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ARTICLE

Phacidium and *Ceuthospora* (*Phacidiaceae*) are congeneric: taxonomic and nomenclatural implications

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Abstract: The morphologically diverse genus *Ceuthospora* has traditionally been linked to *Phacidium* sexual morphs via association, though molecular or cultural data to confirm this relationship have been lacking. The aim of this study was thus to resolve the relationship of these two genera by generating nucleotide sequence data for three loci, ITS, LSU and RPB2. Based on these results, *Ceuthospora* is reduced to synonymy under the older generic name *Phacidium*. *Phacidiaceae* (currently *Helotiales*) is suggested to constitute a separate order, *Phacidiales* (*Leotiomycetes*), as sister to *Helotiales*, which is clearly paraphyletic. *Phacidiaceae* includes *Bulgaria*, and consequently the family *Bulgariaceae* becomes a synonym of *Phacidiaceae*. Several new combinations are introduced in *Phacidium*, along with two new species, *P. pseudophacidioides*, which occurs on *Ilex* and *Chamaespartium* in Europe, and *Phacidium trichophori*, which occurs on *Trichophorum cespitosum* subsp. *germanicum* in The Netherlands. The generic name *Allantophomopsiella* is introduced to accommodate *A. pseudotsugae,* a pathogen of conifers, while *Gremmenia* is resurrected to accommodate the snow-blight pathogens of conifers, *G. abietis, G. infestans,* and *G. pini-cembrae.*

Key words:
Bulgariaceae
coelomycete
discomycete
Gremmenia
Helotiales
LSU
Phacidiales
RPB2
systematics

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INTRODUCTION

The generic name *Phacidium* was introduced by Fries (1815) for *P. coronatum* and *P. integerrimum*. *Phacidium integerrimum* was subsequently transferred to *Excipula*, and *P. coronatum* to *Coccomyces*. *Phacidium lacerum*, a species described later by Fries (1818), was therefore considered the type species of the genus (von Höhnel 1917), even though it was not one of the two species originally described by Fries. Subsequent authors have accepted this typification (Terrier 1942, von Arx & Müller 1954, Reid & Cain 1962, Korf 1973, Dennis 1978). In order to regularise this situation, Hawksworth & Sherwood (1981) proposed the conservation of *Phacidium* with *P. lacerum* as the conserved type species; this proposal was accepted by the Committee for Fungi and Lichens and incorporated into the appendices of the Berlin *Code* of 1988 (Greuter *et al.* 1988). While the proposal to conserve the type was under discussion, DiCosmo *et al.* (1984) followed Höhnel (1917) and accepted *P. lacerum* as the type. Under the Melbourne *Code* (McNeill *et al.* 2013), types for sanctioned names can be selected either from the original protologue (in this case Fries 1815) or the sanctioning work (in this case Fries 1823, where *P. lacerum* was included), so there would be no objection now to the acceptance of *P. lacerum* as type species of *Phacidum* but that option was not available in 1981.

Tulasne & Tulasne (1861–65) recognised that *Phacidium ilicis* was a single fungus with two morphs (pleomorphic), and the conidiomatal states to be representative of *Cytisporae* (spermatial) and *Ceuthosporae* (asexual). *Ceuthospora* has been linked as an asexual morph to *Phacidium* (Sutton 1980, Nag Raj 1993). As with *Phacidium*, however, the typification of the asexual name was also beset by problems.

The generic name *Ceuthospora* was published by Fries (1825) with two species, *Sphaeria phaeocomes* and *Sclerotium inclusum*. Greville (1828) included another three species, *C. phacidioides, C. lauri,* and *C. phaeocomes*, all accepted by Fries (1832). Fries (1849) introduced the generic name *Pyrenophora*, and referred both *Sphaeria phaeocomes* and *Sclerotia inclusum* to that genus. The genus *Ceuthospora*, was thus not clearly typified. Fries (1832) effectively selected *Sphaeria phaeocomes* as type,

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Table 1. Collection details and GenBank accession numbers of isolates included in this study.

Species	Isolate no.[1]	Host	Location	Collector	GenBank accession no.[2]		
					LSU	ITS	RPB2
Allantophomopsiella pseudotsugae	CBS 288.37	*Picea abies*	United Kingdom	–	KJ663863	KJ663824	KJ663904
	CBS 320.53	*Pseudotsuga menziesii*	Norway	H. Robak	KJ663864	KJ663825	KJ663905
	CBS 321.53	*Picea abies*	Norway	H. Robak	KJ663865	KJ663826	KJ663906
	CBS 437.71	*Pinus sylvestris*	Netherlands	J. Gremmen	KJ663866	KJ663827	KJ663907
	CBS 562.63	*Pinus sylvestris*	Norway	F. Roll-Hansen	KJ663867	KJ663828	KJ663908
	CBS 841.91	*Pinus* sp.	Germany	P. Schumacher	KJ663868	KJ663829	KJ663909
Allantophomopsis cytisporea	CBS 262.85	Roots of Conifer species	Germany	H. Courtois	KJ663869	KJ663830	KJ663910
'*Allantophomopsis*' sp.	CBS 109.22	*Oxycoccus macrocarpos*	USA	C.L. Shear	KJ663861	KJ663822	KJ663902
Allantophomopsis sp.	CBS 322.36	*Pinus radiata*	New Zealand	P.C. Birch	KJ663880	KJ663839	KJ663921
Bulgaria inquinans	CBS 118.31	Forest floor	Germany	BIHM	KJ663870	KJ663831	KJ663911
	CBS 129.58	Forest floor	Germany	–	KJ663871	KJ663832	KJ663912
	CBS 145.55	–	Germany	H. Lyr	KJ663872	KM216394	KJ663913
	CBS 315.71	*Quercus robur*	Switzerland	E. Müller	KJ663873	KJ663833	KJ663914
Coleophoma sp.	CBS 449.70	*Liriodendron tulipifera*	Netherlands	H.A. van der Aa	KJ663874	KJ663834	KJ663915
Gremmenia infestans	CBS 396.48	–	Sweden	E. Björkman	KJ663876	KM216393	KJ663917
Hyaloscypha sp.	CBS 109453	*Miconia* sp.	Venezuela	I. Hernandez	KJ663875	KJ663835	KJ663916
Neofabraea sp.	CBS 135481 = CPC 22154	*Polygonatum* sp.	Netherlands	U. Damm	KF251745	KF251242	KJ663942
Phacidium calderae	CBS 287.72	*Arbutus unedo*	Italy	W. Gams & J.A. Stalpers	KJ663878	KJ663837	KJ663919
	CBS 372.81	*Pistacia terebinthus*	Spain	H.A. van der Aa	KJ663879	KJ663838	KJ663920
Phacidium fennicum	CBS 457.83	*Pinus sylvestris*	Finland	H. Butin	KJ663881	KJ663840	KJ663922
Phacidium lacerum	CBS 130.30	*Pinus sylvestris*	Netherlands	J.Y. van Vliet	KJ663882	KJ663841	KJ663923
	CBS 338.70	*Ilex aquifolium*	Netherlands	H.A. van der Aa	KJ663883	KJ663842	KJ663924
	CBS 400.81	*Juniperus communis*	France	O. Petrini	KJ663884	KJ663843	KJ663925
	CBS 540.70	*Pinus sylvestris*	Netherlands	H.A. van der Aa	KJ663885	KJ663844	KJ663926
	CBS 557.70	*Sciadopitys verticillata*	Netherlands	H.A. van der Aa	KJ663886	KJ663845	KJ663927
	CBS 761.73	*Pinus sylvestris*	France	M. Morelet	KJ663887	KJ663846	KJ663928
Phacidium lauri	CBS 198.68	*Vinca minor*	Netherlands	H.A. van der Aa	KJ663890	KJ663849	KJ663930
	CBS 308.68	*Prunus laurocerasus*	Netherlands	H.A. van der Aa	KJ663891	KJ663850	KJ663931
	CBS 443.71	*Ilex aquifolium*	Netherlands	L. Marvanová	KM216397	KM216392	KM216396
	CBS 589.67	*Ilex aquifolium*	Netherlands	H.A. van der Aa	KJ663892	KJ663851	KJ663932
Phacidium mollerianum	CBS 365.72	*Eucalyptus* sp.	Italy	W. Gams	KJ663888	KJ663847	KJ663929
	CBS 574.66	*Polygonatum odoratum*	Netherlands	H.A. van der Aa	KJ663889	KJ663848	KM216395
Phacidium pseudophacidioides	CBS 497.72	*Chamaespartium sagittale*	Switzerland	E. Müller	KJ663893	KJ663852	KJ663933

Table 1. (Ctd).

Species	Isolate no.[1]	Host	Location	Collector	GenBank accession no.[2]		
					LSU	ITS	RPB2
	CBS 590.69	*Ilex aquifolium*	Netherlands	H.A. van der Aa	KJ663894	KJ663853	KJ663934
Phacidium trichophori	CBS 138246 = CPC 22952	*Trichophorum cespitosum* subsp. *germanicum*	Netherlands	W. Quaedvlieg	KJ663895	KJ663854	KJ663935
Phacidium vaccinii	CBS 444.71	*Vaccinium vitis-idaea*	Netherlands	L. Marvanová	KJ663896	KJ663855	KJ663936
Phlyctema vincetoxici	CBS 123726	*Vincetoxicum officinale*	Czech Republic	G. Verkley	KJ663897	KJ663856	KJ663937
	CBS 123727	*Vincetoxicum officinale*	Czech Republic	G. Verkley	KJ663898	KJ663857	KJ663938
	CBS 123743	*Vincetoxicum officinale*	Czech Republic	G. Verkley	KJ663899	KJ663858	KJ663939
Potebniamyces pyri	CBS 282.55	*Pyrus communis*	Netherlands	Zweede	KJ663862	KJ663823	KJ663903
	CBS 322.63	*Pyrus communis*	Netherlands	G.S. Roosje	KJ663900	KJ663859	KJ663940
Pseudophacidium ledi	CBS 377.59	*Picea abies*	Switzerland	J. Gremmen	KJ663901	KJ663860	KJ663941
Sarcotrochila longispora	CBS 273.74	*Pinus contorta*	British Columbia	W.G. Ziller & A. Funk	KJ663877	KJ663836	KJ663918

[1]CBS: CBS-KNAW Fungal Biodiversity Centre, Utrecht, The Netherlands; CPC: Culture collection of Pedro Crous, housed at CBS.

[2]LSU: large subunit (28S) of the nrRNA gene; ITS: internal transcribed spacers and intervening 5.8S nrDNA; RPB2: partial RNA polymerase II second largest subunit gene.

when he excluded *Sclerotium inclusum* from the genus. However, *Pyrenophora phaeocomes* was selected as type species of *Pyrenophora* by Shoemaker (1961), which effectively leaves *Pyrenophora* as a later nomenclatural synonym of *Ceuthospora*. To resolve this situation, Sutton (1972) proposed the conservation of *Ceuthospora* Grev. 1826 with *C. lauri* as type, over *Ceuthospora* Fr. 1825 with *C. phaeocomes* as type; this was accepted by the Committee for Fungi and Lichens and the name included in the appendices to the Leningrad *Code* (Stafleu *et al.* 1978).

The family name *Phacidiaceae* was introduced by Fries (1849) and accepted by Karsten (1871) who stressed that members had a particular apothecium type with a reduced exciple. Nannfeldt (1932) recognised 14 genera in the family, but Terrier (1942) felt that the family contained different elements, and probably should only include five genera. Von Arx & Müller (1954) regarded eight genera as belonging to the family. The circumscription remained a bone of contention, as Kreisel (1969) recognised four genera, Korf (1973) nine, Dennis (1978) 13, and Lanier *et al*. (1978) seven. DiCosmo *et al*. (1984) listed 24 genera in *Phacidiaceae*, stating that it was heterogeneous and in need of further study. In a recent phylogenetic study of *Leotiomycetes* (Wang *et al*. 2006b), *Helotiales* (incl. *Phacidiaceae*) was left untreated as a large, polyphyletic assemblage, due to inadequate molecular data and sampling. However, they did refer to *Phacidiaceae,* based on analyses including a LSU sequence of *Phacidium lacerum* (data not shown), which suggested a sister group relationship with *Phacidiopycnis pyri* (sexual morph: *Potebniamyces pyri*), previously questionably placed in *Rhytismatales*). In the SSU-LSU-5.8S phylogeny (Wang *et al.* 2006b), *P. pyri* formed a strongly supported monophyletic group with *Bulgaria inquinans* (*Bulgariaceae*), and *P. pyri* together with *Holwaya mucida* (although without support) was moved to *Bulgariaceae*. *Bulgaria* has large, brown-black to black, turbinate, gelatinous apothecia with brown-walled ascospores, and is thus quite different from *Phacidium* and *Potebniamyces* in morphology. In the LSU & SSU phylogeny generated by Lantz *et al*. (2011), however, these three genera clustered together in a well-supported clade.

Given the recent decision to abolish dual nomenclature for fungi (Hawksworth 2011, Hawksworth *et al.* 2011, Wingfield *et al*. 2012), we wanted to resolve the issue of whether *Phacidium* and *Ceuthospora* were really congeneric (Johnston *et al*. 2014) and fix the application of these names using genetic data, and further to determine the phylogenetic position of *Phacidiaceae* within *Helotiales*.

MATERIALS AND METHODS

Isolates

Isolates used in this study were obtained from the culture collection of the CBS-KNAW Fungal Biodiversity Centre (CBS). Utrecht, The Netherlands (Table 1). Colonies were established on Petri dishes containing 2 % malt extract agar (MEA), potato-dextrose agar (PDA), and oatmeal

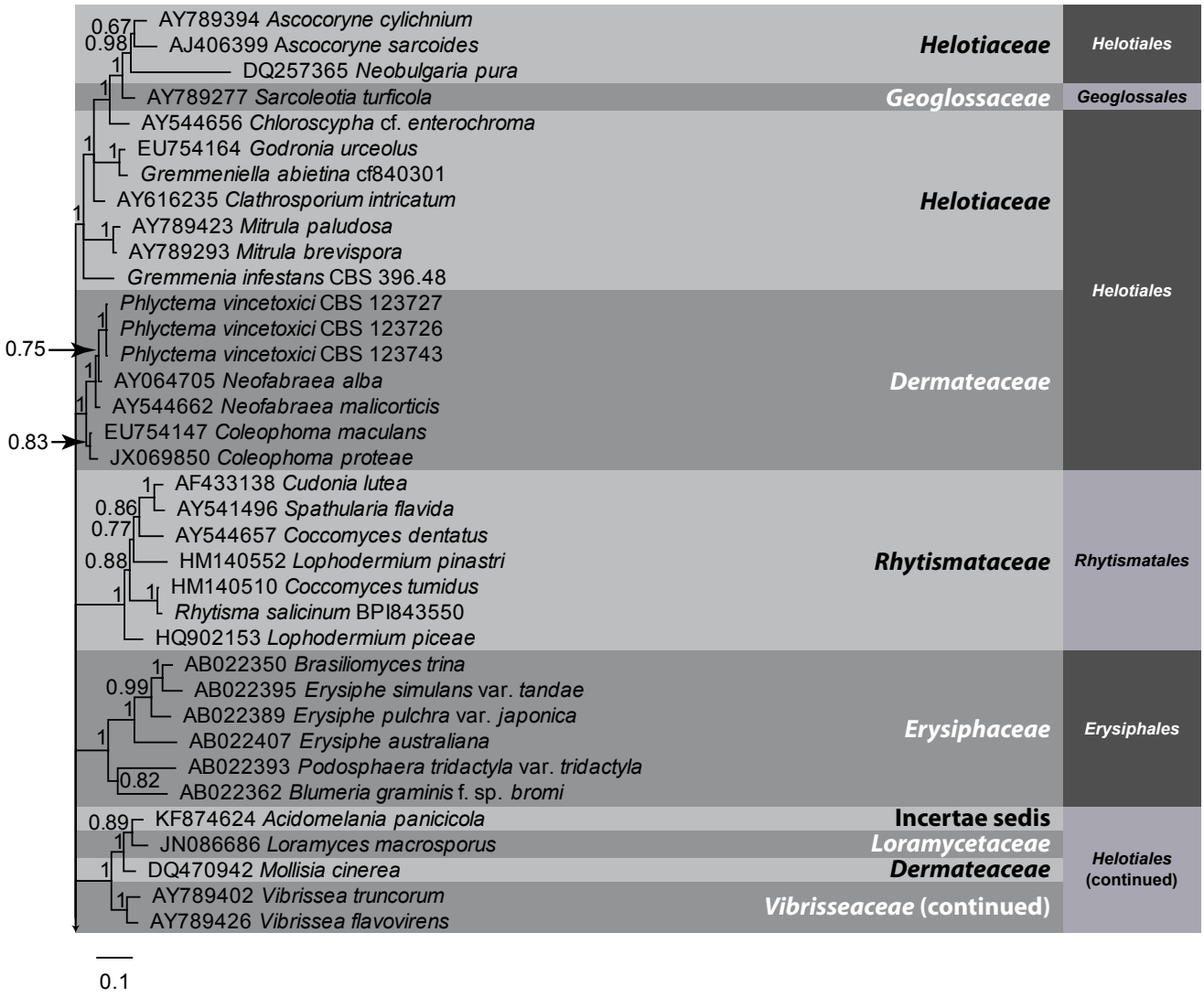

Fig. 1. A Bayesian 50 % majority rule LSU consensus tree containing representative isolates belonging to *Leotiomycetes* and related classes. Bayesian posterior probabilities support values for the respective nodes are displayed in the tree. A stop rule (set to 0.01) for the critical value for the topological convergence diagnostic was used for the Bayesian analysis. The tree was rooted to *Saccharomyces cerevisiae* (GenBank J01355). The scale bar indicates 0.1 expected changes per site.

agar (OA) (Crous *et al*. 2009b), and incubated at 25 °C under continuous near-ultraviolet light to promote sporulation.

DNA isolation, amplification and analyses

Genomic DNA was extracted from fungal colonies growing on MEA using the UltraCleanTM Microbial DNA Isolation Kit (MoBio Laboratories, Solana Beach, CA) according to the manufacturer's protocol. The primers LSU1Fd (Crous *et al*. 2009a) and LR5 (Vilgalys & Hester 1990) were used to amplify the partial 28S rRNA gene (LSU), ITS5 and ITS4 (White *et al*. 1990) were used to amplify the internal transcribed spacer region (ITS), fRPB2-5F (Liu *et al*. 1999), and fRPB2-414R (Quaedvlieg *et al*. 2011) were used to amplify the partial RNA polymerase II second largest subunit locus (RPB2). A basic alignment of the obtained sequence data was first done using MAFFT v. 7 (http://mafft.cbrc.jp/alignment /server/index.html; Katoh *et al*. 2002) and if necessary, manually improved in BioEdit v. 7.0.5.2 (Hall 1999). To check the congruency of the individual datasets, a 70 % neighbour-joining (NJ) reciprocal bootstrap was performed (Mason-Gamer & Kellogg 1996, Lombard *et al*. 2010). A Bayesian analysis (critical value for the topological convergence diagnostic set to 0.01) was performed on both the Multi order LSU (Fig. 1) and the concatenated ITS, LSU and RPB2 (Fig. 2) datasets using MrBayes v. 3.2.1 (Huelsenbeck & Ronquist 2001) as described by Crous *et al*. (2006) using nucleotide substitution models that were selected using the Akaike Information Criterion implemented in MrModeltest v. 2.3 (Nylander 2004). Novel sequences derived from this study were lodged at GenBank, and the alignments and phylogenetic trees in TreeBASE (www.treebase.org/treebase/index.html).

Morphology

Observations were made with a Zeiss V20 Discovery stereomicroscope, and with a Zeiss Axio Imager 2 light microscope using differential interference contrast (DIC) illumination and an AxioCam MRc5 camera and Zen software. Colony characters and pigment production were noted after 2 wk of

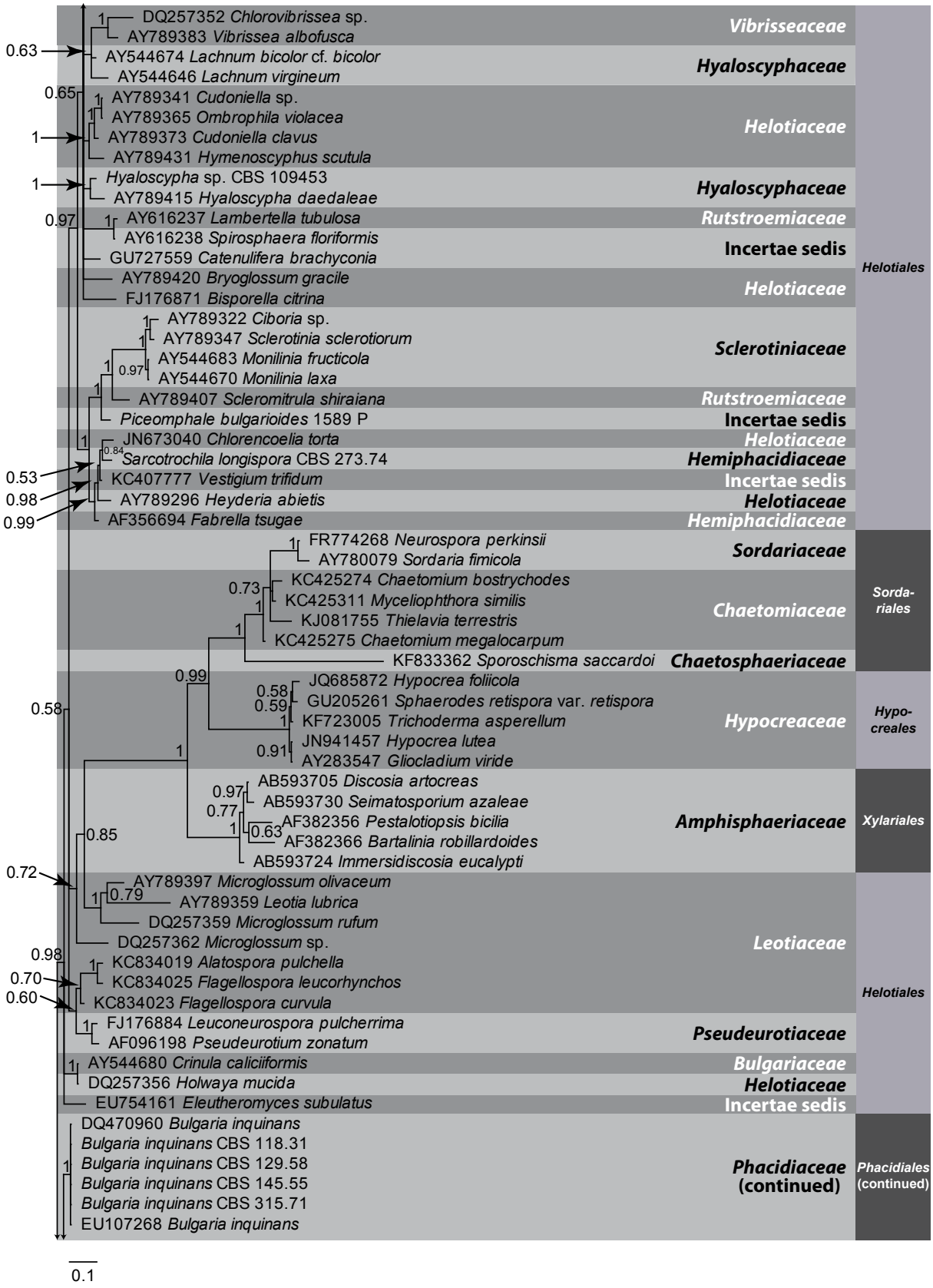

Fig. 1. (Continued).

growth on MEA, PDA and OA incubated at 25 ºC. Colony colours (surface and reverse) were rated according to the colour charts of Rayner (1970). Morphological descriptions were based on cultures sporulating on PDA, and taxonomic novelties and metadata were deposited in MycoBank (www.MycoBank.org; Crous *et al.* 2004).

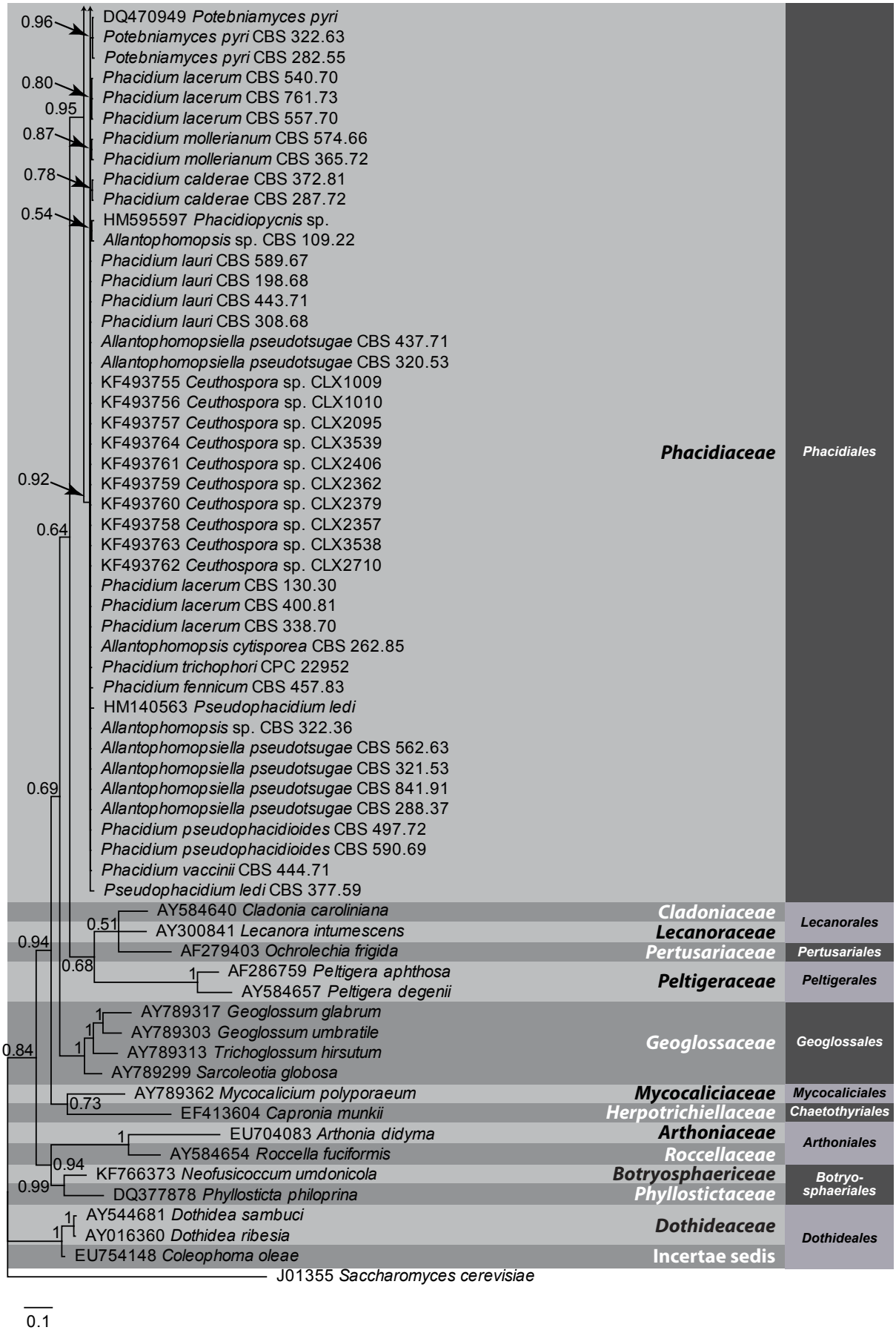

Fig. 1. (Continued).

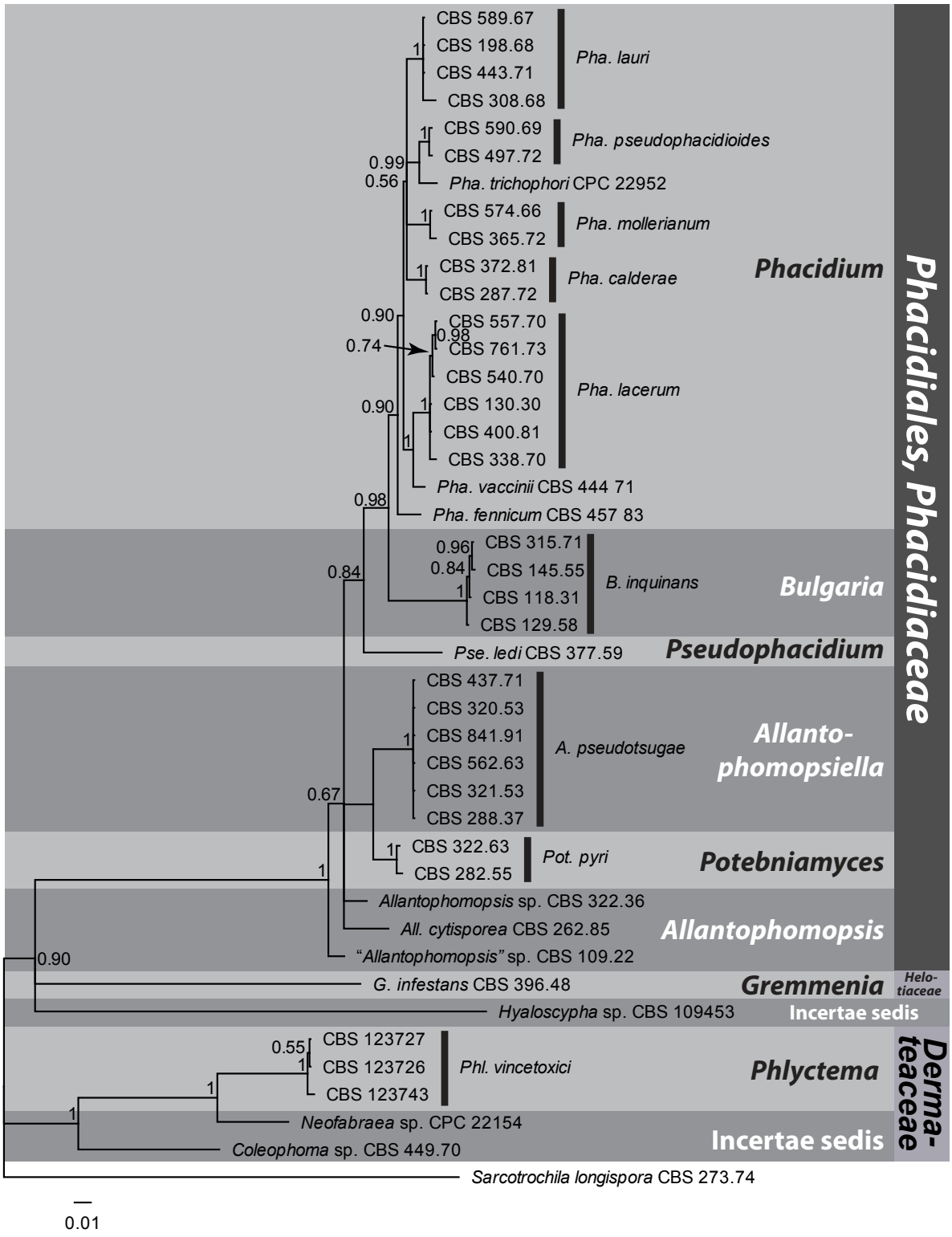

Fig. 2. A Bayesian 50 % majority rule combined ITS, LSU and RPB2 consensus tree containing representative isolates belonging to the *Phacidiales* and related orders. Bayesian posterior probabilities support values for the respective nodes are displayed in the tree. A stop rule (set to 0.01) for the critical value for the topological convergence diagnostic was used for the Bayesian analysis. The tree was rooted to *Sarcotrochila longispora* (CBS 273.74). The scale bar indicates 0.01 expected changes per site.

RESULTS

Phylogeny

The ITS, RPB2 and LSU sequence datasets of 43 sequences (including the outgroup) did not show any conflicts in their tree topology for the 70 % reciprocal bootstrap trees, allowing us to combine them in the multigene analyses. For Fig. 1, the LSU overview dataset of 160 sequences (including the outgroup) contained 830 characters, of which 461 contained unique site patterns. For Fig. 2, the LSU dataset contained

819 characters, of which 101 contained unique site patterns, the RPB2 dataset contained 355 characters, of which 155 contained unique site patterns, and the ITS dataset contained 537 characters, of which 203 contained unique site patterns.

For the combined dataset, all data partitions used the GTR model but the LSU partition was analysed with MrBayes using dirichlet (1,1,1,1) state frequency distribution and inverse gamma-shaped rate variation across sites, the ITS partition was analysed using a fixed (equal) state frequency distribution and gamma-shaped rate variation across sites, and the RPB2 partition was analysed using fixed (equal) state frequency distribution and inverse gamma-shaped rate variation across sites. For the LSU overview tree, MrModeltest suggested the same Bayesian parameters as for the LSU partition in the combined dataset. During the generation of Fig. 1, 72 262 trees were generated of which 54 198 (75 %) were sampled for the final tree; for Fig. 2, 2 672 trees were generated of which 2 004 (75 %) were sampled for the final tree.

Taxonomy

The genus *Phacidium* represents inoperculate discomycetes characterised by erumpent, cleistohymenial apothecia with a covering layer splitting into teeth or lobes, an externally black stroma with vertically arranged pseudoparenchymatous cells, asci that are clavate, (4–)8-spored, with amyloid dehiscence rings, and aseptate, ellipsoid, hyaline ascospores lacking sheaths or appendages. Paraphyses extend above the asci, frequently anastomose, are embedded in mucilage, and arise from the subhymenium. The *Ceuthospora* asexual morphs have phialidic conidiogenesis, and subcylindrical, hyaline conidia with funnel-shaped, mucoid apical appendages.

Leotiomycetes, Phacidiales, Phacidiaceae

Phacidiales Höhn., *Ber. Deutsch. Bot. Ges*. **34**: 416 (1917).

Saprobic or plant pathogenic. *Ascomata* circular, superficial, discoid, or immersed, becoming erumpent, opening by irregular tears in upper layer. *Asci* clavate, unitunicate with or without apical dehiscence ring. *Ascospores* aseptate, ellipsoid to subcylindrical or irregularly so, straight to curved, hyaline or brown, without sheath. *Paraphyses* branched or simple, septate, hyaline, anastomosing, invested in mucilage. *Conidiomata* uni- to multilocular, single to aggregated. *Conidiophores* hyaline, smooth, branched, or reduced to conidiogenous cells. *Conidiogenous cells* phialidic, at times proliferating percurrently, invested in mucilage. *Conidia* subcylindrical, ellipsoid-oblong or subreniform, aseptate, with or without appendages.

Type family: *Phacidiaceae* Fr. 1849.

Phacidiaceae Fr., *Summa veg. Scand*. **2**: 367 (1849); as "*Phacidicei*".

Synonym: *Bulgariaceae* Fr., *Summa veg. Scand.* **2**: 357 (1849); as "*Bulgariacei*".

Foliicolous, caulicolous, corticicolous, parasitic or saprobic (endophytic). *Ascomata* apothecial, discoid, or circular, initially immersed, becoming erumpent, opening by irregular tears in upper layer, teeth opening to expose hymenium; wall of *textura globulosa* to *textura angularis*; inner layer of smooth-walled, hyaline periphysoids invested in mucilage; basal stroma of *textura angularis* to *textura globulosa*. *Asci* arising from croziers, clavate, (4–)8-spored, unitunicate, with or without amyloid dehiscence ring staining blue in Melzer's reagent. *Ascospores* aseptate, ellipsoid, fusoid, subcylindrical or irregularly so, hyaline or brown, with or without germ slit, straight to curved, lacking gelatinous appendages. *Paraphyses* branched or simple, septate hyaline, anastomosing, invested in mucilage or not. *Conidiomata* uni- to multilocular, single to aggregated, with one to several ostioles. Walls of *textura angularis* to *textura globulosa*. *Conidiophores* hyaline, smooth, branched, or reduced to conidiogenous cells, arising from inner layer of conidioma. *Conidiogenous cells* phialidic, at times proliferating percurrently, invested in mucilage. *Conidia* hyaline, smooth, subcylindrical, ellipsoid-oblong or subreniform, with or without apical, mucoid funnel-shaped appendage.

Notes: *Bulgaria inquinans* (formerly *Bulgariaceae*) forms a strongly supported monophyletic group with members of the *Phacidiaceae*, and although its exact placement within this group is unresolved, *Bulgariaceae* is reduced to synonymy because it is genetically very close to these taxa (Figs 1–2). *Holwaya mucida*, placed in *Bulgariaceae* by Lumbsch & Huhndorf (2010) based on the results of Wang (2006b), groups outside *Phacidiaceae* and does not appear to be closely related (Fig. 1). Morphologically *Bulgariaceae* resembles the *Phacidiaceae* in its cleistohymenial development (Bellemère 1968), but is distinguished by having ascomata with a brownish outer exciple, a thick gelatinous medullary exciple, and four of the eight ascospores being dark brown, with a longitudinal germ-slit. *Potebniamyces pyri* (syn. *Phacidiopycnis pyri*), which was also placed in *Bulgariaceae*, clusters in the same clade. The family name *Phacidiaceae* was published in the same publication as *Bulgariaceae*, but is chosen here over the latter, as the family name *Phacidiaceae* is better established in the literature, and has more members.

Type genus: *Phacidium* Fr. 1815. Other genera accepted in *Phacidiaceae* based on DNA data include *Allantophomopsiella, Allantophomopsis, Bulgaria, Potebniamyces,* and *Pseudophacidium.*

Allantophomopsiella Crous, **gen. nov.**
MycoBank MB809673

Etymology: Named after its morphological similarity to the genus *Allantophomopsis*.

Diagnosis: Distinct from *Apostrasseria* and *Allantophomopsis* in lacking percurrent proliferation and in having inequilaterally fusiform or naviculate conidia.

Description: *Conidiomata* pycnidial, immersed, becoming erumpent, irregularly multilocular, dark brown, ostiolate; wall of 3–4 layers of dark brown *textura angularis*. *Conidiophores*

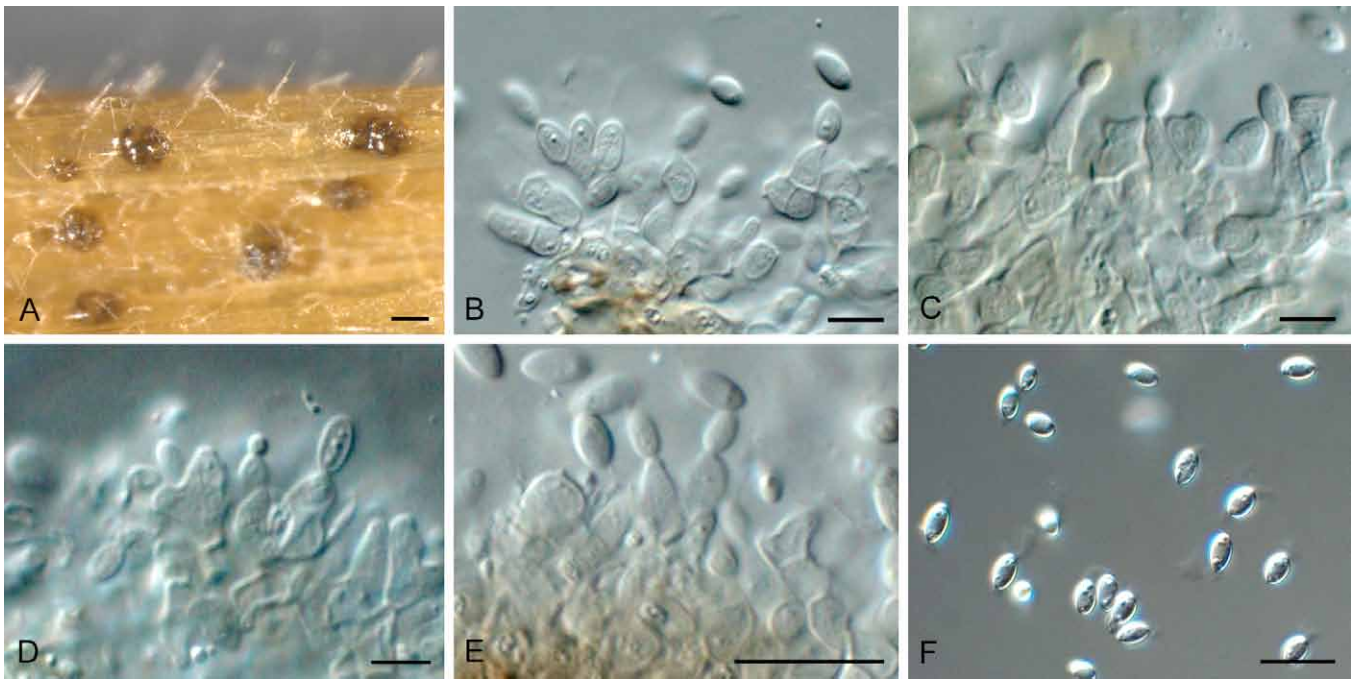

Fig. 3. *Allantophomopsiella pseudotsugae* (CBS 841.91). **A.** Conidiomata forming on autoclaved barley leaves. **B–E.** Conidiogenous cells giving rise to conidia. **F.** Conidia. Bars: A = 300 µm, all others = 10 µm.

arising from inner layer of conidioma, at times reduced to conidiogenous cells, branched, septate. *Conidiogenous cells* integrated or discrete, ampulliform to subcylindrical or lageniform, hyaline, smooth with minute periclinal thickening at apex. *Conidia* ellipsoid to fusiform, hyaline, smooth, aseptate, guttulate, bearing mucoid apical appendages (Type C sensu Nag Raj 1993), flabelliform to irregular in shape.

Type species: *Allantophomopsiella pseudotsugae* (M. Wilson) Crous 2014.

Allantophomopsiella pseudotsugae (M. Wilson) Crous, **comb. nov.**
MycoBank MB809674
(Fig. 3)

Basionym: *Phomopsis pseudotsugae* M. Wilson, *Trans. R. Scottish Arboricult. Soc*. **34**(2): 147 (1920).

Synonyms: *Allantophomopsis pseudotsugae* (M. Wilson) Nag Raj, *Coelom. Anam. App. Conidia*: 116 (1993).

Phacidiella coniferarum G.G. Hahn, *Mycologia* **49**: 227 (1957).

Phacidium coniferarum (G.G. Hahn) DiCosmo, *et al*., *Canad. J. Bot*. **61**: 37 (1983).

Additional synonyms are provided in Nag Raj (1993).

Specimens examined: **Germany**: on *Pinus* wood, Dec. 1991, *P. Schumacher* (CBS 841.91). – **The Netherlands**: Groesbeek, on needles of *Pinus sylvestris*, Nov. 1970, *J. Gremmen* (CBS 437.71). – **Norway**: on needles of *Pinus sylvestris*, July 1963, *F. Roll-Hansen* (CBS H-15946, culture CBS 562.63); Førde in Sunnfjord, shoot of *Pseudotsuga menziesii*, Apr. 1948, *H. Robak* (CBS 320.53); Gyl in Nordmøre, dead bark of *Picea abies*, June 1948, *H. Robak* (CBS 321.53). – **UK**: near Dumfries, dieback of 30-yr-old *Picea abies*, Oct. 1937, *Peace* (CBS 288.37).

Sporulating on PNA: *Conidiomata* pycnidial, immersed, becoming erumpent, irregularly multilocular, to 600 µm diam, dark brown, ostiolate; wall of 3–4 layers of dark brown *textura angularis*. *Conidiophores* arising from inner layer of conidioma, at times reduced to conidiogenous cells, branched, septate, 5–15 × 2.5–3.5 µm. *Conidiogenous cells* integrated or discrete, ampulliform to subcylindrical or lageniform, hyaline, smooth with minute periclinal thickening at apex, 5–8 × 2.5–3 µm. *Conidia* (4–)5–6(–7) × (2–)3 µm, ellipsoid to fusiform, hyaline, smooth, aseptate, guttulate, bearing mucoid apical appendages (Type C *sensu* Nag Raj 1993, only visible in water), flabelliform to irregular in shape.

Culture characteristics: Colonies spreading, flat with sparse aerial mycelium and feathery margins. On PDA surface olivaceous grey, reverse iron-grey. On OA surface olivaceous grey with patches of iron-grey.

Notes: Distinct from *Apostrasseria* and *Allantophomopsis* in that it lacks percurrent proliferation on its conidiogenous cells, and has inequilaterally fusiform or naviculate conidia.

Gremmenia: snow-blight pathogens of conifers

Gremmen (1953) described *Phragmonaevia gigaspora* as a new pathogen associated with needle blight (snow mould disease) of *Pinus cembra* in Europe. In his revision of *Helotiales* occurring on conifers, Korf (1962) established the genus *Gremmenia* to accommodate this pathogen, as it was clearly distinct from *Phacidium s. str*., lacking a distinct upper stroma in its apothecia. He also disagreed with Petrak

(1957), who concluded that *P. gigaspora* represented old and abnormal material of *Phacidium infestans*, which occurs on *Pinus sylvestris*, and its synonym, *Phacidium pini-cembrae*, which occurs on *Pinus cembra*. Korf (1962) distinguished these two species based on the fact that *Phacidium pini-cembrae* frequently has less than eight ascospores in its asci, a feature not observed in *P. infestans*. In a detailed comparison of the two species made by DiCosmo *et al.* (1984), *G. gigaspora* was reduced to synonymy with *Phacidium infestans*. *Phacidium infestans* and *P. pini-cembrae* are morphologically similar, but can be distinguished based on different hosts, as well as ascus and ascospore morphologies (DiCosmo *et al.* 1984). Ascospores of *P. infestans* are elongate-ellipsoid, straight, curved, or curved-fusiform, eight per ascus, with apothecia formed on needles of two-needled pines. In contrast, ascospores of *P. pini-cembrae* are slightly narrower, elongate-ellipsoid, frequently less than eight per ascus, and apothecia occur on needles of five-needled pines. Although DiCosmo *et al.* (1984) listed *Phragmonaevia gigaspora* as synonym of *Phacidium infestans*, this was incorrect, as a *Phragmonaevia gigaspora* occurs on *Pinus cembra*, and frequently has less than 8-ascospores (clearly illustrated by Gremmen 1953), and thus is more correctly placed in synonymy with *Phacidium pini-cembrae*. A third species of this complex is *P. abietis*, which causes disease on *Abies* and *Pseudotsuga*. Although further research is required to define the host range of these species, they are clearly not members of *Phacidium s. str.* (Fig. 2), and thus the genus *Gremmenia* is herewith resurrected to accommodate them.

Gremmenia Korf, *Mycologia* **54**: 27 (1962).

Plant pathogenic, foliicolous. *Ascomata* scattered, gregarious or separate, circular to elliptical in outline, subepidermal, raising host tissue, bursting open via 4–8 teach that curve backwards, exposing the creamy hymenium at maturity; apothecial roof of *textura globulosa*, brown, appearing like a clypeus when viewed in section when ascomata are immature, becoming hyaline towards interior, with inner layer giving rise to periphysoids, invested in mucilage; subhymenium of hyaline smooth-walled hyphae, forming a *textura angularis*. *Paraphyses* simple or branched, septate, hyaline, smooth-walled, invested in mucilage, sometimes slightly swollen at the tip. *Asci* club-shaped, (1–)8-spored, tapering towards base, stipitate, flattened at apex, giving blue reaction in Melzer's reagent. *Ascospores* biseriate, ellipsoid-elongate, straight to curved or reniform, aseptate, finely guttulate, hyaline, smooth.

Type species: *Gremmenia gigaspora* (Gremmen) Korf 1962 (i.e. *G. pini-cembrae* (Rehm) Crous 2014).

Gremmenia abietis (Dearn.) Crous, **comb. nov.**
MycoBank MB809676
Basionym: *Phacidium infestans* var. *abietis* Dearn., *Mycologia* **18**: 237 (1926).
Synonym: *Phacidium abietis* (Dearn.) J. Reid & Cain, *Mycologia* **54**: 482 (1963) ["1962"] (nom. illegit., Art. 53.1; non *P. abietis* Rabenh. 1844).

Notes: *Gremmenia abietis* causes snow-blight of *Abies* spp. and *Pseudotsuga menziesii* (Dearness 1926, Faull 1930). Bega (1978) reported that the disease could reach epidemic proportions in Idaho and Oregon. No cultures are presently available of this pathogen, and it will have to be recollected to clarify its phylogenetic position.

Gremmenia infestans (P. Karst.) Crous, **comb. nov.**
MycoBank MB809677
(Fig. 4)
Basionym: *Phacidium infestans* P. Karst., *Hedwigia* **25**: 232 (1886).

Description and illustrations: DiCosmo *et al*. (1984).

Specimens examined: **Sweden**, Vindeln, host unknown, 1946, *E. Björkman*, CBS 396.48; location unknown, on needles of *Abies balsamea*, Oct 1931, *J.H. Faull*, CBS 265.31; on needles of *A. balsamea*, 30 Nov. 1928, *J.H. Faull*, CBS 264.31; on needles of *Picea*, 22 Nov. 1928, *J.H. Faull*, CBS 263.31. Lappland, Jokkmokk, Kassavare, on dead needles of *Pinus sylvestris*, still attached to a young tree, 31 Aug. 2011, K. *Hansen & I. Olariaga* (S).

Notes: The isolates listed here show variation in the DNA sequence data, suggesting that they could represent more than one taxon. As the cultures proved to be sterile, fresh collections and epitypification is required to settle the application of the name.

Gremmenia pini-cembrae (Rehm) Crous, **comb. nov.**
MycoBank MB809678
Basionym: *Phacidium lacerum* f. *pini-cembrae* Rehm, *Ber. Bayer. Bot. Ges*. **13**: 124 (1912).
Synonyms: *Phacidium pini-cembrae* (Rehm) Terrier, *Beitr. Kryptog-fl. Schweiz* **9**: 73 (1942).
Phragmonaevia gigaspora Gremmen, *Sydowia* **7**: 141 (1953).
Gremmenia gigaspora (Gremmen) Korf, *Mycologia* **54**: 27 (1962).

Description and illustrations: DiCosmo *et al*. (1984).

Phacidium Fr., *Observ. mycol.* **1**: 167 (1815); nom. cons.
Synonyms: *Phacidiostroma* Höhn., *Ber. dt. bot. Ges.* **35**: 420 (1917).
Ceuthospora Grev., *Scot. Crypt. Flora* **5**: 253 (1827); nom. cons.

Foliicolous or caulicolous. *Ascomata* amphigenous, scattered or gregarious, circular, immersed, becoming erumpent, rupturing host tissue by irregular stellate splits, of dark brown pseudoparenchymatal cells of *textura globulosa*, inner layer with periphysoids, invested in mucilage. *Hymenium* of asci and paraphyses; basal stroma present or absent. *Asci* clavate, (4–)8-spored, with amyloid (staining blue in Melzer's reagent) apical discharge mechanism. *Ascospores* aseptate, ellipsoid to ellipsoid-fusoid, uni- to

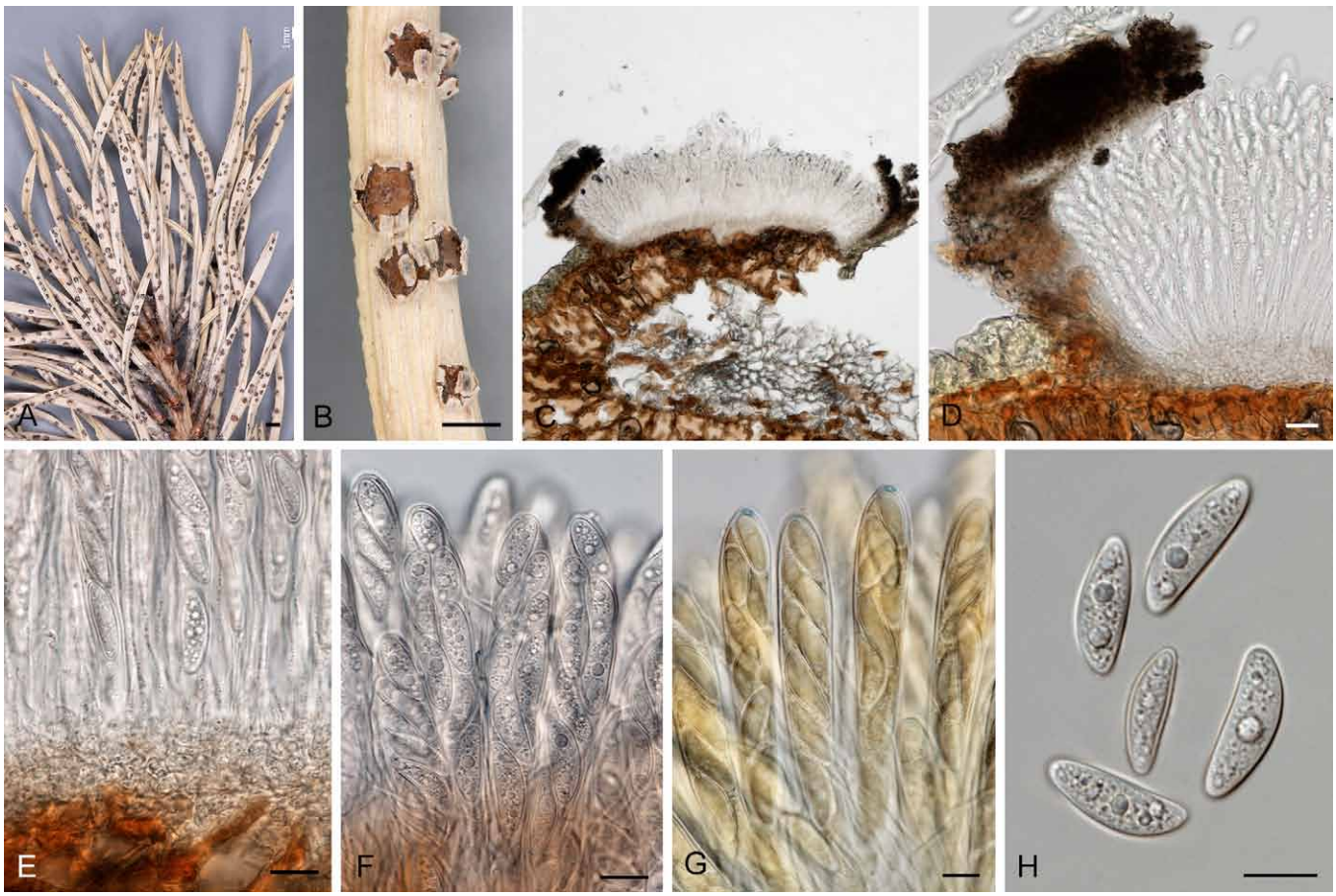

Fig. 4. *Gremmenia infestans* (S-F207441). **A, B.** Ascomata on needles. **C, D.** Vertical section through ascomata. **E–G.** Asci and ascospores (F in Meltzer's solution). **H.** Ascospores. Bars: A = 1 mm, B = 0.5 mm, all others = 10 µm.

biseriate, hyaline, smooth, lacking mucoid appendages. *Paraphyses* septate, hyaline, smooth, branched, anastomosing, invested in mucilage. *Conidiomata* pycnidial, immersed, becoming erumpent, uni- to multilocular, brown, with ostiole; wall of *textura angularis* to *textura globulosa*. *Conidiophores* branched or simple, septate, hyaline, smooth, invested in mucilage. *Conidiogenous cells* phialidic, at times proliferating percurrently, subcylindrical to ampulliform, smooth, hyaline, invested in mucilage. *Conidia* subcylindrical, aseptate, hyaline, smooth, with irregular funnel-shaped apical mucilaginous appendage.

Type species: *Phacidium lacerum* Fr. 1818, typ. cons.

Phacidium calderae (Urries) Crous, **comb. nov.**
MycoBank MB809679
(Fig. 5)
Basionym: *Ceuthospora calderae* Urries, *An. Inst. bot. A.J. Cavanilles* **14**: 165 (1956) ["1955"].

Description: *Conidiomata* multilocular, with large central ostiole, papillate. *Conidiophores* frequently reduced to conidiogenous cells, branched, 1–3-septate, up to 30 µm long, 3–4 µm diam. *Conidiogenous cells* hyaline, smooth, terminal and subterminal, 5–15 × 2.5–3.5 µm, proliferating with periclinal thickening (characteristic of this species). *Conidia* subcylindrical, smooth, granular, hyaline, (17–)18–20(–22) × 3.5(–4) µm, with a flared, funnel-shaped apical mucoid appendage.

Culture characteristics: Colonies flat, spreading, with sparse aerial mycelium and feathery margins. On PDA and OA surface and reverse olivaceous grey.

Specimens examined: **Italy:** *Sardinia*: Tacco di Sta Barbara, fallen leaf of *Arbutus unedo*, 10 May 1971, *W. Gams & J.A. Stalpers* (CBS 287.72). – **Spain**: *Ibiza*: Cala Llonga, fallen leaves of *Pistacia terebinthus*, 17 Apr. 1981, *H.A. van der Aa* (CBS H-10269, culture CBS 372.81).

Notes: *Ceuthospora calderae* was originally described from leaves of *Pistacia lentiscus*, collected from the Canary Islands. Culture CBS 372.81 closely matches the morphology of this species; CBS 287.72 was now sterile.

Phacidium fennicum Butin, *Sydowia* **37**: 21 (1984).

Description and illustration: Butin (1984).

Specimen examined: **Finland**: Lempäälä Kulju, on needles of *Pinus sylvestris*, 18 Apr. 1982, *U. Söderholm* (CBS 457.83 – ex-type culture).

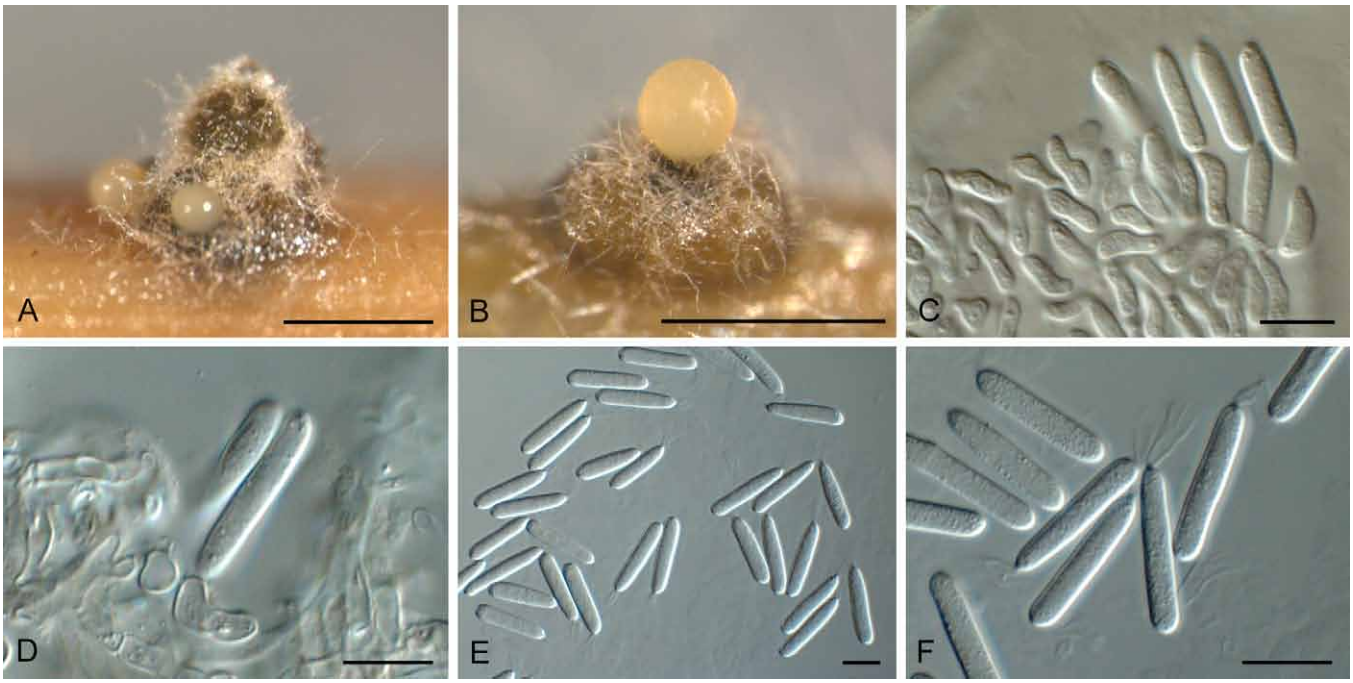

Fig. 5. *Phacidium calderae* (CBS 372.81). **A, B.** Conidiomata. **C, D.** Conidiogenous cells. **E, F.** Conidia. Bars: A, B = 200 µm, all others = 10 µm.

Phacidium lacerum Fr., *Observ. mycol.* **2**: 312 (1818) : Fr., *Syst. mycol.* **2**: 575 (1823).
(Figs 6–7)
Synonyms: *Dothidea pinastri* Fr., *Elench. fung.* **2**: 123 (1828).
Ceuthospora pinastri (Fr.) Höhn., *Mitt. bot. Inst. tech. Hochsch. Wien* **2**(4): 104 (1925).

Additional synonyms are included in Nag Raj (1993).

Description: Foliicolous or on cone scales. *Ascomata* amphigenous, circular, 300–2000 µm diam, aggregated to solitary, initially immersed, subepidermal, becoming erumpent, opening by 3–5 teeth of brown *textura globulosa*, to expose hymenium; inner layer of periphysoids, covered in mucilage. *Asci* clavate, 8-spored, with amyloid (straining blue in Melzer's reagent) discharge mechanism, 70–110 × 7–10 µm. *Ascospores* aseptate, hyaline, smooth, guttulate, biseriate, 9.5–12.5 × 3–3.5 µm. *Paraphyses* simple, septate, hyaline, smooth, anastomosing, invested in mucilage. *Conidiomata* pycnidial, flask-shaped to irregularly subglobose, amphigenous, scattered, gregarious, to aggregated, subepidermal, splitting the epidermis, multilocular, 500–1500 µm diam, brown from surface view, with individual locules up to 170 µm diam, with individual ostioles up to 25 µm diam. *Condiophores* simple or branched, septate, often reduced to phialidic conidiogenous cells, lining the inner layer of conidioma, hyaline, smooth-walled, (5–)7–15 × 2–3(–4) µm, invested in mucilage; proliferating percurrently, or with visible periclinal thickening. *Conidia* aseptate, subcylindrical, base bluntly rounded with central, flattened scar, apex with funnel-shaped mucilaginous appendage, (10–)13–15(–18) × (2.5–) 3(–4) µm.

Culture characteristics: Colonies spreading with sparse to moderate aerial mycelium. On OA surface pale olivaceous grey. On PDA surface olivaceous grey, reverse iron-grey.

Specimens examined: **France**: Mt. Ventoux, living needle of *Juniperus communis*, May 1981, *O. Petrini* (CBS 400.81); Hagenau, Bas Rhin, on needles of *Pinus sylvestris*, 26 Aug. 1968, *M. Morelet* (CBS H-10302 – **neotype** for *Phacidium lacerum* **designated here,** MBT178726; CBS 761.73 – ex-neotype culture). – **Germany**: Baden, Bastadt, on pine needles, Apr. 1877, *Schroeter* [ex herbs Thuemen & Grove] (K(M) 189268); Königstein, on needles of *P. sylvestris*, 30 Apr. 1887, *W. Krieger* [Fungi Saxonici exs. 290] (K(M) 189269). – **The Netherlands**: on needle of *Pinus sylvestris*, Feb. 1930, *J.Y. van Vliet* (CBS 130.30); Baarn, Cantonspark, on leaves of *Sciadopitys verticillata*, 27 Apr. 1970, *H.A. van der Aa* (CBS 557.70); Baarn, Maarschalksbos, on leaves of *Ilex aquifolium*, July 1969, *H.A. van der Aa* (CBS H-10292, culture CBS 338.70); Hulshorsterzand, on needles of *Pinus sylvestris*, 12 Apr. 1970, *H.A. van der Aa* (CBS 540.70). – **Sweden**: on needles of *Pinus sylvestris*, ex-herb Fries (UPS).

Notes: *Phacidium lacerum* was originally described from European collections on needles from *Pinus sylvestris*, and is widely distributed throughout Europe, where it occurs commonly on this host. The material in UPS referred to as the "original collection" by (DiCosmo *et al*. 1984) in UPS was stated to be depauperate. In the sanctioning work, Fries (1823) refers to "(Exs. ined.)" and later "S.S." (Fries 1849) implying that he had intended to distribute material in his exsiccate *Scleromycetes Suecici.* This was not, however, done and the name is listed as "material unknown" by Holm & Nannfeldt (1962: 38). The UPS specimen is unlocalised and has no date, and appears to have been collected after Fries came to Uppsala in 1835 according to Stefan Ekman (pers. comm.) (Fig. 8). That specimen is not, therefore, the "original collection" Fries had before him in 1818 or 1823 and so a neotype is designated for Fries' name here.

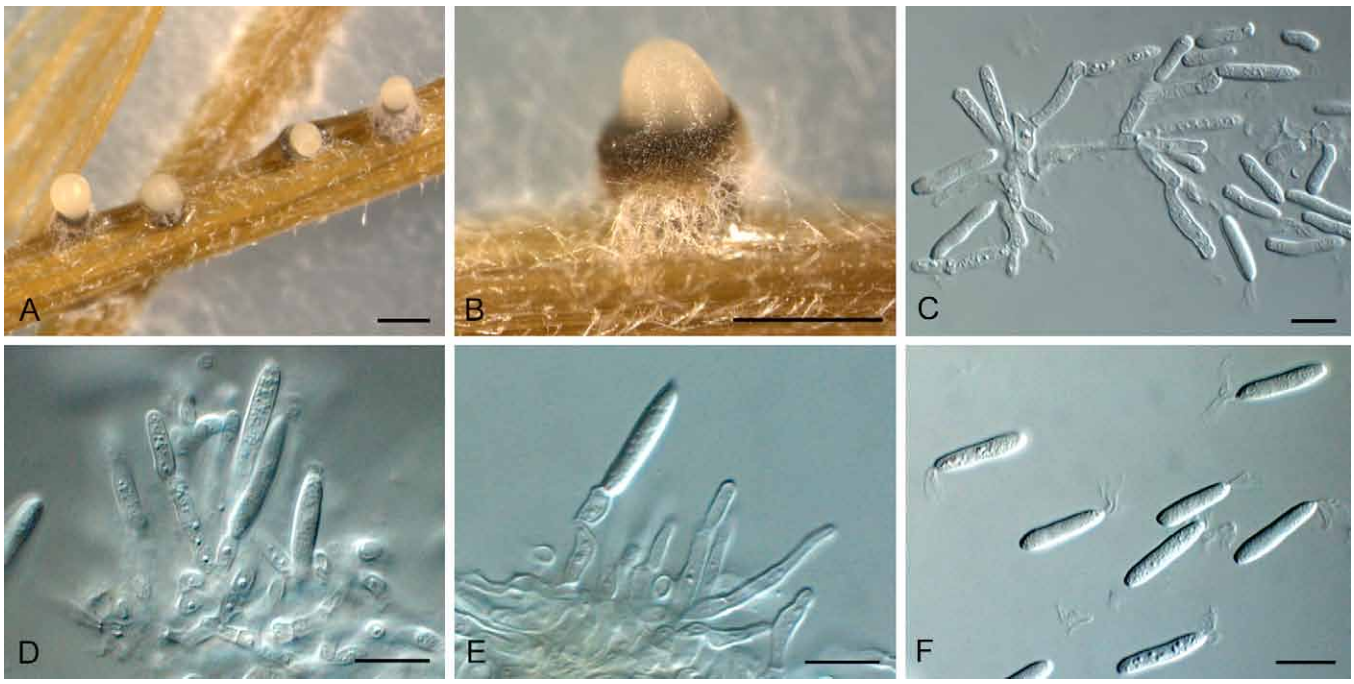

Fig. 6. *Phacidium lacerum* (CBS 761.73). **A, B.** Conidiomata on autoclaved barley leaves. **C–E.** Conidiogenous cells. **F.** Conidia. Bars: A, B = 300 µm, all others = 10 µm.

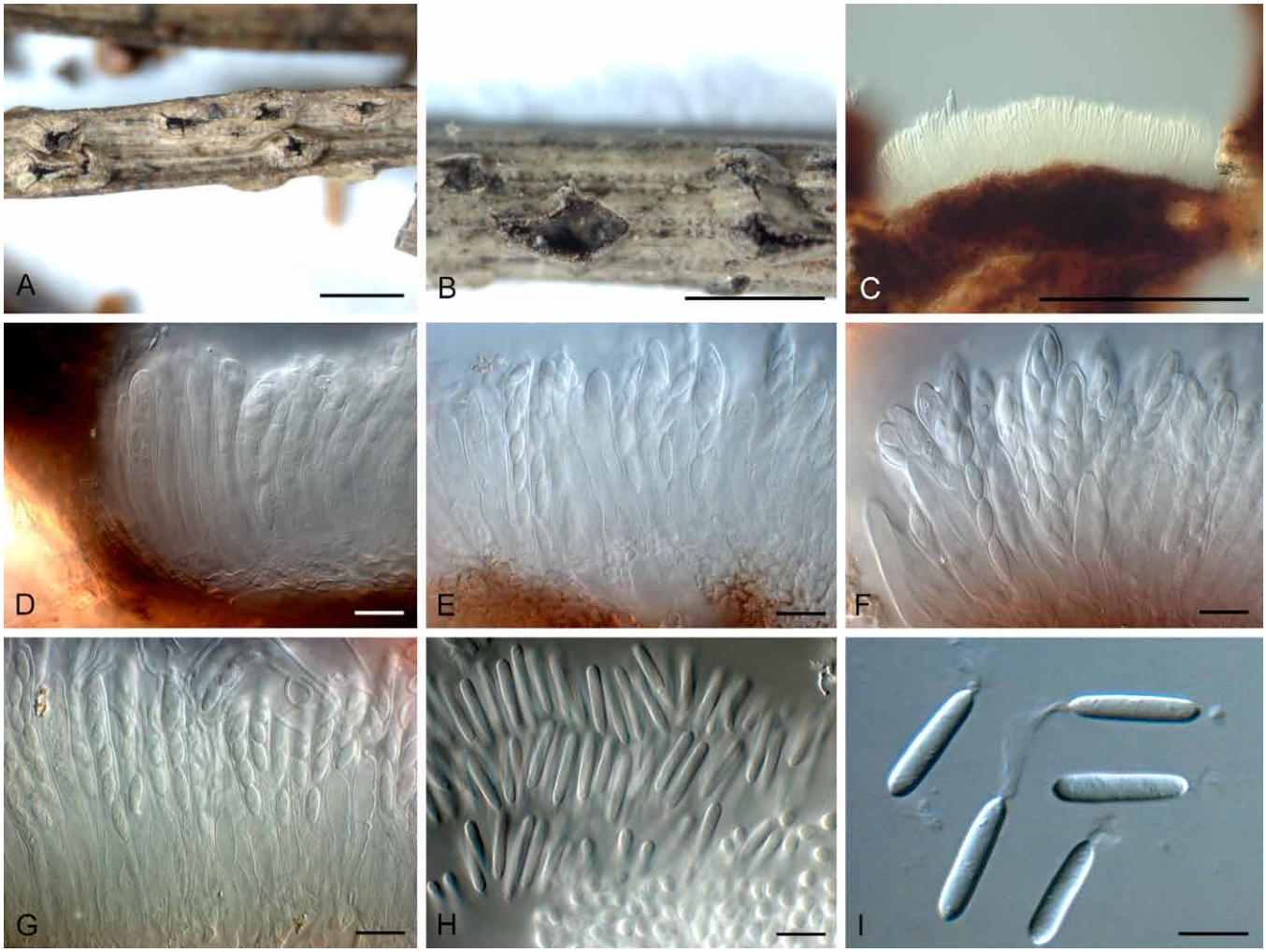

Fig. 7. *Phacidium lacerum* (K(M) 189269). **A, B.** Ascomata on needles. **C–E.** Vertical section through ascomata. **F, G.** Asci and ascospores. **H, I.** Conidia. Bars: A, B = 1000 µm, all others = 10 µm.

Fig. 8. *Phacidium lacerum* (UPS – Fries' specimen). Photo: Stefan Ekman.

Phacidium lauri (Sow.) Crous & D. Hawksw., **comb. nov.**

MycoBank MB810293

Basionym: *Sphaeria lauri* Sow., *Col. Fig. Br. Fungi* **3**: *sine pagin*. [53] (1803[1]).

Synonyms: *Cryptosphaeria lauri* (Sow.) Grev., *Fl. Edin.*: 361 (1824).

Ceuthospora lauri (Sow.) Grev., *Scott. Crypt. Fl.* **5**: 254 (1826) : Fr., *Syst. mycol., Index*: 167 (1832).

Xyloma multivalve DC., *Fl. franç.,* 3rd edn **2**: 303 (1805).

Phacidium multivalve (DC.) J.C. Schmidt, *Mykol. Heft.* **1**: 42 (1817) : Fr., *Syst. mycol.* **2**: 576 (1823).

Ceuthospora phacidioides Grev., *Scott. Crypt. Fl.* **5**: 253 (1826); nom. illegit. (Art. 52,1).

Additional synonyms are listed in Nag Raj (1993).

Descriptions and illustrations: Sutton (1972, asexual morph), DiCosmo *et al*. (1984; sexual and asexual morph) and Nag Raj (1993; asexual morph only).

Specimens examined: **The Netherlands**: Baarn, Drakenburgerweg, on *Ilex aquifolium*, 8 Oct. 1967, *H.A. van der Aa* (CBS 589.67, as *C. phacidioides*); Baarn, Cantonspark, on leaves of *Prunus laurocerasus*, 2 Mar. 1968, *H.A. van der Aa* (CBS H-10276 – **epitype of *Sphaeria lauri* designated here**, MBT178727; CBS 308.68 – culture ex-epitype); Wageningen, on leaves of *Ilex aquifolium*, May 1969, *L. Marvanová* (CBS 443.71, as *C. phacidioides*); Baarn, Eemnesserweg 90, on leaves of *Vinca minor*, 3 Mar. 1968, *H.A. van der Aa* (CBS H-10271, culture CBS 198.68, as *C. feurichii*). – **UK**: *sine loc.,* on dead leaves of *Prunus laurocerasus*, *G.B.W. Kirby* (K – holotype of *Sphaeria lauri* [not traced]; K (M) IMI 153020 – slides ex holotype).

[1]The text to illustrate the plates in this work are not numbered, and the diagnosis for this fungus appears on the 53rd; the illustration is on pl. 371 fig. 4 (Fig. 9), which has no diagnosis or name, and is dated "1802", but it seems unlikely that the text was issued before the whole volume was completed in 1803.

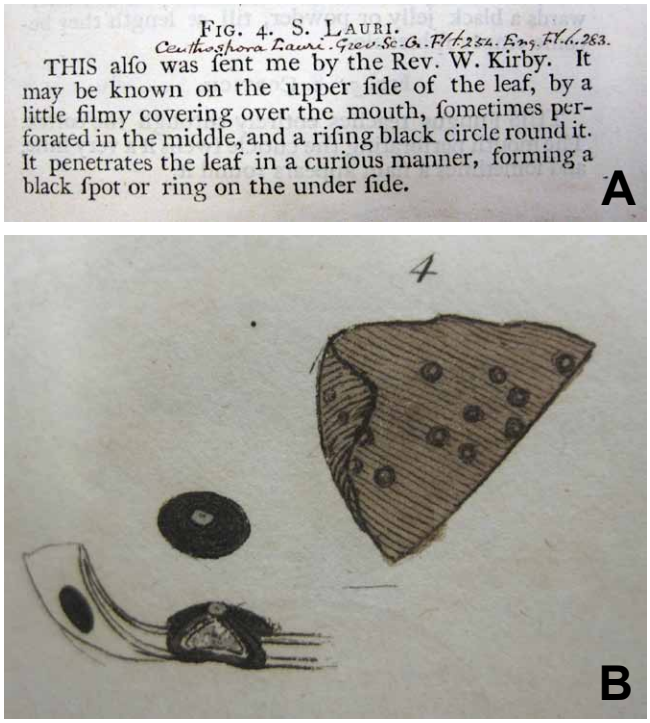

Fig. 9. Sowerby's original diagnosis **(A)** and illustrations **(B)** of *Sphaeria lauri*. From Sowerby (1803).

Notes: Conidia of the present strains (12–)13–15(–16) × 3(–3.5) µm fall into the variation of *C. lauri* (7–17 × 2–3 µm, Nag Raj 1993), which has several synonyms, including *C. phacidioides* (Nag Raj 1993). Furthermore, DiCosmo *et al.* (1984) link *C. phacidioides* (conidia 10–17 × 2.5–3 µm) to *Phacidium multivalve* as sexual morph. *Ceuthospora lauri*, which is the type species of the genus *Ceuthospora* (on *Prunus laurocerasus*, Europe), and *C. phacidioides* (*Ilex aquifolium*, Europe), have been commonly confused in the past, but appear to be synonymous based on the cultures we investigated in this study. Di Cosmo *et al.* (1984) designated a lectotype for *Xyloma multivalve* in G but did not provide more details. However, we have been unable to locate the original material of all these synonyms (also see Sutton 1980, Nag Raj 1993), and suspect that they have been lost. The names *Ceuthospora lauri* and *Phacidium multivalve* were both sanctioned by Fries, and as the earliest species epithet which is legitimate under the ICN is *Sphaeria lauri*, that name has priority. *Ceuthospora lauri* also appears more commonly used in literature than *Phacidium multivalve*. Note that the name *Ceuthospora phacidioides* is illegitimate as *Xyloma multivalve* was listed as a synonym when it was introduced; it is therefore a superfluous name.

The choice of the epithet "*lauri*" by Sowerby is explained by Grove (1935: 291–292): "Owing to the custom, in Britain, of speaking of *Prunus Laurocerasus* as 'the Laurel', great confusion has arisen. It has frequently been erroneously regarded as the true Bay Laurel (*Laurus nobilis*), and its leaves are still sometimes used by our cooks as such." He also confirmed that Greville's specimens were on the *Prunus*

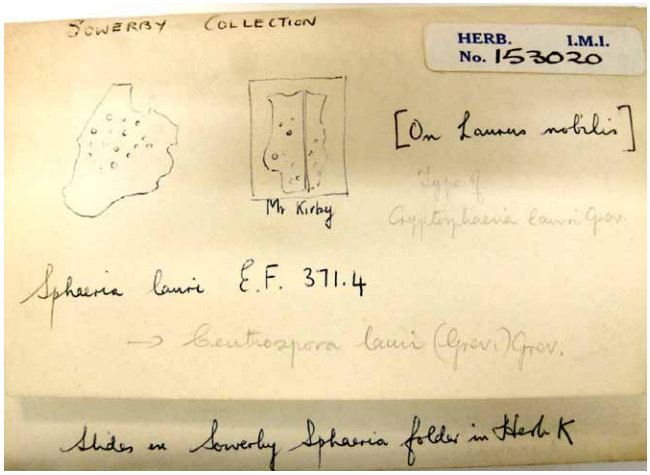

Fig. 10. *Sphaeria lauri* packet with slides made Brian Sutton from Sowerby's holotype (K(M) IMI 153020).

and not *Laurus*, contrary to his publications, which led to that error being perpetuated although the misidentification was soon recognized, for example, by Berkeley (1836: 283) who gave it the English name "Cherry-laurel Ceuthospora" and stated "On dead leaves of *Prunus Lauro-cerasus* (not *Laurus nobilis* as is stated by Dr. Greville)".

Sowerby (1803) referred to a single unlocalized, but presumably English (as his work was devoted to fungi from that country) collection made by the Rev. William Kirby (1759–1850) when introducing the name *Sphaeria lauri* (Fig. 9); Kirby was born in and died in Suffolk, England. The original material was located in K by Sutton (1972) who prepared sections (now preserved as K(M) IMI 153020; Fig 10) and published drawings made from Kirby's specimen (Sutton 1972: 323 fig. 1). That specimen could not now be re-located in K, despite extensive searches by Begoña Aguirre-Hudson, Heidi Döring, and D.L.H. Sutton did, however, include a sketch of the material he saw which evidently comprised two specimens, the right-hand one of which had Kirby's name below it and is therefore the holotype of Sowerby's name.

Sutton (1972, 1980) attributed the epithet "*lauri*" to Greville and not Sowerby, in accordance with the *Code* then in operation which ruled that names of "Fungi caeteri" published before 1 January 1821 were not validly published; that situation changed with the deletion of the later starting point dates for fungi at the Sydney IBC in 1981. In using the term "lectotype", Sutton meant as the type of *Ceuthospora lauri* "Grev.", and that is clear from his annotation on the packet with the slides (Fig. 10) and not Sowerby's original binomial. The use of that term was correct for Greville's name, under the pre-1981 *Code*, as Greville had studied collections other than Sowerby's.

Phacidium mollerianum (Thüm.) Crous, **comb. nov.**
MycoBank MB809680
(Fig. 11)

Basionym: *Sphaeropsis molleriana* Thüm., *Inst. Coimbra* **27**: 40 (1879).

Synonyms: *Phoma molleriana* (Thüm.) Sacc., *Syll. fung.* **3**: 110 (1884).
Macrophoma molleriana (Thüm.) Berl. & Voglino, *Syll. fung.*, Addit. **I**: 314 (1886).
Ceuthospora molleriana (Thüm.) Petr., *Annls mycol*. **23**: 29 (1925).

Description: *Conidiomata* uni- to multilocular, up to 400 µm diam. *Conidiophores* branched, up to 45 µm long, 2–3 µm diam. *Conidiogenous cells* terminal and lateral, 5–10 × 2–3 µm, with prominent periclinal thickening, rarely proliferating percurrently. *Conidia* hyaline, smooth, granular, subcylindrical, (9–)10–12(–13) × (2–)2.5 µm; apical mucoid appendage only visible when mounted in water.

Culture characteristics: Colonies spreading with sparse aerial mycelium and feathery margins. On PDA and OA surface and reverse olivaceous grey.

Cultures examined: **Italy**: *Sardinia*: Su Cologone, on leaves of *Eucalyptus*, 6 May 1971, *W. Gams* (CBS H-10285, 10286; CBS 365.72 – culture). – **The Netherlands**: Baarn, leaf spot on *Polygonatum odoratum*, 8 Aug. 1966, *H.A. van der Aa* (CBS 574.66).

Notes: *Ceuthospora molleriana* was originally described from *Eucalyptus* leaves collected in Portugal (conidia 10–13 × 2–2.5 µm, Petrak 1925), and closely fits the morphology observed in the present collections. Although originally described from *Eucalyptus*, this taxon appears to have a wider host range.

Phacidium pseudophacidioides Crous, **sp. nov.**
MycoBank MB809681
(Fig. 12)

Etymology: Named after its morphological similarity to the asexual morph, *Ceuthospora phacidioides*.

Diagnosis: *Conidiogenous cells* discrete or integrated, subcylindrical with perominent periclinal thickening or percurrent proliferation, 7–19 × 2–2.5 µm. *Conidia* hyaline, smooth, granular, subcylindrical, tapering at ends, bearing a funnel-shaped mucoid apical appendage, (11–)11.5–12.5(–13) × (2–)2.5 µm.

Type: **The Netherlands**: Baarn, Eenmnesserweg 92, on *Ilex aquifolium*, 8 Aug. 1968, *H.A. van der Aa* (CBS H-10289 – holotype; CBS 590.69 – ex-type culture).

Description: *Conidiomata* stromatic, pycnidioid, scattered, black, subepidermal, multiloculate, up to 600 µm diam, with papillate ostioles. *Conidiophores* arising from inner layers of cavity, subcylindrical, hyaline, smooth, extensively branched, up to 120 µm long, 2.5–3 µm diam, invested in mucus. *Conidiogenous cells* discrete or integrated, subcylindrical with perominent periclinal thickening or percurrent proliferation, hyaline, smooth, 7–19 × 2–2.5 µm. *Conidia* hyaline, smooth, granular, subcylindrical, tapering at ends, apex subobtuse, base with truncate hilum, 1 µm diam, bearing a funnel-shaped mucoid apical appendage, (11–)11.5–12.5(–13) × (2–)2.5 µm.

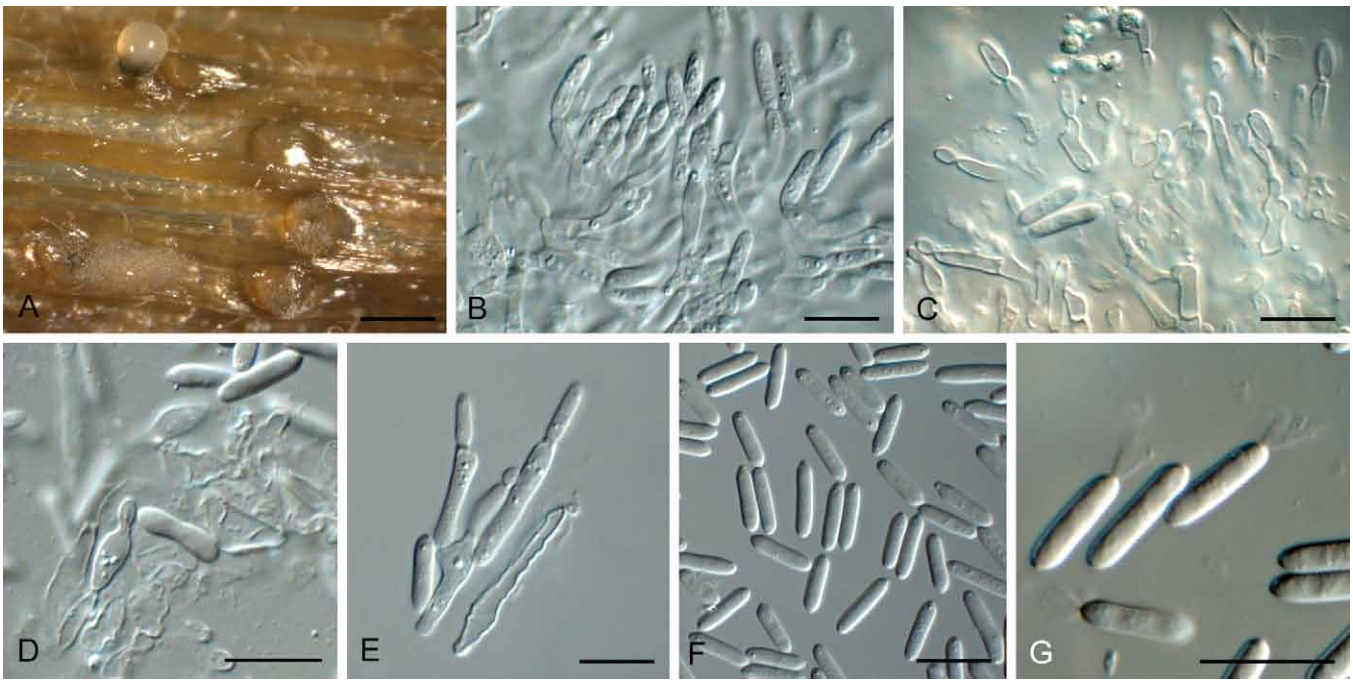

Fig. 11. *Phacidium molleriana* (CBS 574.66). **A.** Conidiomata on autoclaved barley leaves. **B–E.** Conidiogenous cells. **F, G.** Conidia. Bars: A = 300 µm, all others = 10 µm.

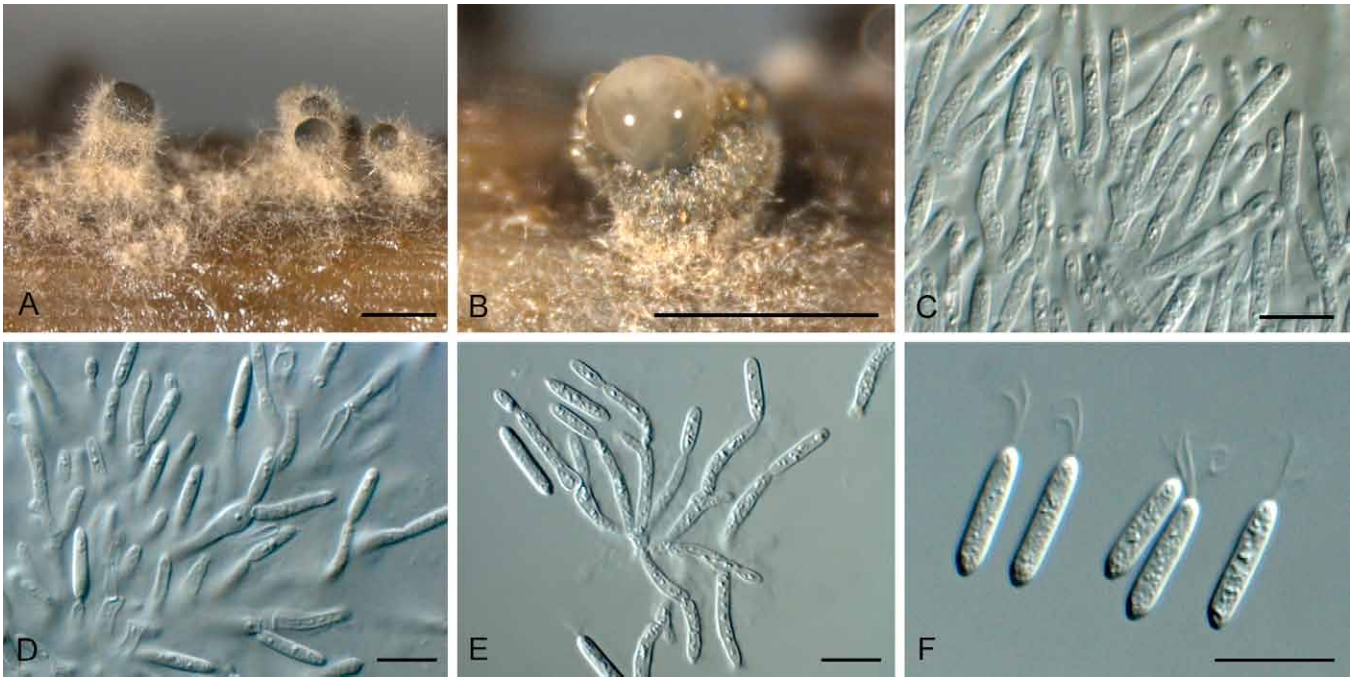

Fig. 12. *Phacidium pseudophacidioides* (CBS 590.69). **A, B.** Conidiomata on autoclaved barley leaves. **C–E.** Conidiophores, conidiogenous cells and conidia. **F.** Conidia. Bars: A = 300 µm, B = 400 µm, all others = 10 µm.

Other specimen examined: **Switzerland**: *Zürich*: Weiacherberg, on dead leaf of *Chamaespartium sagittale*, 3 May 1952, *E. Müller* (CBS 497.72).

Notes: The two isolates of *C. pseudophacidioides* were originally identified as *C. phacidioides* (i.e. *P. lauri*). However, *P. lauri* has larger conidia, and the conidiophores are much more extensively branched than in *P. pseudophacidioides*.

Phacidium trichophori Crous & Quaedvlieg, **sp. nov.**
MycoBank MB809682
(Fig. 13)

Etymology: Named after the host genus on which it was collected, *Trichophorum*.

Diagnosis: *Conidiogenous cells* discrete or integrated, subcylindrical with prominent periclinal thickening, 5–12 ×

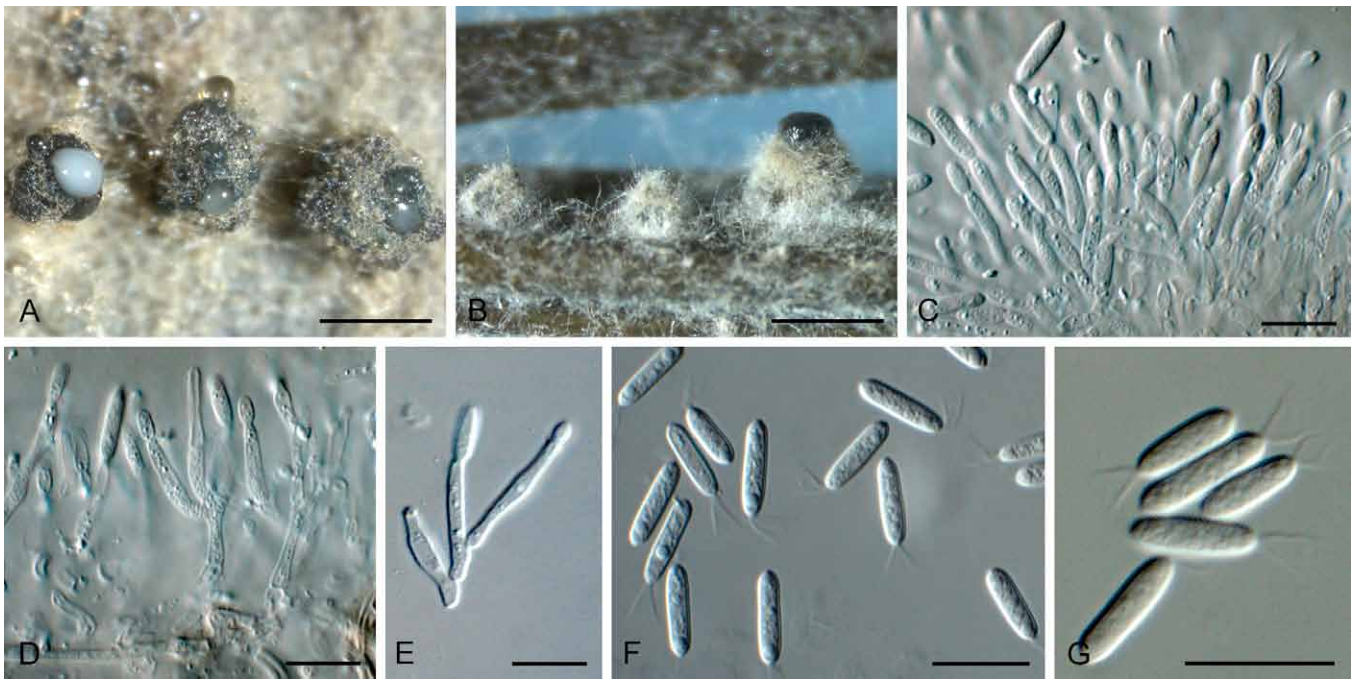

Fig. 13. *Phacidium trichophori* (CPC 22952). **A, B.** Conidiomata in culture. **C–E.** Conidiophores, conidiogenous cells and conidia. **F, G.** Conidia. Bars: A, B = 300 µm, all others = 10 µm.

2–3 µm. *Conidia* hyaline, smooth, granular, subcylindrical, tapering towards a truncate basal scar, 0.5–1 µm diam, bearing a funnel-shaped mucoid apical appendage, 3–5 µm long, 2–4 µm diam at apex, (9–)10–11(–13) × (2–)2.5(–3) µm.

Type: **The Netherlands**: Korenburgerveen, Winterswijk, on *Trichophorum cespitosum* subsp. *germanicum*, 29 Apr. 2013, *W. Quaedvlieg* (CBS H-21816 – holotype; CBS 138246 = CPC 22952 – ex-type culture).

Description: Foliicolous. *Conidiomata* pseudostromatic, pycnidioid, scattered to gregarious, black, subepidermal, uniloculate, up to 300 µm diam; walls of the pseudostroma 40–90 µm thick. *Conidiophores* arising from inner layers of cavity, subcylindrical, hyaline, smooth, thin-walled, branched, to 30 µm long, invested in mucus. *Conidiogenous cells* discrete or integrated, subcylindrical with prominent periclinal thickening, hyaline, smooth, 5–12 × 2–3 µm. *Conidia* hyaline, smooth, granular, subcylindrical, tapering towards a truncate basal scar, 0.5–1 µm diam, apex subobtuse, bearing a funnel-shaped mucoid apical appendage, 3–5 µm long, 2–4 µm diam at apex, (9–)10–11(–13) × (2–)2.5(–3) µm.

Notes: *Phacidium trichophori* resembles *P. lauri* (conidia (12–)13–15(–16) × 3(–3.5) µm), but is morphologically distinct in having smaller conidia. *Ceuthospora gaeumannii* (conidia 8–11 × 2–2.5 µm, av. 9 × 2.2 µm; Nag Raj 1993) has slightly smaller conidia, much larger conidiomata (500–1500 µm diam).

Phacidium vaccinii Fr., *Syst. Mycol.* **2**(2): 575 (1823).

Synonyms are listed in DiCosmo *et al*. (1984).

Culture examined: **The Netherlands**, Loenen, on leaves of *Vaccinium vitis-idaea*, May 1969, *L. Marvanová* (CBS 444.71).

Note: Unfortunately this culture proved to be sterile, and thus its morphology could not be confirmed.

Pseudophacidium P. Karst., *Acta Soc. Fauna Fl.fenn.* **2**: 157 (1885) [“1881–1885”].

Synonym: *Myxofusicoccum* Died., *Annls mycol*. **19**: 68 (1912).

Caulicolous. *Ascomata* scattered to gregarious, immersed, raising the host epidermis, causing it to rupture; ascomata oblong, hemispherical to irregularly pulvinate, black, carbonaceous; wall of brown *textura globulosa*, becoming pale brown towards interior; inner layers of subglobose, hyaline cells, invested in mucilage; subhymenium of hyaline *textura intricata*; basal stroma of pale brown pseudoparenchymatal cells. *Asci* club-shaped, 8-spored flattened at apex which does not strain in Melzer’s reagent. *Ascospores* irregularly biseriate, oblong-ellipsoidal, straight to curved, hyaline, smooth-walled. *Conidiomata* brown, pycnidioid, stromatic, gregarious to crowded, immersed, discoid to orbicular, opening by means of irregular ruptures, multilocular; wall of brown *textura globulosa*; basal stroma of pale brown *textura epidermoidea*. *Conidiogenous cells* phialidic, lining inner cavity, lageniform to ampulliform, hyaline, smooth-walled; proliferating percurrently at apex. *Conidia* ellipsoid to oblong or subreniform, apex rounded, base with truncate scar, guttulate, hyaline, smooth-walled.

Type species: *Pseudophacidium ledi* (Alb. & Schwein.) P. Karst. 1885.

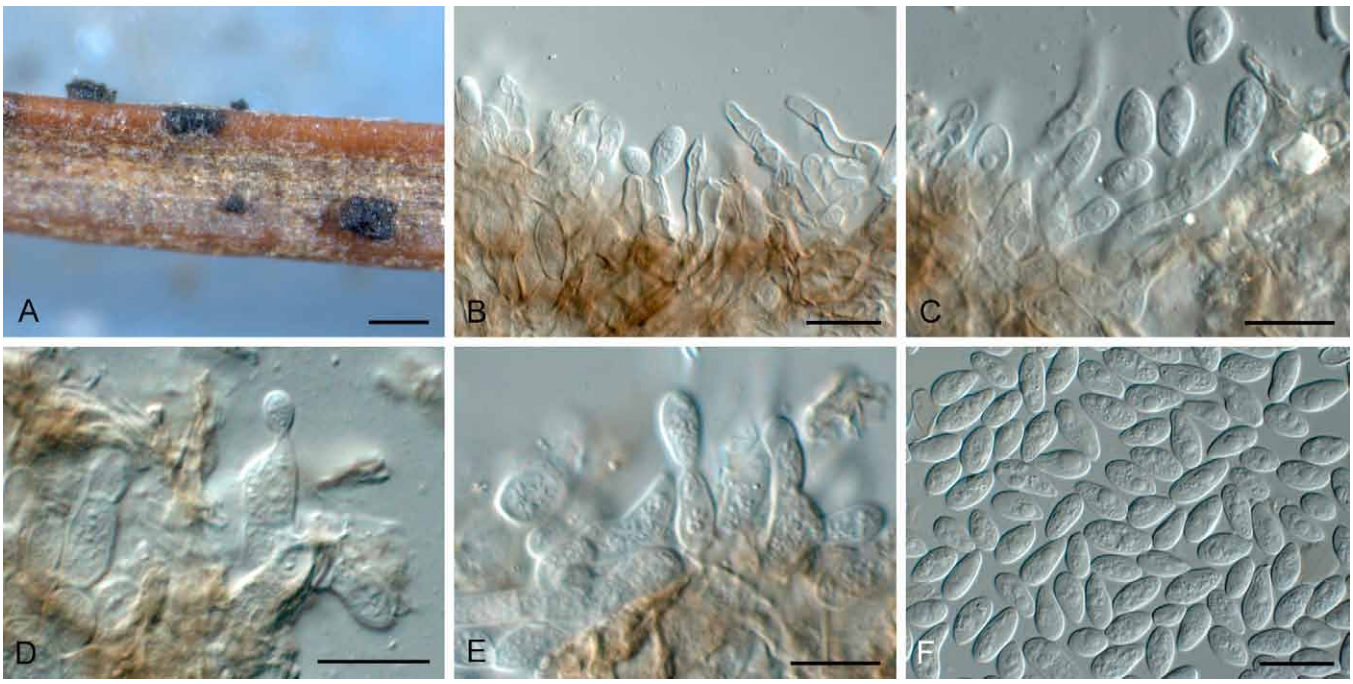

Fig. 14. *Pseudophacidium ledi* (CBS 377.59). **A.** Conidiomata forming on PNA. **B–E.** Conidiogenous cells giving rise to conidia. **F.** Conidia. Bars: A = 500 µm, all others = 10 µm.

Pseudophacidium ledi (Alb. & Schwein.) P. Karst., *Acta Soc. Fauna Flora fenn.* **2**: 157 (1885) ["1881–1885"].
(Fig. 14)
Basionym: *Xyloma ledi* Alb. & Schwein., *Consp. fung.*: 60 (1805)l

Description: Sporulating on PNA. *Conidiomata* stromatic, scattered, erumpent, irregular to pulvinate, brown, opening by irregular rupture, multilocular, up to 500 µm diam. *Conidiophores* arising from inner cavity, hyaline, subcylindrical, branched or not, 1–3-septate, to 30 µm long, 3–4µm diam, or reduced to condiogenous cells. *Conidiogenous cells* subcylindrical or ampulliform, phialidic, hyaline, smooth, 5–10 × 3–4 µm, proliferating 1–2 times percurrently near apex. *Conidia* solitary, ellipsoid to oblong, hyaline, guttulate, thin-walled, mostly widest in upper third, apex subobuse, base truncate, 1 µm diam, (8–)9–11(–12) × (4–)5(–6) µm.

Specimen examined: **Switzerland**, Graubünden, Bergün, on *Picea abies*, Apr. 1959, *J. Gremmen* (CBS 377.59).

Notes: Species of *Pseudophacidium* are immersed discomycetes that occur on bark of hard- or softwood. Ascomata open by means of an irregular rupture of the covering layer, exposing cream to greyish or brownish discs. The genus contains saprobic, and plant pathogenic species (Smerlis 1969).

Potebniamyces Smerlis, *Canad. J. Bot.* **40**: 352 (1962).

Caulicolous and corticolous. *Ascomata* scattered to gregarious, initially immersed, becoming erumpent, irregular in outline, opening by irregular rupture to expose hymenium; apical roof of brown *textura globulosa*, becoming paler towards inner region, which consists of subcylindrical, branched, septate, hyaline periphysoids, invested in mucilage; hymenium red-brown in water, turning blue-green in 2 % KOH. *Paraphyses* numerous, subcylindrical, branched or septate, hyaline, smooth-walled. *Asci* club-shaped, 8-spored, with apex not staining in Meltzer's reagent. *Ascospores* uni- to biseriate, subglobose to ellipsoid, aseptate, guttulate, hyaline to pale yellow, smooth-walled. *Conidiomata* scattered to aggregated, immersed, subepidermal, depressed globose, papillate, non-ostiolate, multilocular, brown, opening by irregular rupture; wall of brown *textura globulosa* to *textura epidermoidea* above, pale brown below, with wall of yellow-brown textura prismatica. *Conidiogenous cells* phialidic, lining the inner cavity, subcylindrical, lageniform to ampulliform, straight to curved, hyaline, smooth-walled. *Conidia* subglobose to obovoid, guttulate, aseptate, base truncate, hyaline to pale yellow, smooth-walled (adapted from Sutton 1980, and DiCosmo *et al*. 1984).

Type species: *Potebniamyces pyri* (Berk. & Broome) Dennis 1978.

Potebniamyces pyri (Berk. & Broome) Dennis, *Brit. Ascom.*, 2nd edn: 231 (1978).
Basionym: *Stictis lecanora* var. *pyri* Berk. & Broome, *Ann. Mag. nat. Hist.*, ser. 4 **17**: 144 (1876).

Specimen examined: **The Netherlands**: Wilhelminadorp, bark of *Pyrus communis*, Mar. 1963, *G.S. Roosje*,(CBS 322.63); Wageningen, on peduncle of *P. communis*, Mar. 1955, *Zweede* (CBS 282.55).

Notes: Although we assume that *Phacidiopycnis* is the asexual morph of *Potebniamyces*, the type species of *Phacidiopycnis*, *P. malorum*, still needs to be recollected to confirm this assumption. For this reason the synonymy between these two generic names remains unconfirmed. If shown to be synonymous, the older name, *Phacidiopycnis*, will have preference for the holomorph (Johnston *et al*. 2014).

DISCUSSION

The primary aim of this study was to obtain molecular support for the assumption that *Ceuthospora* and *Phacidium* are congeneric, and at the same time elucidate the position of *Phacidiaceae* within *Leotiomycetes*, as the latter family and order were not represented in the phylogenetic study of Wang *et al*. (2006b).

The order *Helotiales* contains members that represent a broad range of ecologies, including species that are plant pathogenic, saprobic, endophytic, mycorrhizal or ectomycorrhizal parasites, aquatic saprobes, or wood rotting fungi (Wang *et al.* 2006a). Although lacking many genera of *Helotiales* in their phylogenetic analysis, Wang *et al.* (2006b) concluded that the concept of *Helotiales* adopted by Eriksson (2005) included many non-monophyletic taxa. They placed 13 families in the order. In spite of earlier work on the class (Gernandt *et al*. 2001, Lutzoni *et al*. 2004, Wang *et al.* 2005), no members of *Phacidium* were present in the phylogeny of Wang *et al.* (2006b). By adding *Phacidiaceae* to *Helotiales* data present in GenBank, *Phacidiales* clearly separated from *Helotiales*, which still appear heterogeneous (Fig. 1). The separation of *Phacidiales* from *Helotiales* is also supported by the phylogeny of Wang *et al.* (2006b), as *Bulgaria inquinans* and *Phacidiophicnes pyri* cluster outside of the *Helotiales* clade in their study.

A surprising result of our study concerns the phylogenetic position of *Bulgariaceae*. The genus *Bulgaria*, based on *B. inquinans*, effectively clusters in *Phacidiaceae* (based on *P. lacerum*). A second species has been reported, *B. nana* (Döring & Triebel 1998, Wang 2006b), but that is considered a species of *Austrocenangium* (see Gamundi 1997). *Bulgaria inquinans* is characterised by large (up to 4 cm), dark brown to black turbinate, gelatinous apothecia with brown ascospores. It occurs on bark of fallen trunks and branches, but has also been observed on living trees. The species is considered saprobic, and possibly facultatively plant pathogenic. The relationship of *Bulgaria* has been debatable. It has been placed close to other species producing gelatinous apothecia in *Leotiaceae/Helotiaceae*, e.g. *Leotia*, *Neobulgaria, Ombrophila* (in *Leotieae*, Korf 1973; in *Ombrophiloideae*, Dennis 1978), or considered to be rather distinct, and placed as the sole genus in *Bulgariaceae* (*Helotiales*) (e.g. Eriksson 2006). Although some molecular phylogenetic studies have not been able to place *Bulgaria* in a larger group with support, and instead suggest species such as *Leotia, Neobulgaria* and *Ombrophila* (*Helotiaceae*) are not closely related (Wang 2006a, b), Lantz *et al*. (2011) placed *Bulgaria* in a strongly supported clade with *Phacidium* and *Potebniamyces.* The relationship between *Bulgaria* and *Phacidium* was also confirmed by Hustad & Miller (2011). The ultrastructure of the ascus apical apparatus of *Bulgaria*, however, is unique compared to other members of *Helotiales* (Verkley 1992, 1994). For the present, we treat *Bulgariaceae* as a synonym of *Phacidiaceae*, but it could be that the family is still heterogeneous, and as more members of *Phacidiaceae* and *Helotiaceae* get added in future molecular studies, the *Phacidiaceae* may yet prove to be paraphyletic.

In our results, the genus *Allantophomopsis* (based on *A. cytisporea*), clusters sister to the canker pathogen *Potebniamyces pyri* (asexual morph: *Phacidiopycnis pyri*). *Potebniamyces* produces black, gelatinous discs, erumpent from submerged stromata in tree bark. Although DiCosmo *et al*. (1984) considered this genus a possible member of *Phacidiaceae*, *Rhytismataceae* or *Dermateaceae*, it appears to be a member of an independent family. As the majority of the families in *Helotiales* still lack molecular data, we consider it premature to introduce any new family name here to accommodate *Potebniamyces*. DiCosmo *et al*. (1984) discussed the morphological differences between *Potebniamyces* and *Phacidium*, and Wang *et al*. (2006b) suggested a possible sister relationship between the two genera.

In the present study we introduce the generic name *Allantophomopsiella* to accommodate *A. pseudotsugae,* a pathogen of conifers (Roll Hansen 1992). The genus *Gremmenia* is resurrected to accommodate the snow-blight pathogens of conifers, namely *G. abietis* (on *Abies* spp. and *Pseudotsuga menziesii*), *G. infestans* (on *Abies balsamea*), and *G. pini-cembrae* (on *Pinus cembra*).

Finally, the position of the *Phacidiaceae* is clarified within the resurrected *Phacidiales*, with respectively a neotype and an epitype designated to fix the phylogenetic application of the names *Phacidium lacerum* (type of *Phacidium*) and *Sphaeria lauri* (type of *Ceuthospora*) (i.e. *Phacidium lauri*). *Phacidium* (1815) is accepted as the correct name for this genus over *Ceuthospora* (1827), based on nomenclatural priority, as both names are conserved; it also has a greater number of species.

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