fresh specimens where available, and on dried specimens which were rehydrated in water. Studies of ascocarps were made by using squash mounts and sections cut either by hand or on a microtome. Apothecia were fixed in formalin-aceto-alcohol (5 ml formalin, 5 ml glacial acetic acid, 90 ml 70% ethyl alcohol), then dehydrated in a graded butyl alcohol series, embedded in paraffin, and sectioned at 8–10 μ m thickness. Observations were made in water, Melzer's reagent, methyl blue in lactic acid (cotton blue) and safranin-fast green; the staining of apothecial sections in safranin-fast green follows the protocol of Johansen (1940).

To determine the extent of intraspecific, interspecific, and intergeneric genetic differences we sequenced the nuclear ribosomal ITS region, which consist of the ITS1 and ITS2, and the 5.8S rRNA gene, from up to four specimens each of *S. shiraiana* (type species of *Scleromitrula*), the new species *S. rubicola* nov. sp. (see below), *V. calthicola* (type species of *Verpatinia*), *V. spiraeicola* Dennis, *Ciborinia whetzelii* (Seaver) Seaver (type species of *Ciborinia*), *C. foliicola* (E.K. Cash & R.W. Davids.) L.R. Batra, and *C. candolleana* (Lév.) Whetzel. *Rutstroemia firma* (Pers.:Fr.) P. Karst. (type species of *Rutstroemia*) and *R. bolaris* (Batsch:Fr.) Rehm were selected as suitable reference taxa based on an observed close relationship between *Verpatinia* spp. and *Rutstroemia* spp. in a study of the phylogeny of the family Sclerotiniaceae (Holst-Jensen et al., 1995).

The fungal material used for the rDNA analyses is listed in Table 1. Other specimens examined are listed in the taxonomic part of the manuscript.

DNA extraction, PCR reactions and sequencing of the ITS1, ITS2 and 5.8S rRNA gene were done as described by Holst-Jensen et al. (1997). DNA sequences were visually aligned with legal character states being the bases A, C, G, T and gap (-). Uncertainties in sequence determination were either scored as missing (?), or, in accordance with the IUPAC nucleic acid code, by the letters B=CGT, D=AGT, H=ACT, K=GT, M=AC, N=ACGT, R=AG, S=CG, V=ACG, W=AT and Y=CT. The sequences were aligned visually, and each nucleotide was treated as a single character in the phylogenetic analyses. The new sequences have been submitted to EMBL/GenBank under accession numbers Z73768, Z80877 - Z80894. To examine the biasing effect of minor length mutations (indels) on the phylogenetic trees, we performed phylogenetic analyses both with and without indel segments.

Phylogenetic analyses were performed using maximum parsimony (PAUP version 3.1.1; Swofford, 1993). First, we analysed the matrix to detect all ITS sequence genotypes, including the intraspecific variation within each taxon. Then, phylogenetic analyses were performed on a subset of isolates representing all the observed DNA genotypes. All analyses were performed with the Branch and Bound search algorithm and the

Species ^{a)}	Collection site	Collection no.	Host	DNA source ^{b)}
Ciborinia candolleana	Norway, Østfold, Hvaler	93/050	Quercus sp.	1657.1
	Norway, Østfold, Moss	93/055		1676.2
	Norway, Telemark, Bamble	93/116		1774.P
Ciborinia foliicola	Canada, Ontario, Wawa	93/232	<i>Salix</i> sp.	1932.H
Ciborinia whetzelii*	Canada, Ontario, Wawa	93/252	Populus tremuloides	1927.H
Rutstroemia bolaris	Norway, Akershus, Eidsvoll	92/156	Betula pubescens	1526.P
Rutstroemia firma*	Norway, Østfold, Halden	94/114	Quercus sp.	2089.1
Scleromitrula shiraiana*	Japan	95/080	Morus alba	2213.P ^{c)}
Verpatinia calthicola*	Canada, Ontario, Wawa	93/231	Caltha palustris	1871.P
	Norway, Vestfold, Brunlanes	94/068		2021.P
	Norway, Telemark, Bamble	92/085	Iris pseudacorus	1368.1
	Norway, Vestfold, Brunlanes	94/088		2049.P
	Norway, Telemark, Bamble	94/094		2057.P
	Norway, Vestfold, Brevik	94/095		2060.P
Verpatinia spiraeicola	Norway, Akershus, Fet	90/063	Filipendula ulmaria	1844.2
	Norway, Akershus, Fet	92/070		1331.1
	Norway, Akershus, Fet	92/071		1337.1
	Norway, Akershus, Bærum	94/003		1946.P
Scleromitrula rubicola, sp. nov.	Norway, Akershus, Eidsvoll	94/064	Rubus chamaemorus	2016.P

Table 1. List of fungal specimens included in the phylogenetic study.

a) Generic type is indicated by an asterisk (*).

b) Ascomycete research group (ARO) culture collection number, University of Oslo; symbols: digit=single ascospore isolate, P=mass ascospore isolate, H=dried herbarium specimen.

c) Culture obtained from Institute for Fermentation, Osaka, Japan=IFO 30255.

constitute separate monophyletic lineages, and 2) forcing the three *Ciborinia* species to constitute a single monophyletic lineage. The support for each internode was examined by bootstrapping (Felsenstein, 1985) with



Figs. 1–4. Axenic culture morphology of *Ciborinia candolleana*, *Scleromitrula rubicola*, *Verpatinia calthicola*, and *V. spiraeicola* on PDA incubated for 8 wk at 20°C in the dark.

Note the scattered, clustered irregular, black pyramidal to globose stromata. Bars=1 cm. Fig. 1. *Ciborinia candolleana*, culture 2444.P. Fig. 2. *Scleromitrula rubicola*, culture 2419.P. Fig. 3. *Verpatinia calthicola*, culture 2442.P. Fig. 4. *Verpatinia spiraeicola*, culture 2445.P.

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CTRORINIA CANDOLLEANA 1657	CATTACAGAG TTCATGCC	CT AACGGGTAG	A CCTCCCACCC	TTGTGTAT	TTATACTATG	TTGCTTTGGC	GGGTAGCACC	rcc	G
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SCIEDONITEULA SUIDAIANA		T	N			T	TG	. G	
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VERPATINIA SPIRAEICOLA 1331	33333322222 222222						T TT	-	22
VERPATINIA SPIRAEICOLA 1337	10000						T TT	-	
VERPATINIA SPIRAEICOLA 1946		_							0000110001
VERPATINIA CALTHICOLA "Iris" 1368									
VERPATINIA CALTHICOLA "Caltha" 1871							TTT	T	CCCAAGGA
SCLEROMITRULA RUBICOLA					C		TT		AA
CIBORINIA FOLIICOLA	?????????? T	.G CGA		cc	GAT		.A.CCC	F	
CIBORINIA WHETZELII		.G .GA		GT	CAT.T		.AC.CC.T	CGT	
RUTSTROEMIA FIRMA		c			CAT		.A.CTCTT	GG.CTTAACT	GCCCC AA
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VERPATINIA SPIRAEICOLA 1331	AA					G			
VERPATINIA SPIRAEICOLA 1337	AA			A					
VERPATINIA SPIRAEICOLA 1946	AA					G			
VERPATINIA CALTHICOLA "Iris" 1368									
VERPATINIA CALTHICOLA "Caltha" 1871									
SCLEROMITRULA RUBICOLA	A			A.C				C	
CTROPINIA FOLICOLA			AG	G.AC	NN.	.CA		–	
CIBORINIA WEETZELIT	C		AGT .	CATC	A.C	.ca	.AC.T	. T	
BUTCHEORMIA FIDMA	CA .CTCGA	. CTGAGAG	G	A . AA	.CAA.				
NUISIRUEMIA FIRMA	ACA .CTCGA	. CTGAGAG	.T	A . A	.CAA				N
RUTSTROEMIA BOLARIS									Contraction of the
				5	8S				300
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CIBORINIA CANDOLLEANA 1676									********
SCLEROMITRULA SHIRAIANA		· · · · · · · · · · · · · · · · · · ·							
VERPATINIA SPIRAEICOLA 1844		G							********
VERPATINIA SPIRAEICOLA 1331		G					*********		*********
VERPATINIA SPIRAEICOLA 1337	· · · · · · · · · · · · · · · · · · ·	G							
VERPATINIA SPIRAEICOLA 1946			********			********		********	
VERPATINIA CALTHICOLA "Tris" 1368		Q							*********
VERRATINIA CALTHICOLA "Caltha" 1871		G							
PERFECTIVE CALIFICOLA CALCHA 10/1		G							
SCHEROMITROLA ROBICOLA									
CIBORINIA FOLIICOLA			and the second second						
CIBORINIA WHETZELII		G-							
RUTSTROEMIA FIRMA		0						and a second	
RUTSTROEMIA BOLARIS									
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CIBORINIA CANDOLLEANA 1657	ACATTGCGCC CCTTGGTA	5.8s TCCGGGGGGGCA	TOCCTOTTCG	AGCGICATI-	TCAACCCTCA	 AGCTCTGCTT	• GGTATTGGGC	CTCCGCCAGT	*** * 400 AAAATGGC
CIBORINIA CANDOLLEANA 1657 CIBORINIA CANDOLLEANA 1676	ACATTGCGCC CCTTGGTA	5.85 T CCGGGGGGGC	TOCCTOTICG	AGCGTCATT-	TC AACCCTCA	AGCTCTGCTT	GGTATTGGGC	CTCCGCCAGT	AAAATGGC
CIBORINIA CANDOLLEANA 1657 CIBORINIA CANDOLLEANA 1676 SCLEROMITRULA SHIRAIANA	ACMTTGCGCC CCTTGGTA	5.8s T CCGGGGGGGC	TOCCTOTICG	AGCGTCATT-	TORACCOTCA	AGCTCTGCTT	* GGTATTGGGC	CTCCGCCAGT T.TA.	AAAATGGC
CIBORINIA CANDOLLEANA 1657 CIBORINIA CANDOLLEANA 1676 SCLEROMITRULA SHIRAIANA VERPATINIA SPIRAEICOLA 1844	ACATTGEGEE CETTGETA	5.8S	TGCCTGTTCG	AGCGICATI-	TCAACCCTCA	AGCTCTGCTT	GGTATTGGGC	CTCCGCCAGT T.TA.	400 AAAATGGC
CIBORINIA CANDOLLEANA 1657 CIBORINIA CANDOLLEANA 1676 SCLEKOMITRULA SHIRAIANA VERPATINIA SPIRAEICOLA 1844 VERPATINIA SPIRAEICOLA 1331	ACAPTGCGCC CCTTGGTA	5.8s T ccggggggcz	TGCCTGPTCG	AGCGTCATT-	TO ACCOTCA	AGCTCTGCTT	• GGTATTGGGC	CTCCGCCAGT T.TA.	AAAATGGC
CIBORINIA CANDOLLEANA 1657 CIBORINIA CANDOLLEANA 1676 SCLEROMITRULA SHIRAIANA VERPATINIA SPIRAEICOLA 1331 VERPATINIA SPIRAEICOLA 1337	ACMTTGCGCC CCTTGGEN	5.85 T CCGGGGGGGC	TGCCTOPPICG	AGCGTCATT-	TCRACCCTCA	AGCTCTGCTT	GGTATTGGGC	CTCCGCCAGT T.TA.	AAAATGGC
CIBORINIA CANDOLLEANA 1657 CIBORINIA CANDOLLEANA 1676 SCLEROMITRULA SHIRAIANA VERPATINIA SPIRAEICOLA 1844 VERPATINIA SPIRAEICOLA 1331 VERPATINIA SPIRAEICOLA 1337 VERPATINIA SPIRAEICOLA 1946	ACNITICOCC CCTIGGTN	5.85 TT CCGGGGGGGCA	1 TGCCTOTTCG	AGCOTCATT-	TOACCOTCA	AGCTCTGCTT	GGTATTGGGC	CTCCGCCAGT T.TA.	AAAATGGC
CIBORINIA CANDOLLEANA 1657 CIBORINIA CANDOLLEANA 1676 SCLEROMITRULA SHIRAIANA VERPATINIA SPIRAEICOLA 1844 VERPATINIA SPIRAEICOLA 1331 VERPATINIA SPIRAEICOLA 1337 VERPATINIA SPIRAEICOLA 1946 VERPATINIA CALTHICOLA "Iris" 1368	ACNITICCCC CCTTGGTN	5.85 T CCGGGGGGCA	1 TGCCTOTTCG	AGCOTCATT-	TORACCOTCA	AGCTCTGCTT	GGTATTGGGC	CTCCGCCAGT T.TA.	+++ 400 AAAATGGC
CIBORINIA CANDOLLEANA 1657 CIBORINIA CANDOLLEANA 1676 SCLEROMITRULA SHIRAIANA VERPATINIA SPIRAEICOLA 1844 VERPATINIA SPIRAEICOLA 1831 VERPATINIA SPIRAEICOLA 1337 VERPATINIA SPIRAEICOLA 1946 VERPATINIA CALTHICOLA "Caliba" 1871	ACNITIGCOCC CCTIGGTN	5.85 T CCG00GGC3	1 TOCCTOTICG	AGCGTCAPT	TOACCCTCA	AGCTCTGCTT	CGTATTGGGC	CTCCGCCAGT T.TA.	+++ 400 AAAATGGC
CIBORINIA CANDOLLEANA 1657 CIBORINIA CANDOLLEANA 1676 SCLEROMITRULA SHIRAIANA VERPATINIA SPIRAEICOLA 1844 VERPATINIA SPIRAEICOLA 1331 VERPATINIA SPIRAEICOLA 1337 VERPATINIA SPIRAEICOLA 1346 VERPATINIA CALTHICOLA "Iris" 1368 VERPATINIA CALTHICOLA "Caltha" 1871 SCLEPONTRULA BUBCOLA	ACNITICOCC CCTIGGTN	5.8S	1 TGCCTGPTCG	AGCGTCATT	TGACCCTCA	AGCTCTGCTT	GGTATTGGGC	CTCCGCCAGT T.TA.	AAAATGGC
CIBORINIA CANDOLLEANA 1657 CIBORINIA CANDOLLEANA 1676 SCLERCMITRULA SHIRAIANA VERPATINIA SPIRAEICOLA 1844 VERPATINIA SPIRAEICOLA 1331 VERPATINIA SPIRAEICOLA 1337 VERPATINIA SPIRAEICOLA 1337 VERPATINIA CALTHICOLA "Lris" 1368 VERPATINIA CALTHICOLA "Caltha" 1871 SCLERCMITRULA RUBICOLA	ACATTGCCC CCTTGGTA	5.8S	T9CCT0FFC0	AGCGTCATT	TORACCCTCA	* * AGCTCTGCTT	* GGTATTGGGC	CTCCGCCAGT	+++ + 400 AAAATGGC
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CIBORINIA CANDOLLEANA 1657 CIBORINIA CANDOLLEANA 1676 SCLEROMITRULA SHIRAIANA VERPATINIA SPIRAEICOLA 1844 VERPATINIA SPIRAEICOLA 1844 VERPATINIA SPIRAEICOLA 1337 VERPATINIA SPIRAEICOLA 1337 VERPATINIA SPIRAEICOLA 1946 VERPATINIA CALTHICOLA "Caltha" 1871 SCLEROMITRULA RUBICOLA "Caltha" 1871 SCLEROMITRULA RUBICOLA CIBORINIA FOLIICOLA CIBORINIA FOLIICOLA CIBORINIA HETZELII RUTSTOEMIA FIRMA RUTSTROEMIA BOLARIS	ACATTGCGCC CCTTGGTA	5.85 TT CCGGGGGGC		- AGCOTCATT-	TC AACCOTCA	AGCTCTGCTT	GGTATTGGGC	CTCCGCCAGT T.TA. 	*** * 400 AAAATGGC
CIBORINIA CANDOLLEANA 1657 CIBORINIA CANDOLLEANA 1676 SCLEROMITRULA SHIRAIANA VERPATINIA SPIRARICOLA 1331 VERPATINIA SPIRARICOLA 1331 VERPATINIA SPIRARICOLA 1337 VERPATINIA SPIRARICOLA 1346 VERPATINIA CALTHICOLA "LIS" 1368 VERPATINIA CALTHICOLA "Caltha" 1871 SCLEROMITRULA RUBICOLA CIBORINIA HEIZELII RUTSTROEMIA FIRMA RUTSTROEMIA FIRMA RUTSTROEMIA FIRMA CIBORINIA CANDOLLEANA 1657	ACATTGCCCC CCTTGGTA	5.85 TCCCGGGGGGC	TOCCTOPTCO	- AGCGTCATT-	TC AACCOTCA	AGCTCTGCTT 	GGTATTGGGC	CTCCGCCAGT T.TA. 	+++ + 400 AAAATGGC
CIBORINIA CANDOLLEANA 1657 CIBORINIA CANDOLLEANA 1657 SCLEROMITRULA SHIRAIANA VERPATINIA SPIRAEICOLA 1844 VERPATINIA SPIRAEICOLA 1331 VERPATINIA SPIRAEICOLA 1331 VERPATINIA SPIRAEICOLA 1346 VERPATINIA CALTHICOLA "Iris" 1368 VERPATINIA CALTHICOLA "Calta" 1871 SCLEROMITRULA RUBICOLA CIBORINIA FOLLICOLA CIBORINIA MHETZELII RUTSTROEMIA BOLARIS CIEDORINIA CANDOLLEANA 1657 CIBORINIA CANDOLLEANA 1657	ACATTGCCCC CCTTGGTA	5.85 TT CCGGGGGGC	Goteeraac	• AGCOTCATT- ···································	TCAACCCTCA	AGCTCTGCTT 	GGTATTGGGC	CTCCGCCAGT T.TA. 	*** * 400 AAAATGGC
CIBORINIA CANDOLLEANA 1657 CIBORINIA CANDOLLEANA 1676 SCLEROMITRULA SHIRAIANA VERPATINIA SPIRAEICOLA 1844 VERPATINIA SPIRAEICOLA 1831 VERPATINIA SPIRAEICOLA 1337 VERPATINIA SPIRAEICOLA 1946 VERPATINIA CALTHICOLA "CAltha" 1871 SCLEROMITRULA RUBICOLA CIBORINIA VHETZELII RUTSTROEMIA PIRMA RUTSTROEMIA PIRMA RUTSTROEMIA BOLARIS CIBORINIA CANDOLLEANA 1657 CIBORINIA CANDOLLEANA 1676 SCLEROMITRULA SHIRAIANA	ACATTGCGCC CCTTGGTA	5.85 TT CCGGGGGGC	Gotterrand	• AGCGTCATT	TC AACCOTCA	AGCTCTGCTT 	GGTATTGGGC	CTCCGCCAGT T.TA. 	+++ + 400 AAAATGGC
CIBORINIA CANDOLLEANA 1657 CIBORINIA CANDOLLEANA 1676 SCLEROMITRULA SHIRAIANA VERPATINIA SPIRAEICOLA 1344 VERPATINIA SPIRAEICOLA 1331 VERPATINIA SPIRAEICOLA 1337 VERPATINIA SPIRAEICOLA 1346 VERPATINIA CALTHICOLA "Iris" 1368 VERPATINIA CALTHICOLA "Iris" 1368 VERPATINIA CALTHICOLA "Iris" 1368 CIBORINIA CALTHICOLA "Iris" 1368 CIBORINIA FIRMA RUTSTROEMIA FIRMA RUTSTROEMIA FIRMA RUTSTROEMIA FIRMA CIBORINIA CANDOLLEANA 1657 CIBORINIA CANDOLLEANA 1657 SCLEROMITRULA SHIRAIANA VERPATINIA SPIRAEICOLA 1844	ACATTGCOCC CCTTGGTA	5.85 T CCGGGGGGC	GOTECTGAGE	- AGCGTCATT-	TC AACCOTCA	AGCTCTGCTT 	GGTATTGGGC	CTCCGCCAGT T.TA. 	+++ 400 AAAATGGC
CIBORINIA CANDOLLEANA 1657 CIBORINIA CANDOLLEANA 1676 SCLERONITRULA SHIRAINAA VERPATINIA SPIRAEICOLA 1844 VERPATINIA SPIRAEICOLA 1844 VERPATINIA SPIRAEICOLA 1337 VERPATINIA SPIRAEICOLA 1337 VERPATINIA CALTHICOLA "CAItha" 1871 SCLEROMITRULA RUBICOLA "CAItha" 1871 SCLEROMITRULA RUBICOLA CIBORINIA CALTHICOLA "CAItha" 1871 SCLEROMITRULA RUBICOLA CIBORINIA MHETZELII RUTSTROEMIA FIRMA RUTSTROEMIA FIRMA RUTSTROEMIA ELANA 1657 CIBORINIA CANDOLLEANA 1657 CIBORINIA CANDOLLEANA 1676 SCLEROMITRULA SHIRAINAA VERPATINIA SPIRAEICOLA 1844	ACATTGCOCC CCTTGGTA	5.85 TT CCGGGGGGCA	GOTECTGACC	• AGCOTCATT- ···································	• • • • • • • • • • • • • • • • • • •	AGCTCTGCTT 	GGTATTGGGC	CTCCGCCAGT T.TA. 	+++ + 400 AAAATGGC
CIBORINIA CANDOLLEANA 1657 CIBORINIA CANDOLLEANA 1676 SCLEROMITRULA SHIRAIANA VERPATINIA SPIRAEICOLA 1344 VERPATINIA SPIRAEICOLA 1331 VERPATINIA SPIRAEICOLA 1337 VERPATINIA SPIRAEICOLA 1346 VERPATINIA CALTHICOLA "LI'IS" 1368 VERPATINIA CALTHICOLA "Caltha" 1871 SCLEROMITRULA RUBICOLA CIBORINIA WHETZELII RUTSTROEMIA FIRMA RUTSTROEMIA FIRMA RUTSTROEMIA BOLARIS CIBORINIA CANDOLLEANA 1657 CIBORINIA CANDOLLEANA 1657 SCLEROMITRULA SHIRAIANA VERPATINIA SPIRAEICOLA 1331 VERPATINIA SPIRAEICOLA 1337	ACATTGCCCC CCTTGGTA	5.85 TT CCGGGGGGCA	GOTECTGATE	- AGCGTCATT-	TC AACCOTCA A. A. ATT. A. TTCTCGCT C. C.	AGCTCTGCTT 	GGTATTGGGC	CTCCGCCAGT T.TA. CAT.T.TC .CAT.T.TC .CAT.T.G. .CAT.T.G. .CAT.T.G. .CAT.T.G.	
CIBORINIA CANDOLLEANA 1657 CIBORINIA CANDOLLEANA 1676 SCLEROMITRULA SHIRAIANA VERPATINIA SPIRAEICOLA 1344 VERPATINIA SPIRAEICOLA 1331 VERPATINIA SPIRAEICOLA 1331 VERPATINIA SPIRAEICOLA 1346 VERPATINIA CALTHICOLA "Iris" 1368 VERPATINIA CALTHICOLA "Iris" 1368 VERPATINIA CALTHICOLA "Iris" 1368 CIBORINIA FLINA CIBORINIA FLINA RUTSTROEMIA FLIMA RUTSTROEMIA FLIMA RUTSTROEMIA FLIMA CIBORINIA CANDOLLEANA 1657 CIBORINIA CANDOLLEANA 1657 CIBORINIA CANDOLLEANA 1657 CIBORINIA CANDOLLEANA 1657 SCLEROMITRULA SHIRAIANA VERPATINIA SPIRAEICOLA 1331 VERPATINIA SPIRAEICOLA 1337 VERPATINIA SPIRAEICOLA 1337	ACATTGCCC CCTTGGTA	5.85 TT CCG000GGCA	GOTECTGAGE	- AGCGTCATT-	TC AACCCTCA	AGCTCTGCTT 	GGTATTGGGC	CTCCGCCAGT T.TA. 	••• • • 400 AAAATGGC
CIBORINIA CANDOLLEANA 1657 CIBORINIA CANDOLLEANA 1676 SCLEROMITRULA SHIRAIANA VERPATINIA SPIRAEICOLA 1844 VERPATINIA SPIRAEICOLA 1844 VERPATINIA SPIRAEICOLA 1331 VERPATINIA SPIRAEICOLA 1337 VERPATINIA SPIRAEICOLA 1337 VERPATINIA CALTHICOLA "15" 1368 VERPATINIA CALTHICOLA "Caltha" 1871 SCLEROMITRULA RUBICOLA "Caltha" 1871 SCLEROMITRULA RUBICOLA "Caltha" 1871 SCLEROMITRULA RUBICOLA "Caltha" 1871 RUTSTROEMIA FIRMA RUTSTROEMIA FIRMA RUTSTROEMIA BOLARIS CIBORINIA CANDOLLEANA 1657 CIBORINIA CANDOLLEANA 1657 CIBORINIA SPIRAEICOLA 1657 SCLEROMITRULA SHIRAIANA VERPATINIA SPIRAEICOLA 1331 VERPATINIA SPIRAEICOLA 1331 VERPATINIA SPIRAEICOLA 1337 VERPATINIA SPIRAEICOLA 1336	ACATTGCCCC CCTTGGTA	5.85 TT CCGGGGGGCA	GOTECTGARC	• AGCGTCATT- ···································	• • • • • • • • • • • • • • • • • • •	AGCTCTGCTT		CTCCGCCAGT T.TA. CAT.T.TC .CAT.T.TC .CAT.T.G. .CT.G. .CT.G. TG-CCATTAA	*** * 400 AAAATGGC
CIBORINIA CANDOLLEANA 1657 CIBORINIA CANDOLLEANA 1676 SCLEROMITRULA SHIRAIANA VERPATINIA SPIRARICOLA 1331 VERPATINIA SPIRARICOLA 1331 VERPATINIA SPIRARICOLA 1337 VERPATINIA SPIRARICOLA 1337 VERPATINIA CALTHICOLA "1ris" 1368 VERPATINIA CALTHICOLA "1ris" 1368 VERPATINIA CALTHICOLA "1ris" 1368 VERPATINIA CALTHICOLA "1ris" 1368 CIBORINIA FIRMA RUTSTROEMIA FIRMA RUTSTROEMIA FIRMA RUTSTROEMIA FIRMA RUTSTROEMIA FIRMA VERPATINIA CANDOLLEANA 1657 CIBORINIA CANDOLLEANA 1657 CIBORINIA SPIRARICOLA 1331 VERPATINIA SPIRARICOLA 1331 VERPATINIA SPIRARICOLA 1337 VERPATINIA SPIRARICOLA 1337 VERPATINIA SPIRARICOLA 1337 VERPATINIA CALTHICOLA "1676	ACATTGCOCC CCTTGGTA	5.85 TT CCGGGGGGC	TOCCTOPTEG	- AGCGTCATT-	TC AACCOTCA	AGCTCTGCTT 		CTCCGCCAGT T.TA. 	
CIBORINIA CANDOLLEANA 1657 CIBORINIA CANDOLLEANA 1676 SCLEROMITRULA SHIRAIANA VERPATINIA SPIRAEICOLA 1331 VERPATINIA SPIRAEICOLA 1331 VERPATINIA SPIRAEICOLA 1331 VERPATINIA SPIRAEICOLA 1337 VERPATINIA CALTHICOLA "Iris" 1368 VERPATINIA CALTHICOLA "Iris" 1368 VERPATINIA CALTHICOLA "Caltha" 1871 SCLEROMITRULA RUBICOLA CIBORINIA FOLIICOLA CIBORINIA FOLIICOLA CIBORINIA FILMA RUTSTROEMIA FIRMA RUTSTROEMIA BOLARIS CIBORINIA CANDOLLEANA 1657 CIBORINIA CANDOLLEANA 1657 CIBORINIA CANDOLLEANA 1657 CIBORINIA SPIRAEICOLA 1864 VERPATINIA SPIRAEICOLA 1331 VERPATINIA SPIRAEICOLA 1337 VERPATINIA SPIRAEICOLA 1337 VERPATINIA SPIRAEICOLA 1346 VERPATINIA CALTHICOLA "Iris" 1368 VERPATINIA CALTHICOLA "Iris" 1368	ACATTGCCCC CCTTGGTA	5.85 TT CCGGGGGGC	GOTECTGAGE	- AGCOTCATT-	TCAACCCTCA	AGCTCTGCTT 	GGTATTGGGC	CTCCGCCAGT T.TA. 	*** * 400 AAA ATGGC
CIBORINIA CANDOLLEANA 1657 CIBORINIA CANDOLLEANA 1676 SCLEROMITRULA SHIRAIANA VERPATINIA SPIRAEICOLA 1844 VERPATINIA SPIRAEICOLA 1331 VERPATINIA SPIRAEICOLA 1337 VERPATINIA SPIRAEICOLA 1346 VERPATINIA CALTHICOLA "Lis" 1368 VERPATINIA CALTHICOLA "Caltha" 1871 SCLEROMITRULA RUBICOLA CIBORINIA WHETZELII RUTSTROEMIA FIRMA RUTSTROEMIA FIRMA RUTSTROEMIA FIRMA RUTSTROEMIA BOLARIS CIBORINIA CANDOLLEANA 1657 CIBORINIA SPIRAEICOLA 1657 CIBORINIA SPIRAEICOLA 1657 SCLEROMITRULA SHIRAIANA VERPATINIA SPIRAEICOLA 1331 VERPATINIA SPIRAEICOLA 1331 VERPATINIA SPIRAEICOLA 1331 VERPATINIA SPIRAEICOLA 1337 VERPATINIA SPIRAEICOLA 1337 VERPATINIA CALTHICOLA "LIS" 1368 VERPATINIA CALTHICOLA "CALTHA" 1871 SCLEROMITRULA RUBICOLA	ACATTGCGCC CCTTGGTA	5.85 TT CCGGGGGGCA	TOCCTOPTCG	- AGCGTCATT-		AGCTCTGCTT 		CTCCGCCAGT T.TA. CAT.T.TC .CAT.T.TC .CAT.T.G. .CT.G. TG-CCATTAA	*** * 400 AAAATGGC
CIBORINIA CANDOLLEANA 1657 CIBORINIA CANDOLLEANA 1676 SCLEROMITRULA SHIRAIANA VERPATINIA SPIRAEICOLA 1331 VERPATINIA SPIRAEICOLA 1331 VERPATINIA SPIRAEICOLA 1337 VERPATINIA SPIRAEICOLA 1337 VERPATINIA CALTHICOLA "Iris" 1368 VERPATINIA CALTHICOLA "Iris" 1368 VERPATINIA CALTHICOLA "Iris" 1368 VERPATINIA CALTHICOLA "Iris" 1368 CIBORINIA FILMA RUTSTROEMIA FILMA RUTSTROEMIA FILMA RUTSTROEMIA FILMA RUTSTROEMIA FILMA RUTSTROEMIA FILMA VERPATINIA CANDOLLEANA 1657 CIBORINIA CANDOLLEANA 1657 CIBORINIA SPIRAEICOLA 1844 VERPATINIA SPIRAEICOLA 1331 VERPATINIA SPIRAEICOLA 1337 VERPATINIA SPIRAEICOLA 1337 VERPATINIA SPIRAEICOLA 1337 VERPATINIA SPIRAEICOLA 1337 VERPATINIA SPIRAEICOLA 1337 VERPATINIA CALTHICOLA "CILMA" 1871 SCLEROMITRULA RUBICOLA COLLA" 1871 SCLEROMITRULA RUBICOLA	ACATTGCCC CCTTGGTA	5.85 TT CCG000GGCA	TOCCTOPTICG	- AGCGTCATT-			GGTATTGGGC C A.T	CTCCGCCAGT T.TA. CAT.T.TC .CAT.T.TC .CAT.T.C .CT.G. TG-CCATTAA C.C.AC .CC	*** * 400 AAAATGGC
CIBORINIA CANDOLLEANA 1657 CIBORINIA CANDOLLEANA 1676 SCLEROMITRULA SHIRAIANA VERPATINIA SPIRAEICOLA 1331 VERPATINIA SPIRAEICOLA 1337 VERPATINIA SPIRAEICOLA 1337 VERPATINIA SPIRAEICOLA 1337 VERPATINIA CALTHICOLA "LIS" 1368 VERPATINIA CALTHICOLA "Caltha" 1871 SCLEROMITRULA RUBICOLA CIBORINIA CALTHICOLA "Caltha" 1871 SCLEROMITRULA RUBICOLA CIBORINIA CHICALEANA 1657 CIBORINIA CHICALEANA 1657 CIBORINIA CANDOLLEANA 1657 CIBORINIA CANDOLLEANA 1657 CIBORINIA SPIRAEICOLA 1331 VERPATINIA SPIRAEICOLA 1346 VERPATINIA CALTHICOLA "LIS" 1366 VERPATINIA CALTHICOLA "Caltha" 1871 SCLEROMITRULA RUBICOLA CIBORINIA FOLICOLA	ACATTGCCCC CCTTGGTA	5.85 TT CCGGGGGGCA 	TOCCTOPTICG	- AGCOTCATT	• • • • • • • • • • • • • • • • • • •	AGCTCTGCTT 	- GGTATTGGGC 	CTCCGCCAGT T.TA. 	
CIBORINIA CANDOLLEANA 1657 CIBORINIA CANDOLLEANA 1676 SCLEROMITRULA SHIRAIANA VERPATINIA SPIRAEICOLA 1844 VERPATINIA SPIRAEICOLA 1831 VERPATINIA SPIRAEICOLA 1337 VERPATINIA SPIRAEICOLA 1337 VERPATINIA CALTHICOLA "LI'IS" 1368 VERPATINIA CALTHICOLA "Calthe" 1871 SCLEROMITRULA RUBICOLA CIBORINIA WHETZELII RUTSTROEMIA FIRMA RUTSTROEMIA FIRMA RUTSTROEMIA BOLARIS CIBORINIA CANDOLLEANA 1657 CIBORINIA SPIRAEICOLA 1844 VERPATINIA SPIRAEICOLA 1331 VERPATINIA SPIRAEICOLA 1331 VERPATINIA SPIRAEICOLA 1331 VERPATINIA SPIRAEICOLA 1331 VERPATINIA SPIRAEICOLA 1337 VERPATINIA SPIRAEICOLA 1337 VERPATINIA SPIRAEICOLA 1337 VERPATINIA SPIRAEICOLA 1337 VERPATINIA SPIRAEICOLA 1337 VERPATINIA SPIRAEICOLA 1346 VERPATINIA SPIRAEICOLA 1346 VERPATINIA CALTHICOLA "Calthe" 1871 SCLEROMITRULA RUBICOLA CIBORINIA WHETZELII RUTSTROEMIA FIRMA	ACATTGCGCC CCTTGGTA	5.85 Tr CCGGGGGGCA 	TOCCTOPTICG	- AGCGTCATT-		AGCTCTGCTT 	- GGTATTGGGC 	CTCCGCCAGT T.TA. 	
CIBORINIA CANDOLLEANA 1657 CIBORINIA CANDOLLEANA 1676 SCLEROMITRULA SHIRAIANA VERPATINIA SPIRAEICOLA 1344 VERPATINIA SPIRAEICOLA 1331 VERPATINIA SPIRAEICOLA 1331 VERPATINIA SPIRAEICOLA 1337 VERPATINIA CALTHICOLA "Iris" 1368 VERPATINIA CALTHICOLA "Iris" 1368 VERPATINIA CALTHICOLA "Iris" 1368 VERPATINIA CALTHICOLA "Iris" 1368 CIBORINIA FILMA RUTSTROEMIA FILMA RUTSTROEMIA FILMA RUTSTROEMIA FILMA RUTSTROEMIA FILMA VERPATINIA CANDOLLEANA 1657 CIBORINIA CANDOLLEANA 1657 CIBORINIA CANDOLLEANA 1657 CIBORINIA SPIRAEICOLA 1844 VERPATINIA SPIRAEICOLA 1331 VERPATINIA SPIRAEICOLA 1337 VERPATINIA SPIRAEICOLA 1337 VERPATINIA SPIRAEICOLA 1337 VERPATINIA SPIRAEICOLA 1337 VERPATINIA SPIRAEICOLA 1337 VERPATINIA CALTHICOLA "CILMA" 1871 SCLEROMITRULA RUBICOLA CIBORINIA HETZELII RUTSTROEMIA FILMA RUTSTROEMIA FILMA RUTSTROEMIA FILMA	ACATTGCCC CCTTGGTA	5.85 TT CCG00000000 	TOCCTOTICG	- AGCOTCATT	TCAACCCTCA	AGCTCTGCTT 	- GGTATTGGGC	CTCCGCCAGT T.TA. CAT.T.TC .CAT.T.TC .CAT.T.G. .CT.G. .TG-CCATTAA .C.AC C.	
CIBORINIA CANDOLLEANA 1657 CIBORINIA CANDOLLEANA 1676 SCLEROMITRULA SHIRAIANA VERPATINIA SPIRAEICOLA 1844 VERPATINIA SPIRAEICOLA 1831 VERPATINIA SPIRAEICOLA 1337 VERPATINIA SPIRAEICOLA 1337 VERPATINIA CALTHICOLA "Caltha" 1871 SCLEROMITRULA RUBICOLA "Caltha" 1871 SCLEROMITRULA RUBICOLA "Caltha" 1871 CIBORINIA CALTHICOLA "Caltha" 1871 RUTSTROEMIA FIRMA RUTSTROEMIA FIRMA RUTSTROEMIA BOLARIS CIBORINIA CANDOLLEANA 1657 CIBORINIA CANDOLLEANA 1657 CIBORINIA SPIRAEICOLA 1844 VERPATINIA SPIRAEICOLA 1844 VERPATINIA SPIRAEICOLA 1331 VERPATINIA SPIRAEICOLA 1331 VERPATINIA SPIRAEICOLA 1331 VERPATINIA SPIRAEICOLA 1331 VERPATINIA CALTHICOLA "Caltha" 1871 SCLEROMITRULA RUBICOLA CIBORINIA CALTHICOLA "Caltha" 1871 SCLEROMITRULA RUBICOLA CIBORINIA FOLICOLA	ACATTGCCCC CCTTGGTA	5.85 Tr CCGGGGGGCA 	TOCCTOPTICG	• AGCOTCATT	TC ACCOTCA A. A. A. A. A. TTCTCQCT C. C. TTCTCQCT T. A. A. T. A. T. A. T. T. T. T. T. T. T. T. T. A. T. T. T. <tr tr=""> <tr tr=""></tr></tr>	AGCTCTOCTT 	- GGTATTGGGC 	CTCCGCCAGT T.TA. CAT.T.TC .CAT.T.TC .CATTC .C.T.G. TG-CCATTAA 	
CIBORINIA CANDOLLEANA 1657 CIBORINIA CANDOLLEANA 1676 SCLEROMITRULA SHIRAIANA VERPATINIA SPIRARICOLA 1331 VERPATINIA SPIRARICOLA 1331 VERPATINIA SPIRARICOLA 1337 VERPATINIA SPIRARICOLA 1337 VERPATINIA CALTHICOLA "LI'Is" 1368 VERPATINIA CALTHICOLA "Caltha" 1871 SCLEROMITRULA RUBICOLA CIBORINIA WHETZELII RUTSTROEMIA FIRMA RUTSTROEMIA BOLARIS CIBORINIA CANDOLLEANA 1657 CIBORINIA SPIRARICOLA 1844 VERPATINIA SPIRARICOLA 1844 VERPATINIA SPIRARICOLA 1844 VERPATINIA SPIRARICOLA 1337 VERPATINIA SPIRARICOLA 1337 VERPATINIA SPIRARICOLA 1337 VERPATINIA SPIRARICOLA 1337 VERPATINIA SPIRARICOLA 1337 VERPATINIA SPIRARICOLA 1345 VERPATINIA SPIRARICOLA 1345 VERPATINIA CALTHICOLA "LI'IS" 1368 VERPATINIA CALTHICOLA "Caltha" 1871 SCLEROMITRULA RUBICOLA CIBORINIA HETZELII RUTSTROEMIA FIRMA RUTSTROEMIA FIRMA RUTSTROEMIA BOLARIS	ACATTGCCC CCTTGGTA	5.85 TT CCGGGGGGCA 	TOCCTOPTICG	- AGCGTCATT-	TC A. A. A. A. A. A. TTCTCGCT C. C. T. T. A. A. T. A. T. C. T.	AGCTCTGCTT 	- GGTATTGGGC 	CTCCGCCAGT T.TA 	
CIBORINIA CANDOLLEANA 1657 CIBORINIA CANDOLLEANA 1676 SCLERONITRULA SHIRAIANA VERPATINIA SPIRAEICOLA 1844 VERPATINIA SPIRAEICOLA 1844 VERPATINIA SPIRAEICOLA 1837 VERPATINIA SPIRAEICOLA 1337 VERPATINIA CALTHICOLA "Inis" 1368 VERPATINIA CALTHICOLA "Caltha" 1871 SCLEROMITRULA RUBICOLA CIBORINIA CALTHICOLA "Caltha" 1871 SCLEROMITRULA RUBICOLA CIBORINIA FOLIICOLA CIBORINIA FIRMA RUTSTROEMIA FIRMA RUTSTROEMIA FIRMA RUTSTROEMIA SPIRAEICOLA 1857 CIBORINIA CANDOLLEANA 1657 CIBORINIA SPIRAEICOLA 1331 VERPATINIA CALTHICOLA "LAIS" 1368 VERPATINIA CALTHICOLA "Caltha" 1871 SCLEROMITRULA RUBICOLA CIBORINIA FOLIICOLA CIBORINIA FOLICOLA CIBORINIA FOLICOLA CIBORINIA FOLIA FIRMA RUTSTROEMIA BOLARIS	ACATTGCCC CCTTGGTA	5.85 Tr CCGGGGGGGA 	TOCCTOPTICG	- AGCOTCATT- 	TC AACCCTCA	AGCTCTOCTT 	- GGTATTGGGC C C A.T 	CTCCGCCAGT T.TA. CAT.T.TC .CAT.T.TC .CATTC .C.T.G. TG-CCATTAA 	
CIBORINIA CANDOLLEANA 1657 CIBORINIA CANDOLLEANA 1676 SCLEROMITRULA SHIRAIANA VERPATINIA SPIRAEICOLA 1844 VERPATINIA SPIRAEICOLA 1831 VERPATINIA SPIRAEICOLA 1331 VERPATINIA SPIRAEICOLA 1337 VERPATINIA CALTHICOLA 'Inis' 1368 VERPATINIA CALTHICOLA 'Caltha' 1871 SCLEROMITRULA RUBICOLA CIBORINIA WHETZELII RUTSTROEMIA FILMA RUTSTROEMIA FILMA RUTSTROEMIA BOLARIS CIBORINIA CANDOLLEANA 1657 CIBORINIA SPIRAEICOLA 1844 VERPATINIA SPIRAEICOLA 1331 VERPATINIA SPIRAEICOLA 134 CIBORINIA CALTHICOLA 'Caltha' 1871 SCLEROMITRULA RUBICOLA CIBORINIA WHETZELII RUTSTROEMIA FIRMA RUTSTROEMIA BOLARIS	ACATTGCGCC CCTTGGTA	5.85 TT CCGGGGGGCA 	TOCCTOPTICG TOCCTOPTI	- AGCGTCATT	TC ACCCTCA	AGCTCTGCTT 	- GGTATTGGGC C A.T 	CTCCGCCAGT T.TA. 	
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2,000 replicates (Hedges, 1992), using the Bootstrap option in PAUP. We also examined the Bremer index (Bremer, 1988) using AutoDecay version 3.0 (Eriksson, 1995). Evaluation of the resulting phylogenetic hypotheses (tree topologies) was done with the Kishino and Hasegawa test (Kishino and Hasegawa, 1989) in DNAML (PHYLIP version 3.57c, Felsenstein, 1995), with a specified transition-transversion ratio of 1.5.

Results

Fresh specimens of *V. calthicola*, *V. spiraeicola*, *C. candolleana* and *S. rubicola* all produced felty, adpressed, greyish brown mycelial mats and determinate, convoluted, pyramidal stromata in concentric rings on PDA after 1 to 8 wk (Figs. 1–4). *Rutstroemia firma* and *R. bolaris* typically produced pale yellowish-brown mycelial mats and indeterminate, undifferentiated brownish black stromata of heavily pigmented interwoven hyphae. *Ciborinia foliicola* and *C. whetzelii* did not grow on PDA in axenic culture.

The complete sequence matrix of the 19 specimens of the nine species included in this study consisted of 546 aligned nucleotide positions (characters; Fig. 5), of which 124 characters were parsimony informative. The ITS1 and ITS2 contributed 187 (75 parsimony informative) and 162 (46 parsimony informative) of the 546 characters, respectively. Two genotypes, differing by a single substitution in position 450 were found in C. candolleana. Four genotypes, differing by 2, 4, 6 or 8 characters were found in V. spiraeicola. Specimens of V. calthicola from Canada and Norway, as well as on Caltha (dicot: Ranunculaceae) and Iris (monocot: Iridaceae) had identical genotypes. Parsimony analysis of the complete matrix yielded a single most parsimonious tree (MPT; L=259; Fig. 6), in which the specimens of Scleromitrula, C. candolleana and Verpatinia together constituted a strongly supported monophyletic clade (99% bootstrap support; Bremer index = 11).

Within the ITS1 a central segment (characters 81-135) could not be aligned without introducing gaps, due to presence of several small indel motifs. Phylogenetic analysis excluding this segment yielded 20 MPTs (L=181). A strict consensus tree of these 20 MPTs is shown in Fig. 7.

The analyses consistently yielded three strongly supported evolutionary lineages corresponding to the three cultural phenotypes described above. The first and second lineages (LIN 1 and LIN 2) consisted of the *Rutstroemia* spp. (group I), and two *Ciborinia* spp. including the type species (group II), respectively. The third lineage (LIN 3) constituted an assemblance of specimens representing five subclades or groups: *C. candolleana* on *Quercus* species (group III); *S. shiraiana* on *M. alba* (group IV); *V. calthicola* on *Caltha palustris* and *Iris pseudacorus* (group V); *S. rubicola* on *Rubus chamaemorus* (group VI); and *V. spiraeicola* on *Filipendula ulmaria* (group VII). With (and without) the indel segment included, the maximum parsimony bootstrap support for the three lineages LIN1, LIN2 and LIN3, was 100 (93), 100 (100) and 99 (99) %, and the Bremer index was 27 (5), 39 (28) and 11 (9), respectively.

With a constraint retaining *Scleromitrula* and *Verpatinia* as separate monophyletic entities, PAUP yielded five trees (Fig. 8) two steps longer than the MPT (Fig. 6) when all characters were included, and 29 trees (Fig. 9) one step longer than the MPTs (Fig. 7) when the indel segment was excluded from the analysis. It should be noted that *C. candolleana* and the new taxon *S. rubicola* were treated as *Verpatinia* species when we defined the constraint.

Constraining *C. candolleana*, *C. whetzelii* and *C. foliicola* to constitute a single monophyletic lineage yielded two trees (Fig. 10) twelve steps longer than the MPT (Fig. 6) when all characters were included, and 2 trees (Fig. 11) ten steps longer than the MPTs (Fig. 7) when the indel segment was excluded from the analysis. A separation of *C. candolleana* from *C. foliicola* and *C. whetzelii* and the inclusion of the former species in the *Scleromitrula*/*Verpatinia* lineage, was strongly supported.

A maximum likelihood analysis with DNAML was performed using the obtained tree topologies as userdefined trees (Table 2). Among the trees compared with DNAML, the MPTs (Figs. 6, 7) were found to be the best trees. The difference in log likelihood of the MPTs (Figs. 6, 7) and the trees obtained with a constraint retaining *Scleromitrula* and *Verpatinia* as separate monophyletic entities (Figs. 8, 9) was not significant. The difference in log likelihood between the MPTs (Figs. 6, 7) and the trees obtained with a constraint forcing the three *Ciborinia* species together (Figs. 10, 11) was significant when all characters were included, but not when the indel segment was excluded.

Discussion

Culture morphology and molecular phylogeny This study provides supporting data for a new phylogenetic framework of the genus *Scleromitrula*. The observed

Fig. 5. Sequence matrix of the ITS region for phylogenetic analyses.

The matrix consists of 546 characters, and spans from the 3'-end of the nuclear SSU rRNA gene (positions 1–5; first dark box) through the entire internal transcribed spacer 1 (ITS1; positions 6–193), the 5.8S rRNA gene (positions 194–351; second dark box), and the ITS2 (positions 352–513), to the 5'-end of the LSU gene (positions 514–546; terminal dark box). *Ciborinia can-dolleana* isolate 1657.1 was used as reference, and sequence similarity is indicated by dots (.). Gaps are indicated by hyphens (--), and missing characters are indicated by question marks. The segment consisting of positions 81–135 (grey box) was excluded from some analyses (see text) due to uncertainties with the alignment of the many indels within the segment. Parsimony informative characters are indicated by asterisks (*) above. The specimens 1774.P (*C. candolleana*), and 2021.P, 2049.P, 2057.P and 2060.P (*Verpatinia calthicola*) were omitted from the figure because of 100% sequence similarity to specimens 1657.1 (*C. candolleana*), and 1871.P and 1368.1 (*V. calthicola*).



Fig. 6. The single most parsimonious tree (MPT) yielded with a branch and bound algorithm in PAUP and the complete sequence matrix.

Tree statistics are: length (L)=259, consistency index (CI)=0.830, CI excluding uninformative characters (CIx)=0.774, retention index (RI)=0.803, rescaled CI (RC)=0.666. Three major evolutionary lineages (LIN1, LIN2 and LIN3) are indicated. The first lineage, LIN1 consists of the reference taxa *Rutstroemia bolaris* and *R. firma* (group I). The second lineage, LIN2 consists of two *Ciborinia* spp., i.e., *C. foliicola* and the type species *C. whetzelii* (group II). The third lineage, LIN3 consists of *Ciborinia* candolleana on *Quercus* species (group III), *Scleromitrula shiraiana* on *Morus alba* (group IV), *Verpatinia calthicola* on *Caltha palustris* and *Iris pseudacorus* (group V), *Scleromitrula rubicola* on *Rubus chamaemorus* (group VI) and *Verpatinia spiraeicola* on *Filipendula ulmaria* (group VII). Placing *Verpatinia, Ciborinia* candolleana as well as the type species of *Scleromitrula* (*S. shiraiana*) in separate genera would make the former genus paraphyletic. The type species are indicated by asterisks (*) behind the species names. The values above the internodes are bootstrap values (>50%) obtained from 2,000 bootstrap replicates; thick internodes indicate $\geq 99\%$ bootstrap support. The Bremer support (\geq 1), indicating the number of character state changes postulated for each internode. Scale bar corresponds to 20 character state changes (CSCs). The specimens 1774.P (*C. candolleana*), and 2021.P, 2049.P, 2057.P and 2060.P (*Verpatinia calthicola*) were omitted from the figure due to 100% sequence similarity to specimens 1657.1 (*C. candolleana*) and 1871.P and 1368.1 (*V. calthicola*), respectively.

growth pattern of *V. calthicola*, *V. spiraeicola*, *C. candolleana* and *S. rubicola* on PDA (Figs. 1–4) corresponds well with the growth pattern of *S. shiraiana* reported by Kohn and Nagasawa (1984). The phylogenetic analyses of the ITS rDNA sequences also strongly support the inseparable status of *Scleromitrula* and *Verpatinia*. The



Fig. 7. Strict consensus tree based on the 20 equally most parsimonious trees (MPTs) yielded with a branch and bound algorithm in PAUP when positions 81-135 were excluded. Tree statistics are: L=181, CI=0.829, CIx=0.742, RI=0.782, RC=0.648. The trees contain the same three major evolutionary lineages (LIN1, LIN2 and LIN3) as those which were found with the complete sequence matrix (Fig. The MPTs consistently placed Scleromitrula shiraiana 6). and Ciborinia candolleana in derived positions within the Verpatinia clade, indicating that placing C. candolleana, Scleromitrula and Verpatinia in separate genera would make the latter genus paraphyletic (data not shown). The type species are indicated by asterisks (*) behind the species The values above the internodes are bootstrap names. values (>50%) obtained from 2,000 bootstrap replicates; thick internodes indicate $\geq 99\%$ bootstrap support. The Bremer support (≥ 1) is shown below the internodes. The tree only reflects the branching topology, and internode lengths are not drawn to scale. The specimens included in the figure are the same as shown in Figs. 5 and 6.

sequence data may question the taxonomic relevance of certain morphological characters such as texture of ectal excipular tissues and staining of the ascus pore plug in Melzer's reagent, which traditionally have been major criteria in separating *Scleromitrula* and *Verpatinia* and genera of the family Sclerotiniaceae and the order Helotiales as a whole (Korf, 1973; Kohn and Nagasawa, 1984).

The same set of morphological and sequence data also supports the distinctiveness of the genera *Ciborinia* and *Verpatinia*. This conclusion is further supported by the level of SSU and LSU rDNA divergence observed in a recent study of the phylogeny of the family Sclerotiniaceae based on a combined data set of rDNA sequences (Holst-Jensen et al., 1995). Cultural features and ITS sequences in *C. candolleana* diverged significantly from the other Ciborinia spp., e.g., C. foliicola and C. whetzelii (the type species), but demonstrated strong affinities to the Scleromitrula/Verpatinia assemblance of species. Except for the stipitate-cupulate shape in C. candolleana, the apothecial morphology is not as different from the stipitate-capitate forms of Scleromitrula and Verpatinia as it might first seem. As already pointed out in the original description by Léveille (1843), ".... in this Peziza (candolleana) the stalk is slender, filiform, naked, rather firm and dark reddish; it forms at first only erect or tortuous threads, later the tip swells resembling a small pin; finally it dilates and forms a small flattened cup, red, whose edge is thin, sometimes regular, completely spread out and even decurved." The occasional flattened and decurved apothecial shape in fresh specimens of C. candolleana has also been observed by us. As pointed out by Kohn and Nagasawa (1984), the stipitate-capitate Verpatinia may represent a mere modification of development of gross morphology of the ascocarp in the typical cupulate apothecium in Ciborinia; the mechanisms are not difficult to imagine; the stipe continues to proliferate, expanding more rapidly lengthwise than the developing subhymenial and medullary tissues of the apothecial disc" (Kohn and Nagasawa, 1984).

The inseparable status of *C. candolleana*, *Scleromitrula* and *Verpatinia* species was strongly supported by the ITS rDNA phylogenies (Figs. 6, 7). Transferring *C. candolleana* to the *Scleromitrula*/*Verpatinia* lineage was significantly supported by the Kishino and Hasegawa tests (Table 2).

The failure to obtain axenic cultures from specimens of *C. foliicola* and *C. whetzelii* was also noted by Whetzel (1945), and may probably be explained by the obligate parasitic life history of the species.

Verpatinia has traditionally been treated as a member of the sclerotial group of taxa of the family Sclerotiniaceae, e.g., *Sclerotinia* and *Ciborinia* (Whetzel, 1945; Batra and Korf, 1959; Kohn, 1979). Recent molecular studies, however, suggest a closer relationship with taxa producing a substratal stroma, e.g., *Poculum* and *Rutstroemia* (Holst-Jensen, 1995; Holst-Jensen et al., 1995). This is also in agreement with the observations on the stromatal anamorph of *S. shiraiana* by Kohn and Grenville (1989), who referred the species to the substratal stromatal group. Although having determinate, well-circumscribed sclerotia, the stroma in *Scleromitrula* and *Verpatinia* is poorly differentiated into a cortex and medulla compared to the highly differentiated stroma of the true sclerotial group of taxa.

Taxonomy On the basis of gross morphology, axenic culture morphology and the set of aligned ITS sequences, *Scleromitrula* turns out as a well-circumscribed genus of stipitate-capitate and very similar stipitate-cupulate forms of stromatic discomycetes of the family Sclero-tiniaceae. In the synopsis of taxa which follows, only characters of importance in identifying and discriminating the genus and the included species are summarized.

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Figs. 8, 9. Strict consensus trees based on a constraint compatible with a classification in which *Scleromitrula* and *Verpatinia* constitute separate monophyletic evolutionary lineages (thick lines).

Note that *Ciborinia candolleana* and the new taxon *S. rubicola* are treated as *Verpatinia* species. The generic types are indicated by asterisks (*) behind the species names. The specimens included are the same as shown in Figs. 5 and 6. Fig. 8. Strict consensus tree based on the 5 MPTs yielded with a branch and bound algorithm in PAUP and the complete sequence matrix. Tree statistics are: L=261, CI=0.824, CIx=0.766, RI=0.794, RC=0.654. Fig. 9. Strict consensus tree based on the 29 MPTs yielded with a branch and bound algorithm in PAUP and the complete sequence matrix. RI=0.775, RC=0.638.



Figs. 10, 11. Strict consensus trees based on a constraint forcing *Ciborinia* to be monophyletic (thick lines). The generic types are indicated by asterisks (*) behind the species names. The specimens included are the same as shown in Figs. 5 and 6. Fig. 10. Strict consensus tree based on the 2 MPTs yielded with a branch and bound algorithm in PAUP and the complete sequence matrix. Tree statistics are: L=271, CI=0.793, CIx=0.729, RI=0.749, RC=0.594. Fig. 11. Strict consensus tree based on the 2 MPTs yielded with a branch and bound algorithm in PAUP and the complete sequence matrix. Tree statistics are: L=271, CI=0.793, CIx=0.729, RI=0.749, RC=0.594. Fig. 11. Strict consensus tree based on the 2 MPTs yielded with a branch and bound algorithm in PAUP when positions 81-135 were excluded. Tree statistics are: L=191, CI=0.785, CIx=0.685, RI=0.711, RC=0.559.

Table 2. Maximum likelihood results from the Kishino and Hasegawa tests, comparing tree topologies obtained with maximum parsimony methods in PAUP with and without constraints.

Each tree topology was introduced	as a user defined	tree in DNAML
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Tree	Tree length	Log likelihood	Difference LnLª)	SD of tree ^{b)}	Significantly worse? ^{c)}
With co	omplete matrix:				
The	unconstrained mo	st parsimonious t	ree (Fig. 6)		
	259	-1647.498	←		Best
The	constrained trees	accepting both ge	enera: <i>Scleromit</i>	trula and Verpatin	<i>ia</i> (Fig. 8)
	261	-1655.206	-7.708	7.593	No
		-1665.435	-17.937	11.352	
The	constrained trees	keeping <i>Ciborinia</i>	monophyletic (Fig. 10)	
	271	-1680.589	-33.091	11.928	Yes
		-1680.598	-33.100	11.947	
Withou	ut positions 81-13	35:			
The	unconstrained mo	st parsimonious t	ree (Fig. 7)		
	181	-1452.954	←		Best
		- 1458.936	-5.982	11.495	No
The	constrained trees	accepting both g	enera: <i>Scleromi</i> t	trula and Verpatin	<i>ia</i> (Fig. 9)
	182	- 1459.959	-7.005	5.270	
		- 1464.373	-11.419	13.062	No
The	constrained trees	keeping Ciborinia	monophyletic (Fig. 11)	
	191	- 1477.683	-24.729	15.689	No
		-1478.767	-25.813		

a) Difference in log likelihood compared to that of the best tree.

b) The standard deviation of log likelihood.

c) The difference is considered significant if the difference of log likelihood is more than 1.96 SD.

Scleromitrula S. Imai, J. Fac. Agric. Hokkaido Univ. 45: 177. 1941. emend.

- Verpatinia Whetzel & Drayton in Whetzel, Mycologia
 37: 690. 1945.
- = Scleroglossum Hara, Manual of pests and diseases, p. 158. 1948.
- Illustrations: Stromatal anamorph: Kohn and Nagasawa (1984): 133, Fig. 5.

Microconidial anamorph: Kohn and Nagasawa (1984), Fig. 4.

Axenic culture morphology: Kohn and Nagasawa (1984), Fig. 2.

Ascomata stipitate-capitate, exceptionally stipitatecupulate, the capitate forms with a pendent margin forming a collar around stipe apex interrupting the continuity between the hymenium and stipe. Ectal excipulum of head (cup) of globose to angular to brick-shaped cells in chains perpendicular to stipe axis, medullary excipulum of textura intricata, subhymenium distinct, of densely packed hyphae. Ectal excipulum of stipe of dense textura porrecta, medullary excipulum of bundles of densely packed hyphae; hyphae short-segmented. Stroma determinate, of the lenticular to pyramidal type, developing on surface of infected host fruits, leaves or stems; stroma black outside, white to greyish inside, with a well-developed dorsiventral rind composed of thick-walled, melanized, globose to prismatic cells, stromatal cortex and medulla not much differentiated, of compact textura oblita with heavily gelatinized walls enveloping partly digested or undigested host tissues. Ascus inoperculate, with a thickened apex, pore channel wall J + or J -after pretreatment in 2% KOH. Ascospores hyaline, ellipsoidal to allantoid, unicellular, eguttulate or with one or two internal, minute polar guttules.

In culture on PDA mycelium greyish to olive-grey to brown, mostly adpressed and submerged in agar; aerial mycelium scarce, white, in cushions in center after 1 to 2 wk; after 3 to 4 wk mycelial mat becoming convoluted and sometimes furrowed, darkening and becoming heavily pigmented and black with age; first generation mycelium producing clusters of determinate, irregularly lenticular to pyramidal, convoluted, soft, sclerotioid stromata in hyphal cushions in concentric zones on surface of mycelial mat, upper surface usually convex and irregularly convoluted (cerebriform), lower surface flat to concave, broadly attached to the agar surface. Microconidia a *Myrioconium* Sydow state produced on discrete phialides in mucilaginous pustules or spermodochia on surface of mycelium.

Macroconidial anamorph wanting.

Morphologically differing from other genera assigned to the Sclerotiniaceae by the stipitate-capitate gross morphology of the ascomata (except in *S. candolleana*), and the relatively small asci and narrowly ellipsoid to allantoid ascospores, the pyramidal and convoluted, scarcely differentiated stroma as opposed to the indeterminate, flat substratal stroma in *Rutstroemia* P. Karst.; from the true, differentiated hollow-sphaeroid (i.e., *Monilinia* Honey), mummioid (i.e., *Ciboria* Fuckel), discoid (i.e., *Ciborinia*) or tuberoid (i.e., *Botryotinia* Whetzel, *Sclerotinia* Fuckel, *Myriosclerotinia* N. F. Buchw., *Dumontinia* L. M. Kohn) type of sclerotium in the sclerotioid group of the family, and from *Botryotinia* and *Monilinia* by the absence of a macroconidial anamorph referable to *Botrytis* Micheli: L. and *Monilia* Bonorden, respectively.

Notes Groves and Elliott (1961) succeeded in obtaining apothecia from single ascospore culture isolates of *V*.

calthicola and concluded that the fungus was self-fertile. Whetzel (1945) in describing Verpatinia, included the non-congeneric taxon V. duchesnayensis (see below), thus opening for an intermingling of characters in the generic diagnosis of Verpatinia (see Whetzel, 1945). Kohn and Nagasawa (1984) provided full description and illustrations of axenic culture isolates, and stromatal and microconidial anamorphs in S. shiraiana, the generic type, which is applicable to other Scleromitrula species as well. Scleromitrula shiraiana was credited a conidial stage by Endo (1927) and Imai (1941), that was found comparable with those of the microconidiophores and microconidia by Kohn and Nagasawa (1984).

Key to the species of Scleromitrula

1.	Apothecia stipitate-capitate, cap with longitudinal ridges and furrows, arising from lenticular to pyramidal stromata on its host
1.	Apothecia stipitate-cupulate to applanate to slightly decurved, arising from small, lenticular stromata on petioles and leaf nerves of <i>Quercus</i> species and <i>Castanea sativa</i>
2.	Cap minute, 2–5 mm high, 0.8–2 mm broad; asci 35–55 μ m; on leaves and stems of its host
2.	Cap large, 3-16 mm high, 2-7 mm broad; asci 65-90 μm; on fruits of Morus alba S. shiraiana
З.	Ascospores exceeding 7 µm in length
3.	Ascospores $5-7 \times 1.5-2.5 \mu$ m; cap 1-3 mm high, 0.8-1.5 mm broad; stipe $10-30 \times 0.2-0.4$ mm; on leaves of <i>Filipendula</i> and <i>Calystegia</i>
(3	Ascospores 5.5–7 \times 2 μ m; host unknown
4.	Cap 2–5 mm high, 1–2 mm broad; stipe 10–40×0.3–0.7 mm; ascospores 6.0–9.4×2.0–3.0 μm; on leaves of <i>Rubus</i> chamaemorus ····································
4.	Cap 2–3 mm high, 1–2 mm broad; stipe $10-30 \times 0.2-0.6$ mm; ascospores $6.3-9.8 \times 1.5-2.6 \mu$ m; on leaves of <i>Caltha palustris</i> and <i>Iris pseudacorus S. calthicola</i>

Scleromitrula calthicola (Whetzel) T. Schumach. & Holst-Jensen, comb. nov.

Basionym: Verpatinia calthicola Whetzel, Mycologia 37: 692. 1945.

Ascomata stipitate-capitate, 2–3 mm long, 1–2 mm broad, greyish brown to pale brown, long-stipitate, stipe 5-18 mm long, 0.2-0.5 mm thick. Stromata determinate, lenticular to pyramidal, soft, $1-2 \times 0.5-1.5$ mm; in culture stromata more irregular in shape, convoluted, up to 3 to 5 to 8 mm in diam, clustered, in concentric zones, partly submerged in agar, aerial mycelium whitish, submerged mycelium brownish. Asci 8-spored, 38-50 \times 4-7 μ m, with a thickened apex, ascus pore bluing (J+) in Melzer's reagent, gradually tapering to a short bifurcate or blunt base. Ascospores narrowly fusold to allantoid, $6.3-9.8 \times 1.5-2.6 \,\mu m$, in fresh specimens with one minute globule at each pole. Paraphyses abundant, unbranched, straight or slightly bent, 2.0-2.8 μ m broad below, not inflated or narrowed (to 1.5 μ m) above.

Substrate: On decaying plant remnants of *Caltha palustris* and *Iris pseudacorus*.

Distribution: Canada, U.S.A. (Whetzel, 1945), England (Clark, 1980; Cannon et al., 1985), Czechia (Svrček, 1966), Norway (Schumacher, 1997).

Cultures and specimens examined: -On decaying leaf remnants of *Caltha palustris*: USA. New York, Syracuse, Labrador Lake, swamp N of Woods road, May 23, 1937, H. H. Whetzel and A. P. Viegas-Whetzel S1319

(holotype-CUP 25926; isotype-Korf and Gruff, Discomycetes exsiccati no. 50); New York, McLean, S of stream opposite old shelter near foot bridge, May 5, 1933, Whetzel S 990 (CUP 21996). Canada. Ontario, Ottawa, apothecia produced in culture, March, 1954, C. Bowerman (TRTC-ex DAOM 45991); Ontario, 35 km N of Wawa, June 7, 1993, L.M. Kohn and T. Schumacher 93/231 (O), 1871.P -mass ascospore isolate; Ontario, Ottawa, Gatineau Park, apothecia produced in culture, Series C 1962-63, February 25, 1963, M. E. Elliott 726 (CUP 48463-ex DAOM 91252); apothecia produced in culture, Series C XII, April, 1964, M. E. Elliott 733 (CUP 51967-ex DAOM 128284); Quebec, SE of Coaticook, June 11, 1959, R.F. Cain (TRTC 34605). Norway. Vestfold, Brunlanes, Oddane Sand, June 16, 1992, A. Holst-Jensen and T. Schumacher 92/080 (0), 1356.P mass ascospore isolate; same locality June 22, 1994, T. Schumacher 94/068 (0), 2021.P -mass ascospore isolate.

-On decaying leaf sheets of *Iris pseudacorus*: Norway. Telemark, Bamble, Stokkevann, June 20, 1990, A. Holst-Jensen 90/119 (O); same locality, June 16, 1992, A. Holst-Jensen and T. Schumacher 92/085 (O), 1368.P-1369.P -mass ascospore isolates; same locality June 22, 1994, T. Schumacher, N. Sletvold and M. Vaage 94/094 (O), 2057.P -mass ascospore isolate; 94/095 (O), 2060.P -mass ascospore isolate; same locality June 29, 1996, A. Holst-Jensen 96/143 (O), 2442.P mass ascospore isolate; Vestfold, Brunlanes, pond at Strandåsen, June 22, 1994, T. Schumacher, N. Sletvold and M. Vaage 94/088 (O), 2049.P -mass ascospore isolate. England. Cheshire, Bidston, West of Bidston Hill, June 22, 1963, J. T. Palmer 11625 (CUP-G 2822; CUP-E 2822 -ex herb. Gremmen).

-On unidentified leaf under *Populus* sp. and *Betula* sp.: Canada. Quebec, Tenaga, May 25, 1937, J. W. Groves and I. L. Conners (Whetzel S 1332 -CUP 26449).

Scleromitrula candolleana (Lév.) T. Schumach. & Holst-Jensen, comb. nov.

Basionym: *Peziza candolleana* Lév., Ann. Sci. Nat. II, **20**: 233. 1843.

= Sclerotinia candolleana (Lév.) Fuckel, Jahrb. Nass. Ver. Naturk. **23**–24: 330. 1870.

=Phialea candolleana (Lév.) Quél., Encheridion Fung. 301. 1886.

Hymenoscypha candolleana (Lév.) W. Phillips, Man. Brit. Discom. 114. 1887.

= Ciborinia candolleana (Lév.) Whetzel, Mycologia **37**: 668. 1945.

Stromatal anamorph: *Sclerotium quercinum* Pers., Disp. Meth. Fung. 15. 1797.

= Sclerotium pustula DC a. roboris DC, Fl. Fr. III, 5(6): 113, 1815.

=*Sclerotium pustula* DC: Fr. (*'pustulla'*), Syst. Mycol. **2**(1): 260. 1822.

Ascomata stipitate-cupulate, cup discoid to slightly decurved, 2-4 mm broad, stipe 10-25 mm long, 0.2-0.5 mm thick. Ectal excipulum of minute, globose cells, 8-16 μm in diam. Stromata black, lenticular, soft, 0.5-2 \times 0.4–0.8 mm; in culture determinate stromata formed after 5-7 wk, irregular in shape, convoluted, pyramidal, clustered, upper surface convex, lower surface flat or concave, up to 5–7 mm long \times 1–4 mm broad \times 1–2 mm thick, superficially and partly submerged in agar, mycelium white to greyish brown, felty, mostly adpressed to agar, deeply furrowed, aerial mycelium whitish, submerged mycelium brownish. Asci 8-spored, 68-80 \times 6-8 μ m, ascus pore bluing (J+) in Melzer's reagent, ascus base blunt. Ascospores ovoid-ellipsoidal, no internal guttules, $6.0-7.8 \times 3.1-4.6 \mu m$. Paraphyses abundant, unbranched, $1.5-2 \mu m$ broad, upper segment slightly bent, tips enlarged to 2.5–3.0 μ m.

Substrate: In leaves of *Castanea sativa* and *Quercus* species.

Distribution: Recorded from several European countries.

Cultures and specimens examined: Germany. Krieger, Fungi Saxonici no. 93 -CUP - (neotype selected (Batra, 1960)). - on leaves of *Quercus*: Germany. Berlin, zoological garden, September, 1885, P. Sydow (S. Rehm, Ascom. no. 802-isotype). Norway. Østfold, Onsøy, Storesandvik, June 8, 1981, R. Kristiansen (O); Østfold, Borge, Dal, Torsnes, June 7, 1981, R. Kristiansen (O); Østfold, Hvaler, Vesterøy, Lerdalen, May 19, 1993, A. Holst-Jensen, 93/050 (O), 1655.1, 1657.1 single ascospore isolates; Østfold, Moss, Jeløya, Røed gåard, May 19, 1993, A. Holst-Jensen, T. Schumacher, C. Holm and T. Vråalstad, 93/055 (O), 1676.2, 1678.1, 1678.2 - single ascospore isolates; Telemark, Bamble, Rørholt, Myrane, June 20, 1993, A. Holst-Jensen and T. Vråalstad 93/116 (O), 1774.P - 1777.P - mass ascospore isolates; Telemark, Bamble, Rugtvedtmyra, N end of Stokkevann, June 29, 1996, A. Holst-Jensen 96/145 (O), 2444.P - mass ascospore isolate.

Scleromitrula morchelloides (Mains) T. Schumach. & Holst-Jensen, comb. nov.

Basionym: *Mitrula morchelloides* Mains, Pap. Mich. Acad. Sci. Arts Lett. **20**: 83. 1934.

= Verpatinia morchelloides (Mains) A. Redhead, Can. J. Bot. 55: 323. 1977.

Ascomata stipitate-cupulate, pale brown, 1 mm broad, 1–2 mm long, stipe 18–20 mm long. Ectal excipulum of subglobose to clavate cells, 11–12.5× 7.5–10.5 μ m, developing apical papillae near the apothecial margin. Stroma unknown. Asci 8-spored, short cylindric, 38–46×5–6.5 μ m, short pedicellate, croziate, apically thickened, ascus pore blueing (J+) in Melzer's reagent. Ascospores fusoid-elliptical to cymbiform, usually flattened on one side, 5.5–7×2 μ m, nonseptate, hyaline, thin-walled, inamyloid, mostly biseriate. Paraphyses abundant, hyaline, thin-walled, nonseptate, equal or slightly enlarged apically.

Substrate: on wet leaves (Redhead, 1977).

Distribution: U.S.A.: Michigan (Mains, 1934); only known from the type collection.

Notes We have not examined the type specimen of this species. The scanty type material (U.S.A., Michigan, Munising, Wagner's Falls, June 12, 1933, E. B. Mains 33–93 [MICH]) i.e., a single apothecium lacking stem base, stroma and host remnants, was reexamined and fully described by Redhead (1977), from where the above description is drawn. *Scleromitrula morchelloides* and *S. spiraeicola* seem to share all important microscopical details, and may well be conspecific. Bearing in mind the subtle morphological characters and the observed level of host speciation in this complex of closely related species, we have refrained from synonymizing the two taxa. Future collections from the Michigan district may eventually prove the inseparable status of the two taxa.

Scleromitrula rubicola T. Schumach. & Holst-Jensen, sp. nov. Figs. 12–14

Ascomate capitato ruguloso, stipitati, umbrino, 1–4 mm longo, 1–2 mm lato; stipite cylindraceo, 15–30 mm longo, 0.2–0.8 mm lato; e sclerotio enato; stroma 1–4×0.5–1.5 mm, subhemisphaericum vel ovatum. Excipulum ectale e cellulis globulosa sistens. Asci cylindrico-clavati, typice octospori, apice rotundati, poro in Melzero caerulescente, 40–55×4–6 μ m. Ascosporae hyalinae, fusoideae vel allantoideae, eguttulatae vel biguttulatae, 6.0–9.4×2.0–3.0 μ m. Paraphyses filiformes, apice paullo incrassatae, c. 2.5–3.5 μ m latae. Hab. in sclerotio nigro ad folia putrida *Rubi chamaemori*, June 21, 1994, T. Schumacher, N. Sletvold and M. Vaage 94/064 (holotypus, O).

Ascomata stipitate-capitate, $1-4 \text{ mm} \log$, 1-2 mm thick, greyish brown to pale brown, stipe 15-30 mm

long, 0.2–0.8 mm thick. Stromata determinate, lenticular to pulvinate, soft, $1-4 \times 0.5-1.5$ mm; in culture stromata formed after 3–6 wk, irregular in shape, convoluted, up to 3 to 5 to 8 mm in diam, clustered, in concentric zones, partly submerged in agar, mycelial mat whitish, submerged mycelium brownish. Asci 8-spored, subclavate, $40-55 \times 4-6 \mu$ m, gradually tapering to a blunt or bifurcate base, ascus-pore bluing (J+) in Melzer's reagent. Ascospores hyaline, much variable in shape and size, fusoid to inequilateral loaf-shaped to incurved on one side (allantoid), eguttulate to uniguttulate to biguttulate $6.0-9.4 \times 2.0-3.0 \mu$ m. Paraphyses scanty, $2.5-3.5 \mu$ m broad, unbranched, straigth, not distinctly enlarged at tips.

Substrate: On leaves of Rubus chamaemorus.

Distribution: Norway; only known from type locality. Cultures and specimens examined: Norway. Akershus, Eidsvoll, Frilsetåasen, June 21, 1994, T. Schumacher, N. Sletvold and M. Vaage, 94/064 (holotype-O), 2016.P - mass ascospore isolate; same locality, June 15, 1996, A. Holst-Jensen, S. Landvik and T. Schumacher

(O), 2418.P-2419.P - mass ascospore isolates.

Notes *Scleromitrula rubicola* has morphological features similar to *Scleromitrula calthicola*, however, the ascocarp is slightly larger and the ascospores somewhat broader and more irregular in shape. Additionally, the ITS sequence data clearly indicate the distinctiveness of the two taxa. *Scleromitrula rubicola* and *S. spiraeicola* which attack the hosts *Rubus chamaemorus* and *Filipendula ulmaria* of the same family (Rosaceae), respectively, are obviously also closely related, however, the ascospores are distinctly larger in the former species. This, together with the degree of host specialization, and the observed ITS sequence divergence between the two taxa, which is twice as large as the variation observed within *V. spiraeicola*, support a distinction on species level.

- *Scleromitrula shiraiana* (Henn.) S. Imai, J. Fac. Agric. Hokkaido Univ. **45**: 177. 1941.
 - For a description, see Kohn and Nagasawa (1984). Substrate: On fruits of *M. alba*.





Figs. 12–14. Scleromitrula rubicola, coll. 94/064 (O-holotype).
 Fig. 12. Camera lucida drawing of longitudinal section of fertile head and upper stipe showing hymenium, subhymenium and excipulum. Scale: 50 μm. Fig. 13. Asci and paraphyses. Scale: 5 μm. Fig. 14. Ascospores. Scale: 5 μm.

Distribution: Japan, China (Ling, 1948).

Culture examined: Japan. IFO 30255 - mass ascospore isolate.

Notes Scleromitrula shiraiana, the nomenclatural type of the genus Scleromitrula, was treated in detail by Kohn and Nagasawa (1984) and Spooner (1987). The stipitate-capitate ascomata (fertile head 3-16 × 2-7 mm; stipe up to 100×1 mm), ectal excipulum of head of angular to prismatic cells, relatively large asci (65–90 μ m) and ascus pore wall J- in Melzer's reagent, are features which contrast its generic accompanions. On PDA, the olive greyish mycelial mat develops a ± zonate stroma and \pm elevated, distinct sclerotia, 2-4 mm broad. The relatively large-sized apothecium in S. shiraiana compared to the more fragile apothecium in other Scleromitrula species may be explained by the relative size of the stroma. Positive correlation of apothecial size and stroma has also frequently been observed in species of Ciboria and Monilinia (Schumacher and Holst-Jensen, unpublished data).

Scleromitrula spiraeicola (Dennis) T. Schumach. & Holst-Jensen, comb. nov.

Basionym: Verpatinia spiraeicola Dennis, Mycol. Pap. (C.M.I.) 62: 162. 1956.

Apothecia singly from a stroma, stipitate-capitate, head light brown, 1-2 mm high, 0.5-0.9 mm broad. Stipe 10-22×0.1-0.3 mm, flexuous and elastic; stroma black, lenticular and slightly acuminate, $2.5-3 \times$ 1-1.5×0.7-1 mm, or globular, 0.8 mm in diam. In culture rapidly growing on PDA, mycelium at first densely applanate, whitish, after 1 to 2 wk turning greyish brown, aerial mycelium sparse, after 1 to 5 wk developing irregular, convoluted, clustered, lenticular stromata superficially or partly immersed in \pm concentric zones on agar, 2-3-5 mm broad. Ectal excipulum of apothecium of textura globulosa. Ascospores allantoid - fusoid, biseriate in ascus, 5.5–7.4 \times 2.0–2.8 μ m (mean 6.4 \times 2.5), without internal globules. Asci 8-spored, cylindrical-clavate, (35-)40-50(-55) \times 4.5-6 μ m, narrowed below to a stout stalk, pore wall faintly blueing (J+) in Melzer's reagent. Paraphyses straight, $1.5 \,\mu m$ below, enlarged to 2.0–2.5 μ m above.

Substrate: on blackened, rotting leaves of *Filipendula ulmaria*; also recorded on stems of *Calystegia sepium* (Dennis, 1956).

Distribution: England (Dennis, 1956; Cannon et al., 1985), Switzerland (Matheis, 1979), Denmark (Elborne and Læssøe, 1983), Norway (Schumacher, 1997), Netherlands (Matheis, 1979).

Cultures and specimens examined: -On leaves of *Filipendula ulmaria*: Norway. Akershus, Fet, Øyeren, Monserudvika, May 24, 1990, L. M. Kohn and T. Schumacher 90/063 (O), 1844.2 - single ascospore isolate; same locality, June 12, 1992, A. Holst-Jensen and T. Schumacher 92/070 (O), 1328.1, 1331.1 - single ascospore isolate; 92/071 (O), 1337.1 - single ascospore isolate; Akershus, Bærum, Sandvika, Engervann, May 18, 1994, T. Schumacher and N. Sletvold 94/003 (O), 1946.P - mass ascospore isolate; Telemark, Bamble, near

Rørholt School, June 29, 1996, A. Holst-Jensen 96/146 (O), 2445.P - mass ascospore isolate). Switzerland. TG, Grütried bei Wängi, June 23, 1974, Walter Matheis 417 (CUP - G 2823; CUP - E 2823 - ex herb. Gremmen); same locality, May 29, 1976, W. Matheis 650 (CUP 56949).

Excluded and imperfectly known taxa Quite a number of *Scleromitrula*-like fungi have been reconsidered by contemporary authors and are now redisposed in other genera (see Knudsen, 1975; Benkert, 1983; Kohn and Nagasawa, 1984; Samuels and Kohn, 1986; Spooner, 1987). Some taxa which have been misplaced or suspected as belonging to *Scleromitrula* or *Verpatinia* by us or others are shortly summarized below.

brassicae, Mitrula –Hammarlund, Ark. for Bot. **25**: 59, Taf. 1, Figs. 7–10. 1932.

Notes This species was recorded from sclerotia of *Typhula gyrans* Batsch on leaves of *Brassica oleracea* f. *capitata* from Sweden (Hammarlund, 1932). Maas Geesteranus (1964) suggested a relationship within *Verpatinia*. The original description indicates *Episclerotium sclerotipus* (Boud.) L. M. Kohn (see below). Dr. Åke. Strid has kindly informed us that no type or authentic specimens are found in Hammarlund's herbarium accessioned in Lund (LD) and Stockholm (S).

duchesnayensis, Verpatinia –Whetzel, Mycologia 37: 694. 1945.

Specimens examined: Canada. Quebec, Duchesnay, Portneuf, near Forest Rangers' School, August 23, 1938, original collection of apothecia, Whetzel S 1391 -CUP 28011 A; CUP 28011 B: original culture from above collection on PDA; same locality, leaves showing stromata, September 30, 1938, R. Pomerleau (CUP 28011 C); same locality, second collection of leaves with stromata, October 27, 1938, R. Pomerleau (CUP 28011 D).

Notes The species is only known from the type collection and entered as four packets, including sketches and notes, as no. 28011 in CUP (see above). The packets include some infected leaves of Betula lutea bearing some black, filiform (to 25 mm long), striate stromata typical of a Ciborinia species along the leaf veins. Collection 28011 A includes a single, pale Mitrula-like fungus emanating from a sclerotium, the stipe being relatively short (5 mm) and thick (0.6 mm). From Whetzel's notes in CUP it is clear that he was unsuccessful in cultivating the fungus. The specimen obviously parasitizes sclerotia of a Ciborinia species, is fruiting in autumn, and has a gross morphology of the ascocarp and associated stromata which in our opinion preclude an assignment to Scleromitrula. The species should be compared with Episclerotium L. M. Kohn (Kohn and Nagasawa, 1984).

pusilla, Cudoniopsis - Speg., Mycologia 17: 210. 1925.

Notes The genus *Cudoniopsis* was erected by Spegazzini (1925) to include a single specimen from stromata on living branches of *Eugenia proba* (type: Argentina. Neuquen, Puerto Blest, August, 1921, C. Spegazzini). According to Dumont and Korf (1971) and Korf (1973) *Cudoniopsis* may represent an older name for *Verpatinia*, and thus *Scleromitrula*. The description of a cylindrical to tuberoid stroma bearing minute, crowded apothecia with a campanulate head and free margin enveloping the stipe, and broadly ellipsoid ascospores is not much indicative of *Scleromitrula*. The genus should be compared with *Episclerotium* L. M. Kohn (Kohn and Nagasawa, 1984) or *Sclerocrana* Samuels & L. M. Kohn (Samuels and Kohn, 1986) (=?*Mitrulina* Spooner (1987)). Repeated inquires to obtain authentic material of the fungus from Herb. Spegazzini have never been answered.

sclerotiorum, Scleromitrula - (Rostrup) S. Imai, J. Fac. Agric. Hokkaido Univ. 45: 177. 1941.

=*Episclerotium sclerotiorum* (Rostrup) L. M. Kohn, Trans. Mycol. Soc. Japan **25**: 141. 1984.

Notes This species produces stipitate-capitate ascocarps hyperparasitic on sclerotia of *Sclerotinia* and *Dumontinia* of the family Sclerotiniaceae (cf. Kohn and Nagasawa, 1984: 142) and is likely to be confused with *Scleromitrula*. The species has been well-redescribed by Røed (1954), Ylimäki (1968), Knudsen (1975), Matheis (1979), and Benkert (1983), and was referred to *Episclerotium* by Kohn and Nagasawa (1984). According to Røed (1954) the fungus produces reddish brown, up to 4.5×1.5 mm, flat cushions in culture, resembling sclerotia. The species is to be excluded from *Scleromitrula*.

sclerotipus, Scleromitrula - (Boud.) S. Imai, J. Fac. Agric. Hokkaido Univ. **45**: 177. 1941.

Episclerotium sclerotipus (Boud.) L. M. Kohn, Trans. Mycol. Soc. Japan **25**: 143. 1984.

Notes This species is parasitic on sclerotia of *Typhula* species and should be excluded from *Scleromitrula*. The species has recently been treated by Benkert (1983) and Kohn and Nagasawa (1984), the latter authors referring it to the new genus *Episclerotium*, together with *E. sclerotiorum* (see above).

ushuaiae, Scleromitrula – (Rehm) Gamundi, Kew Bull. 31: 734, 1976.

= Mitrulina ushuaiae (Rehm) Spooner, Bibl. Mycol. 116: 246. 1987.

Notes This taxon was treated by Kohn and Nagasawa (1984) and Spooner (1987), who both agreed that it should be excluded from *Scleromitrula*. Spooner (1987) referred it to his new genus *Mitrulina* Spooner.

viridis, Scleromitrula –Gamundi, Kew Bull. 31: 737. 1976.

Notes This southern hemisphere taxon on *Nothofagus* wood was re-considered by Kohn and Nagasawa (1984) who found several reasons to exclude it from *Scleromitrula*. The species is, except for the description, unknown to us.

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