

Acremonium phylogenetic overview and revision of *Gliomastix*, *Sarocladium*, and *Trichothecium*

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Abstract: Over 200 new sequences are generated for members of the genus *Acremonium* and related taxa including ribosomal small subunit sequences (SSU) for phylogenetic analysis and large subunit (LSU) sequences for phylogeny and DNA-based identification. Phylogenetic analysis reveals that within the *Hypocreales*, there are two major clusters containing multiple *Acremonium* species. One clade contains *Acremonium sclerotigenum*, the genus *Emericellopsis*, and the genus *Geosmithia* as prominent elements. The second clade contains the genera *Gliomastix sensu stricto* and *Bionectria*. In addition, there are numerous smaller clades plus two multi-species clades, one containing *Acremonium strictum* and the type species of the genus *Sarocladium*, and, as seen in the combined SSU/LSU analysis, one associated subclade containing *Acremonium breve* and related species plus *Acremonium curvulum* and related species. This sequence information allows the revision of three genera. *Gliomastix* is revived for five species, *G. murorum*, *G. polychroma*, *G. tumulicola*, *G. roseogrisea*, and *G. masseei*. *Sarocladium* is extended to include all members of the phylogenetically distinct *A. strictum* clade including the medically important *A. kiliense* and the protective maize endophyte *A. zaeae*. Also included in *Sarocladium* are members of the phylogenetically delimited *Acremonium bacillisporum* clade, closely linked to the *A. strictum* clade. The genus *Trichothecium* is revised following the principles of unitary nomenclature based on the oldest valid anamorph or teleomorph name, and new combinations are made in *Trichothecium* for the tightly interrelated *Acremonium crocogenicum*, *Spicellum roseum*, and teleomorph *Leucosphaerina indica*. Outside the *Hypocreales*, numerous *Acremonium*-like species fall into the *Plectosphaerellaceae*, and *A. atrogriseum* falls into the *Cephalothecaceae*.

Key words: *Acremonium*, *Cephalothecaceae*, *Gliomastix*, holomorph concept, *Leucosphaerina*, nomenclature, *Sarcopodium*, *Sarocladium*, *Trichothecium*.

Taxonomic novelties: *Trichothecium sympodiale* Summerbell, Seifert, & Schroers, nom. nov.; *Gliomastix roseogrisea* (S.B. Saksena) Summerbell, comb. nov., *Gliomastix tumulicola* (Kiyuna, An, Kigawa & Sugiy.) Summerbell, comb. nov., *Sarocladium bacillisporum* (Onions & Barron) Summerbell, comb. nov., *Sarocladium bactrocephalum* (W. Gams) Summerbell, comb. nov., *Sarocladium glaucum* (W. Gams) Summerbell, comb. nov., *Sarocladium kiliense* (Grütz) Summerbell, comb. nov., *Sarocladium ochraceum* (Onions & Barron) Summerbell, comb. nov., *Sarocladium strictum* (W. Gams) Summerbell, comb. nov., *Sarocladium zaeae* (W. Gams & D.R. Sumner) Summerbell, comb. nov., *Trichothecium crocogenicum* (Schol-Schwarz) Summerbell, Seifert, & Schroers, comb. nov., *Trichothecium indicum* (Arx, Mukerji & N. Singh) Summerbell, Seifert, & Schroers, comb. nov., *Trichothecium ovalisporum* (Seifert & Rehner) Seifert & Rehner, comb. nov.

INTRODUCTION

The genus *Acremonium* includes some of the most simply structured of all filamentous anamorphic fungi. The characteristic morphology consists of septate hyphae giving rise to thin, tapered, mostly lateral phialides produced singly or in small groups. Conidia tend to be unicellular, produced in mucoid heads or unconnected chains. They can be hyaline or melanised, but the hyphae are usually hyaline. A preliminary study of the phylogenetic diversity of *Acremonium* by Glenn *et al.* (1996), based on partial nuclear ribosomal small subunit (SSU) sequences, showed that recognised members belonged to at least three groups in distinct orders of fungi. Most species including the type, *A. alternatum*, belong to the order *Hypocreales*. A smaller group of species, *Acremonium* section *Chaetomioidea*, belongs to the *Sordariales*. This section, typified by the *Acremonium alabamense* anamorph of *Thielavia terrestris*, was conceived as including the *Acremonium*-like anamorphs of *Chaetomium* and *Thielavia* species (Morgan-Jones & Gams 1982). A recent study has placed several of these heretofore unnamed *Acremonium*-like anamorphs into the new genus *Taifanglania* (Liang *et al.* 2009), based on the type, *T. hechuanensis*. Another *Acremonium* species included by Glenn *et al.* (1996), *A. furcatum*, belongs to an order of uncertain identity.

Subsequent publications have shown that *A. furcatum* is related to the well-known phytopathogen *Verticillium dahliae* and belongs to the recently established family *Plectosphaerellaceae* (Zare *et al.* 2007, Schoch *et al.* 2009), which groups together with the *Glomerellaceae* in a clade that forms a poorly defined, unnamed, ordinal-level sister-taxon to the *Microascales*. Several other *Acremonium* species such as the phytopathogen *A. cucurbitacearum* also have been shown to belong to the *Plectosphaerellaceae* (Zare *et al.* 2007). The simple structure of *Acremonium* has either convergently evolved in diverse fungal orders within the class *Sordariomycetes* or is symplesiomorphic at a very deep level.

The diversity of fungi throughout the *Ascomycota* that produce *Acremonium*-like anamorphs is high, including genera such as *Gabarnaudia* (*Microascales*), *Lecytophora* (*Coniochaetales*), and *Pseudogliomastix* (*Sordariales incertae sedis*). The present study does not review the vast range of fungi producing simple phialidic conidiophores, but instead, focuses specifically on: 1) anamorphs that have been formally placed into the genus *Acremonium*, and 2) species and genera phylogenetically related to the named *Acremonium* species.

The number of previously phylogenetically unstudied fungi is large. Currently, there are approximately 95 named *Acremonium* species with

traceable material (cultures or specimens in good condition), excluding endophyte species that were transferred to *Neotyphodium* by Glenn *et al.* (1996). In addition, there are an undetermined number of nectriaceous teleomorphs with unnamed *Acremonium*-like anamorphs plus about 15 named and unnamed *Emericellopsis* species with *Acremonium* anamorphs (Zuccaro *et al.* 2004). The preliminary phylogeny done by Glenn *et al.* (1996) includes only seven species that would currently be considered *Acremonium*, inclusive of the *Acremonium berkeleyanum*, anamorph of *Cosmospora berkeleyana*, formerly considered the anamorph of *Cosmospora villosa*, plus two *Emericellopsis* species. Clearly, further work is needed on the phylogeny of *Acremonium*.

Because of the high biodiversity within *Acremonium*, relatively evolutionarily labile, rapidly evolving genes like the ribosomal internal transcribed spacer (ITS) are not alignable across the genus (de Hoog *et al.* 2000) or even within some of the individual orders that the genus spans. Because many *Acremonium* species are derived from relatively closely related families in the *Sordariomycetes*, relatively slowly evolving genes that are alignable such as the ribosomal large subunit (LSU) may yield considerable ambiguity about relationships. To address this problem, we performed an analysis of LSU and whole SSU sequences for a larger number of *Acremonium* isolates than has been examined previously. Based on these results, we chose six of the most phylogenetically distinctive species and included them in the Ascomycetous Tree of Life project (Schoch *et al.* 2009). The elegant phylogenetic analysis in that project was based on two nuclear ribosomal genes, one mitochondrial ribosomal gene, and portions of three protein-coding genes. These results permitted us to gain a clearer picture of relationships among the *Acremonium* groups that were imperfectly resolved in LSU and SSU analysis.

In the present study we present the results of the LSU and small subunit (SSU) phylogenetic analyses for the majority of *Acremonium* species available in pure culture including described and undescribed species. This gives not only a phylogenetic overview of the genus, but also provides identification-enabling sequences for *Acremonium* species that have not been sequenced previously. Taken with the Tree of Life studies, these results shed new light on the biodiversity of these morphologically simple fungi that have long been profoundly problematical in terms of accurate classification and reliable species identification.

MATERIALS AND METHODS

Two separate sets of data matrices were assembled (Table 1). The first is a two-gene analysis that aims at investigating the phylogenetic position of *Acremonium* within the *Sordariomycetes*. The second is a one-gene analysis focusing on the *Acremonium* strains belonging to the order *Hypocreales*. The first set includes the large and small subunits of the nuclear ribosomal RNA gene (nuLSU and nucSSU, respectively) and 166 taxa, including 56 strains of *Acremonium*, 105 reference taxa of *Sordariomycetes*, and five species of *Leotiomyces* as an outgroup (*Botryotinia fuckeliana*, *Chalara aurea*, *Leotia lubrica*, *Microglossum rufum*, and *Pseudeurotium zonatum*). The second set includes only the nuLSU for 331 taxa including 170 strains of *Acremonium*, 158 sequences of *Hypocreales*, and three outgroup species (*Ceratocystis fimbriata*, *Glomerella cingulata*, and *Ophiostoma piluliferum*).

DNA isolation and sequencing

DNA was extracted with a FastDNA kit (Qbiogene, Heidelberg, Germany) from mycelium grown for 5–14 d in liquid Complete

Medium (Raper & Raper 1972). The LSU region of ribosomal DNA (rDNA) was amplified with primers V9G (de Hoog & Gerrits van den Ende 1998) and LR5 (Vilgalys & Hester 1990). The SSU region was amplified with primers NS1 and NS24 and sequenced using primers NS1–NS4, NS6, NS24 (White *et al.* 1990; Gargas *et al.* 1992). The components for the PCR were used as described by Schroers (2000). The PCR program was 60 s at 94 °C (initial denaturation); 35 cycles of 35 s at 94 °C (denaturation), 50 s at 55 °C (annealing), and 120 s at 72 °C (elongation); and 6 min at 72 °C (final elongation) followed by chilling to 4 °C. The PCR products were purified with a GFX purification kit (Amersham Pharmacia Biotech Inc., Roosendaal, The Netherlands) and visualised on an electrophoresis gel after ethidium bromide staining. The rDNA was sequenced with a BigDye terminator cycle sequencing kit (Applied Biosystems, Foster City, Calif.) and analysed on an ABI Prism 3700 instrument (Applied Biosystems) by using the standard conditions recommended by the vendor. The primers used in the sequence reaction were NL1 and NL4 (O'Donnell 1993), and LR5.

Alignments and phylogenetic analyses

Sequences were assembled and edited using SeqMan II software (DNASTar, Inc., Madison, Wis.). Manual alignments were performed using MacClade v. 4.08 (Maddison & Maddison 2003). Ambiguous regions (*sensu* Lutzoni *et al.* 2000) and introns were delimited manually and excluded from the alignments. Congruence was tested using a 70 % reciprocal bootstrap criterion (Mason-Gamer & Kellogg 1996, Reeb *et al.* 2004). Final phylogenetic analyses of the two-gene and one-gene datasets were performed using Stamatakis's "randomised accelerated (sic) maximum likelihood for high performance computing" (RAxML VI-HPC, Stamatakis *et al.* 2005, 2008) on the Cipres Web Portal (http://www.phylo.org/sub_sections/portal/). For the two-gene analysis, the maximum likelihood search followed a "GTRMIX" model of molecular evolution applied to two partitions, nuLSU and nucSSU. The same model was applied to the one-gene analysis without partition. Support values were obtained in RAxML with bootstrap analyses of 500 pseudoreplicates. The trees are labeled with the updated scientific names.

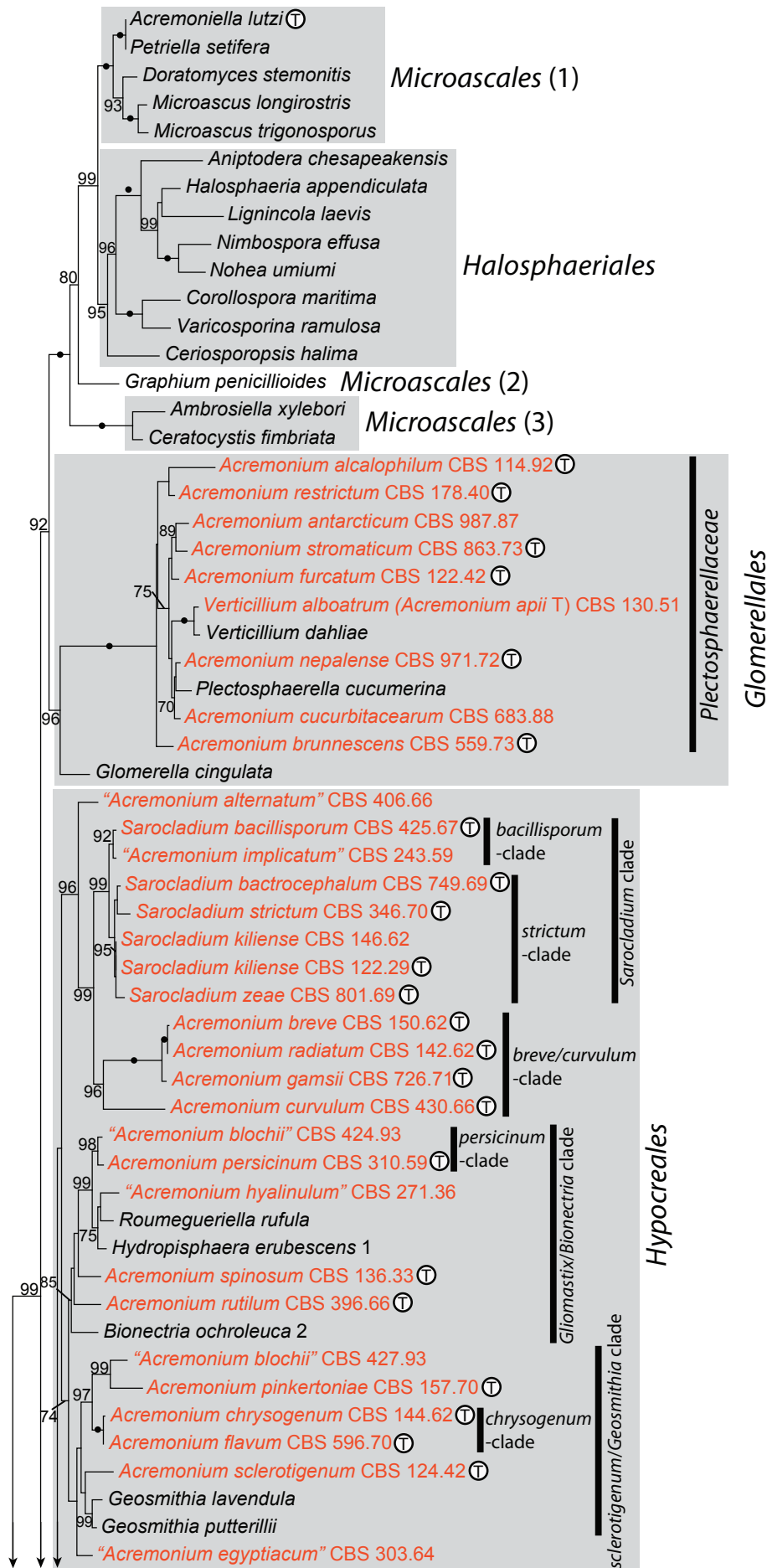
RESULTS

DNA sequence alignments

A total of 228 new sequences were generated for *Acremonium*, 192 nuLSU and 36 nucSSU (Table 1). For the two-gene dataset, one nuLSU and 41 nucSSU sequences were missing. After exclusion of ambiguous regions and introns, the two-gene dataset included 2 955 characters (1 250 nuLSU and 1 705 nucSSU). Among these, 1 739 were constant while 900 were parsimony-informative. After exclusion of ambiguous regions and introns, the one-gene dataset included 848 characters. Among these, 481 were constant while 260 were parsimony-informative.

Phylogenetic inference

As shown in Fig. 1, the species of *Acremonium* mostly fall into three groups, namely the *Hypocreales*, the *Plectosphaerellaceae*, and the *Sordariales*. The bulk of species fall into the *Hypocreales*.



A

Fig. 1.A–C. The phylogenetic position of *Acremonium* and related fungi within the *Sordariomycetes*, as seen in combined analysis of the large and small subunits of the nuclear ribosomal RNA gene (LSU + SSU) analysed by maximum likelihood via RAxML VI-HPC following a GTRMIX model applied to two partitions. 100 % bootstrap values are indicated by a black dot on the relevant internode.

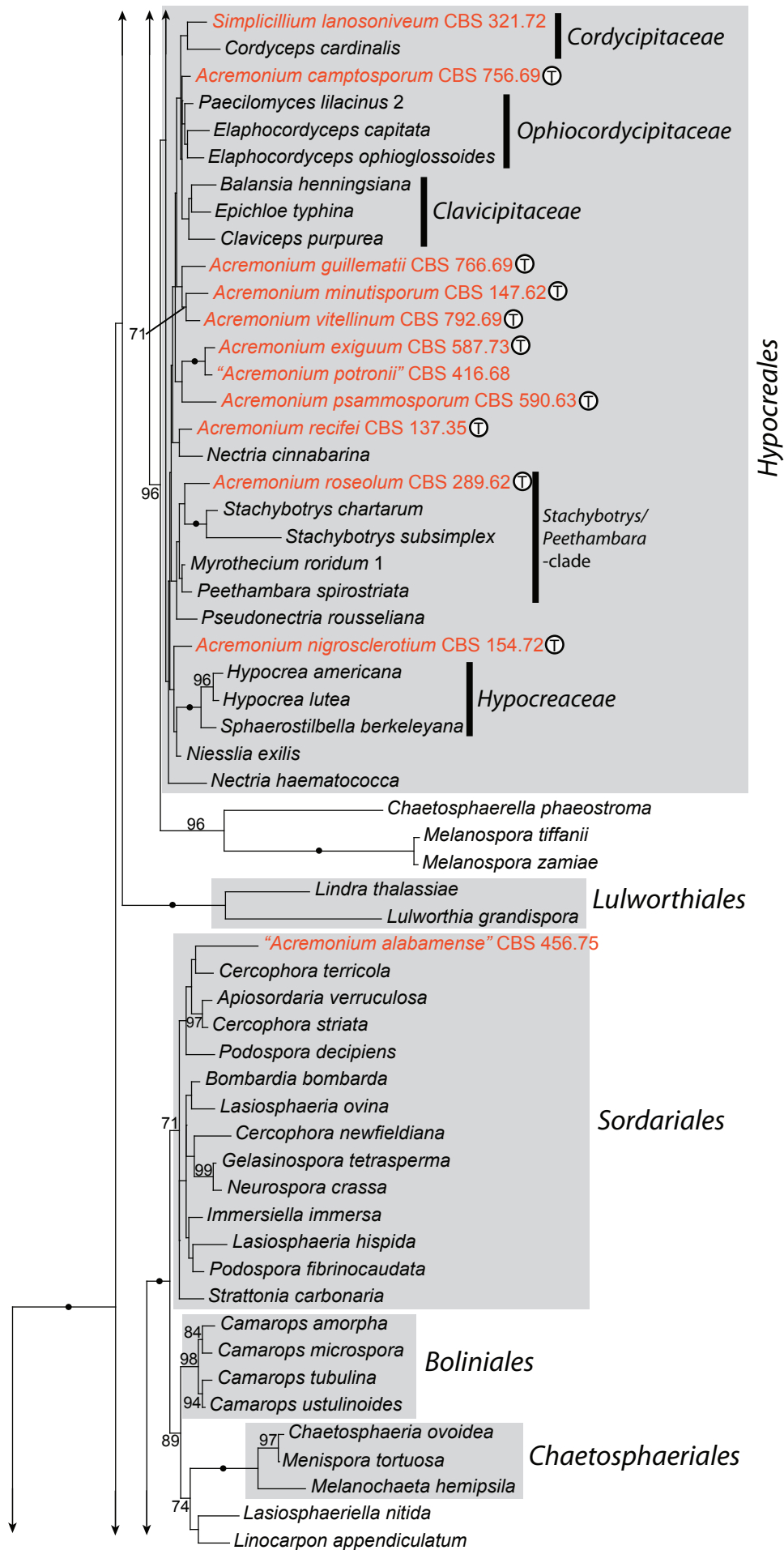


Fig. 1. (Continued).

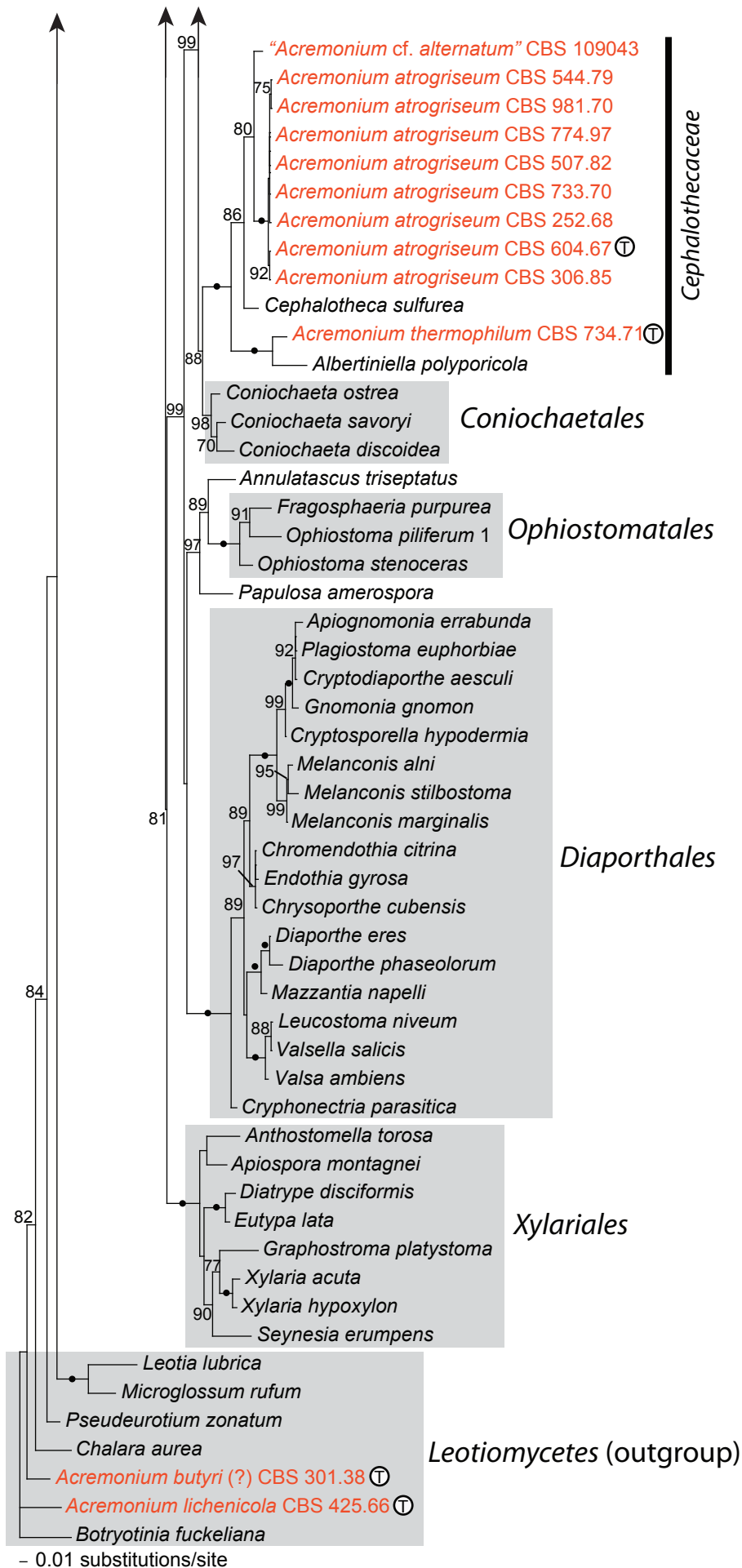


Fig. 1. (Continued).

Table 1. List of *Acremonium* species included in this study as well as other novel or independently redone sequences of related fungi used for comparison. Sequences from GenBank of other comparison taxa are listed in Supplemental Table 1a - see online Supplementary Information. Collection and GenBank numbers are indicated and type strains (T) are mentioned. Sequences generated in this study are shown in bold. Dashes indicate missing data in the two-gene analysis. Isolates that cannot be assigned a phylogenetically confirmed name are listed under the name under which they are currently held in the CBS collection.

Currently assigned species name	Collection numbers	nucLSU	nucSSU	Notes
<i>Acremoniella lutzi</i> T	CBS 103.48	HQ231971	–	Ex-type of <i>Acremoniella lutzi</i>
<i>Acremonium acutatum</i> T	CBS 682.71	HQ231965		
<i>Acremonium alabamense</i>	CBS 456.75	HQ231972	–	
<i>Acremonium alcalophilum</i> T	CBS 114.92	HQ231973	–	Ex-type of <i>Acremonium alcalophilum</i>
<i>Acremonium alternatum</i> T	CBS 407.66	HQ231988		
" <i>Acremonium alternatum</i> "	CBS 381.70A	HQ231986		
	CBS 406.66	HQ231987	HQ232178	
	CBS 831.97	HQ231989		
	CBS 114602	HQ231990		
" <i>Acremonium</i> cf. <i>alternatum</i> "	CBS 109043	HQ231974	–	
<i>Acremonium antarcticum</i>	CBS 987.87	HQ231975	–	
<i>Acremonium atrogriseum</i> T	CBS 604.67	HQ231981	–	Ex-type of <i>Phaeoscopulariopsis atrogrisea</i>
	CBS 252.68	HQ231977	–	
	CBS 306.85	HQ231978	–	
	CBS 507.82	HQ231979	–	
	CBS 544.79	HQ231980	–	
	CBS 733.70	HQ231982	–	
	CBS 774.97	HQ231983	–	
	CBS 981.70	HQ231984	–	
<i>Acremonium biseptum</i> T	CBS 750.69	HQ231998		Ex-type of <i>Acremonium biseptum</i>
" <i>Acremonium blochii</i> "	CBS 324.33	HQ231999		
	CBS 424.93	HQ232000	HQ232181	
	CBS 427.93	HQ232001	HQ232182	
	CBS 993.69	HQ232002		
<i>Acremonium borodinense</i> T	CBS 101148	HQ232003		Ex-type of <i>Acremonium borodinense</i>
<i>Acremonium brachyphenium</i> T	CBS 866.73	HQ232004		
<i>Acremonium breve</i> T	CBS 150.62	HQ232005	HQ232183	Ex-type of <i>Cephalosporium roseum</i> var. <i>breve</i>
<i>Acremonium brunnescens</i> T	CBS 559.73	HQ231966	HQ232184	Ex-type of <i>Acremonium brunnescens</i>
<i>Acremonium butyri</i> T	CBS 301.38	HQ231967	–	Ex-type of <i>Tilachlidium butyri</i> ; synonym of <i>Cadophora malorum</i>
<i>Acremonium camptosporum</i> T	CBS 756.69	HQ232008	HQ232186	Ex-type of <i>Acremonium camptosporum</i>
	CBS 677.74	HQ232007		
	CBS 757.69	HQ232009		
	CBS 835.91	HQ232010		
	CBS 890.85	HQ232011		
<i>Acremonium cavaraeanum</i>	CBS 758.69	HQ232012		
<i>Acremonium cerealis</i>	CBS 207.65	HQ232013		Ex-type of <i>Gliomastix guttuliformis</i>
	CBS 215.69	HQ232014		
<i>Acremonium chrysogenum</i> T	CBS 144.62	HQ232017	HQ232187	Ex-type of <i>Cephalosporium chrysogenum</i>
<i>Acremonium cucurbitacearum</i>	CBS 683.88	HQ231968	–	Previously identified as <i>Acremonium strictum</i>
<i>Acremonium curvulum</i> T	CBS 430.66	HQ232026	HQ232188	Ex-type of <i>Acremonium curvulum</i>
	CBS 104.78	HQ232019		
	CBS 214.70	HQ232020		
	CBS 229.75	HQ232021		
	CBS 333.92	HQ232022		
	CBS 384.70A	HQ232023		
	CBS 384.70C	HQ232024		
	CBS 523.72	HQ232028		
	CBS 761.69	HQ232029		
	CBS 898.85	HQ232030		
	CBS 110514	HQ232032		
" <i>Acremonium</i> aff. <i>curvulum</i> "	CBS 100551	HQ232031		
	CBS 113275	HQ232033		
<i>Acremonium egyptiacum</i>	CBS 303.64	HQ232034	HQ232189	
<i>Acremonium exiguum</i> T	CBS 587.73	HQ232035	HQ232190	Ex-type of <i>Acremonium exiguum</i>
<i>Acremonium exuviarum</i> T	UAMH 9995	HQ232036		
<i>Acremonium flavum</i> T	CBS 596.70	HQ232037	HQ232191	Ex-type of <i>Acremonium flavum</i>
<i>Acremonium fuci</i>	UAMH 6508	HQ232038		
<i>Acremonium furcatum</i> T	CBS 122.42	AY378154	HQ232192	Ex-type of <i>Acremonium furcatum</i>

Table 1. (Continued).

Currently assigned species name	Collection numbers	nucLSU	nucSSU	Notes
<i>Acremonium fusidioides</i> T	CBS 840.68	HQ232039		Ex-type of <i>Paecilomyces fusidioides</i>
<i>Acremonium gamsii</i> T	CBS 726.71	HQ232040	HQ232193	Ex-type of <i>Acremonium gamsii</i>
<i>Acremonium guillematii</i> T	CBS 766.69	HQ232042	HQ232194	Ex-type of <i>Acremonium guillematii</i>
<i>Acremonium hansfordii</i>	CBS 390.73	HQ232043		
<i>Acremonium hennebertii</i> T	CBS 768.69	HQ232044		Ex-type of <i>Acremonium hennebertii</i>
<i>Acremonium hyalinulum</i>	CBS 271.36	HQ232045	HQ232195	
" <i>Acremonium implicatum</i> "	CBS 243.59	HQ232046	HQ232196	Authentic strain of <i>Fusarium terricola</i>
	CBS 397.70B	HQ232047		
<i>Acremonium incrustatum</i> T	CBS 159.70	HQ232049		
<i>Acremonium inflatum</i> T	CBS 212.69	HQ232050		Ex-type of <i>Gliomastix inflata</i>
	CBS 439.70	HQ232051		
	CBS 403.70	HQ231991		In CBS as <i>Acremonium atrogriseum</i>
<i>Acremonium lichenicola</i> T	CBS 425.66	HQ231969	–	Ex-type of <i>Acremonium lichenicola</i>
<i>Acremonium longisporum</i>	CBS 113.69	HQ232057		
" <i>Acremonium luzulae</i> "	CBS 495.67	HQ232058		
	CBS 579.73	HQ232059		
<i>Acremonium minutisporum</i> T	CBS 147.62	HQ232061	HQ232199	Ex-type of <i>Cephalosporium minutisporum</i>
	det 267B	HQ232062		
<i>Acremonium nepalense</i> T	CBS 971.72	HQ231970	–	Ex-type of <i>Acremonium nepalense</i>
<i>Acremonium nigrosclerotium</i> T	CBS 154.72	HQ232069	HQ232200	Ex-type of <i>Acremonium nigrosclerotium</i>
<i>Acremonium persicinum</i> T	CBS 310.59	HQ232077	HQ232201	Ex-type of <i>Paecilomyces persicinum</i>
	CBS 169.65	HQ232072		
	CBS 295.70A	HQ232075		
	CBS 295.70M	HQ232076		
	CBS 330.80	HQ232078		
	CBS 378.70A	HQ232079		
	CBS 378.70D	HQ232081		
	CBS 378.70 E	HQ232082		
	CBS 439.66	HQ232083		
	CBS 469.67	HQ232084		
	CBS 101694	HQ232085		
	CBS 102349	HQ232086		
" <i>Acremonium persicinum</i> "	CBS 378.70C	HQ232080		
	CBS 110646	HQ232088		
" <i>Acremonium aff. persicinum</i> "	CBS 203.73	HQ232073		
	CBS 263.89	HQ232074		
" <i>Acremonium cf. persicinum</i> "	CBS 102877	HQ232087		
<i>Acremonium pinkertoniae</i> T	CBS 157.70	HQ232089	HQ232202	Ex-type of <i>Acremonium pinkertoniae</i>
" <i>Acremonium potronii</i> "	CBS 189.70	HQ232094		
	CBS 379.70F	HQ232096		
	CBS 416.68	HQ232097	HQ232203	
	CBS 433.88	HQ232098		
	CBS 781.69	HQ232099		
<i>Acremonium psammosporum</i> T	CBS 590.63	HQ232100	HQ232204	Ex-type of <i>Acremonium psammosporum</i>
<i>Acremonium pseudozeylanicum</i> T	CBS 560.73	HQ232101		Ex-type of <i>Acremonium pseudozeylanicum</i>
<i>Acremonium pteridii</i> T	CBS 782.69	HQ232102		Ex-type of <i>Acremonium pteridii</i>
	CBS 784.69	HQ232103		
<i>Acremonium radiatum</i> T	CBS 142.62	HQ232104	HQ232205	Ex-type of <i>Cephalosporium acremonium</i> var. <i>radiatum</i>
<i>Acremonium recifei</i> T	CBS 137.35	HQ232106	HQ232206	Ex-type of <i>Cephalosporium recifei</i>
	CBS 135.71	HQ232105		
	CBS 220.84	HQ232107		
	CBS 362.76	HQ232108		
	CBS 402.89	HQ232109		
	CBS 411.91	HQ232110		
	CBS 442.66	HQ232111		
	CBS 541.89	HQ232114		
	CBS 555.73	HQ232115		
	CBS 596.74	HQ232116		
	CBS 976.70	HQ232117		
	CBS 400.85	HQ232025		In CBS as <i>Acremonium curvulum</i>
	CBS 505.94	HQ232027		In CBS as <i>Acremonium cf. curvulum</i>
" <i>Acremonium recifei</i> "	CBS 485.77	HQ232113		
	CBS 482.78	HQ232112		

Table 1. (Continued).

Currently assigned species name	Collection numbers	nucLSU	nucSSU	Notes
	CBS 110348	HQ232118		
<i>Acremonium restrictum</i> T	CBS 178.40	HQ232119	–	Ex-type of <i>Verticillium dahliae</i> f. <i>restrictum</i>
<i>Acremonium rhabdosporum</i> T	CBS 438.66	HQ232120		Ex-type of <i>Acremonium rhabdosporum</i>
<i>Acremonium roseolum</i> T	CBS 289.62	HQ232123	HQ232207	Ex-type of <i>Paecilomyces roseolus</i>
<i>Acremonium rutilum</i> T	CBS 396.66	HQ232124	HQ232208	Ex-type of <i>Acremonium rutilum</i>
<i>Acremonium salmoneum</i> T	CBS 721.71	HQ232125		Ex-type of <i>Acremonium salmoneum</i>
<i>Acremonium sclerotigenum</i> T	CBS 124.42	HQ232126	HQ232209	Ex-type of <i>Cephalosporium sclerotigenum</i>
	CBS 270.86	HQ232127		
	CBS 281.80	HQ232128		
	CBS 384.65	HQ232129		
	CBS 786.69	HQ232130		
	CBS 100816	HQ232131		
	OMH F1648.97	HQ232132		
	OMH F2365.97	HQ232133		
	OMH F2969.97	HQ232134		
	OMH F3691.97	HQ232135		
	CBS 287.700	HQ232140		In CBS as <i>Acremonium strictum</i>
	CBS 379.70D	HQ232095		In CBS as <i>Acremonium potronii</i>
	CBS 223.70	HQ231985		In CBS as <i>Acremonium alternatum</i>
<i>Acremonium sordidulum</i> T	CBS 385.73	HQ232136		Ex-type of <i>Acremonium sordidulum</i>
<i>Acremonium</i> sp.	CBS 314.72	HQ232156		
<i>Acremonium spinosum</i> T	CBS 136.33	HQ232137	HQ232210	Ex-type of <i>Cephalosporium spinosum</i>
" <i>Acremonium strictum</i> "	CBS 106.23	HQ232138		
	CBS 147.49	HQ232139		
<i>Acremonium stromaticum</i> T	CBS 863.73	HQ232143	–	Ex-type of <i>Acremonium stromaticum</i>
<i>Acremonium tectonae</i> T	CBS 725.87	HQ232144		Ex-type of <i>Acremonium tectonae</i>
<i>Acremonium thermophilum</i> T	CBS 734.71	HQ232145	–	Ex-type of <i>Acremonium thermophilum</i>
<i>Acremonium tsugae</i> T	CBS 788.69	HQ232146		Ex-type of <i>Acremonium tsugae</i>
<i>Acremonium tubakii</i> T	CBS 790.69	HQ232148		Ex-type of <i>Acremonium tubakii</i>
" <i>Acremonium tubakii</i> "	CBS 824.69	HQ232149		
<i>Acremonium verruculosum</i> T	CBS 989.69	HQ232150		Ex-type of <i>Acremonium verruculosum</i>
<i>Acremonium vitellinum</i> T	CBS 792.69	HQ232151	HQ232212	Ex-type of <i>Acremonium vitellinum</i>
<i>Acremonium zeylanicum</i>	CBS 746.73	HQ232154		
<i>Acremonium zonatum</i>	CBS 565.67	HQ232155		
" <i>Cephalosporium acremonium</i> var. <i>cereum</i> " T	CBS 140.62	HQ232147		Ex-type of <i>Cephalosporium acremonium</i> var. <i>cereum</i> . In CBS as <i>Acremonium tubakii</i>
" <i>Cephalosporium acremonium</i> var. <i>funiculosum</i> " T	CBS 141.62	HQ232053		Ex-type of <i>Cephalosporium acremonium</i> var. <i>funiculosum</i> . In CBS as <i>Acremonium kiliense</i>
" <i>Cephalosporium ballagii</i> " T	CBS 134.33	HQ232016		Ex-type of <i>Cephalosporium ballagii</i> . In CBS as <i>Acremonium charticola</i>
" <i>Cephalosporium malorum</i> " T	CBS 117.25	HQ232015		Ex-type of <i>Cephalosporium malorum</i> . In CBS as <i>Acremonium charticola</i>
" <i>Cephalosporium purpurascens</i> " T	CBS 149.62	HQ232071		Ex-type of <i>Cephalosporium purpurascens</i> . In CBS as <i>Acremonium persicinum</i>
<i>Cosmospora khandalensis</i> T	CBS 356.65	HQ231996		Ex-type of <i>Cephalosporium khandalense</i> . In CBS as <i>Acremonium berkeleyanum</i>
<i>Cosmospora lavitskiae</i> T	CBS 530.68	HQ231997		Ex-type of <i>Gliomastix lavitskiae</i> . In CBS as <i>Acremonium berkeleyanum</i>
<i>Gliomastix masseei</i>	CBS 794.69	HQ232060		In CBS as <i>Acremonium masseei</i>
<i>Gliomastix murorum</i>	CBS 154.25	HQ232063		Ex-type of <i>Graphium malorum</i> . In CBS as <i>Acremonium murorum</i> var. <i>felina</i>
	CBS 195.70	HQ232064		In CBS as <i>Acremonium murorum</i> var. <i>felina</i>
	CBS 119.67	HQ232066		In CBS as <i>Acremonium murorum</i> var. <i>murorum</i>
	CBS 157.72	HQ232067		In CBS as <i>Acremonium murorum</i> var. <i>murorum</i>
	CBS 378.36	HQ232068		Ex-type of <i>Torula cephalosporioides</i> . In CBS as <i>Acremonium murorum</i> var. <i>murorum</i>
<i>Gliomastix polychroma</i> T	CBS 181.27	HQ232091		Ex-type of <i>Oospora polychroma</i> . In CBS as <i>Acremonium polychromum</i>
	CBS 151.26	HQ232090		Ex-type of <i>Periconia tenuissima</i> var. <i>nigra</i> . In CBS as <i>Acremonium polychromum</i>
	CBS 617.94	HQ232093		In CBS as <i>Acremonium polychromum</i>
<i>Gliomastix roseogrisea</i> T	CBS 134.56	HQ232121		Ex-type of <i>Cephalosporium roseogriseum</i> . In CBS as <i>Acremonium roseogriseum</i>
	CBS 279.79	HQ232122		In CBS as <i>Acremonium roseogriseum</i>
	CBS 213.69	HQ232092		In CBS as <i>Acremonium polychromum</i>
	CCFC 226570	AY283559		Identified as <i>Acremonium murorum</i> var. <i>felina</i>
	CBS 211.69	HQ232065		In CBS as <i>Acremonium murorum</i> var. <i>felina</i>
<i>Lanatonectria flavolanata</i>	CBS 230.31	HQ232157		

Table 1. (Continued).

Currently assigned species name	Collection numbers	nucLSU	nucSSU	Notes
<i>Lanatonectria flocculenta</i>	CBS 113461	HQ232158		
<i>Leucosphaerina arxii</i> T	CBS 737.84	HQ232159		Ex-type of <i>Leucosphaerina arxii</i>
<i>Nalanthamala diospyri</i> T	CBS 560.89	HQ232160		Ex-type of <i>Cephalosporium diospyri</i> = <i>Acremonium diospyri</i>
<i>Nectria rishbethii</i> T	CBS 496.67	HQ232162		Ex-type of <i>Nectria rishbethii</i>
<i>Neocosmospora endophytica</i>	AR 2674	U17411		Anamorph is <i>Acremonium fungicola</i>
<i>Paecilomyces lilacinus</i>	CBS 101068	HQ232163	HQ232214	Atypical monophialidic isolate, <i>Acremonium</i> +E402-like
<i>Pochonia bulbillosa</i>	CBS 102853	HQ232164		Atypical isolate
<i>Sarcopodium circinatatum</i>	CBS 376.81	HQ232167		
	CBS 587.92	HQ232168		
	CBS 114068	HQ232169		
<i>Sarcopodium circinosetiferum</i>	CBS 100251	HQ232170		
	CBS 100252	HQ232171		
	CBS 100998	HQ232172		
	CBS 101116	HQ232173		
<i>Sarcopodium vanillae</i>	CBS 100582	HQ232174		
<i>Sarocladium attenuatum</i> T	CBS 399.73	HQ232165		Ex-type of <i>Sarocladium attenuatum</i>
<i>Sarocladium bacillisporum</i> T	CBS 425.67	HQ231992	HQ232179	Ex-type of <i>Acremonium bacillisporum</i>
<i>Sarocladium bactrocephalum</i> T	CBS 749.69	HQ231994	HQ232180	Ex-type of <i>Acremonium bactrocephalum</i>
	NRRL 20583	HQ231995		
<i>Sarocladium glaucum</i> T	CBS 796.69	HQ232041		Ex-type of <i>Acremonium glaucum</i>
<i>Sarocladium kiliense</i> T	CBS 122.29	HQ232052	HQ232198	Ex-type of <i>Acremonium kiliense</i>
	CBS 146.62	HQ232048	HQ232197	Ex-type of <i>Cephalosporium incoloratum</i> . In CBS as <i>Acremonium incoloratum</i>
	CBS 155.61	HQ232054		Ex-type of <i>Cephalosporium incarnatum</i> . In CBS as <i>Acremonium kiliense</i>
	CBS 156.61	HQ232055		Ex-type of <i>Cephalosporium incarnatum</i> var. <i>macrospora</i> . In CBS as <i>Acremonium kiliense</i>
	CBS 157.61	HQ232056		Ex-type of <i>Cephalosporium infestans</i> . In CBS as <i>Acremonium kiliense</i>
<i>Sarocladium ochraceum</i> T	CBS 428.67	HQ232070		Ex-type of <i>Paecilomyces ochraceus</i> . In CBS as <i>Acremonium ochraceum</i>
<i>Sarocladium oryzae</i>	CBS 180.74	HQ232166		
<i>Sarocladium strictum</i> T	CBS 346.70	HQ232141	HQ232211	Ex-type of <i>Acremonium strictum</i>
" <i>Sarocladium cf. strictum</i> "	JY03-006	HQ232142		
<i>Sarocladium zaeae</i> T	CBS 801.69	HQ232152	HQ232213	Ex-type of <i>Acremonium zaeae</i>
	KAS 965	HQ232153		
<i>Simplicillium lanosoniveum</i>	CBS 321.72	HQ232006	HQ232185	Ex-type of <i>Acremonium byssoides</i>
<i>Simplicillium obclavatum</i> T	CBS 311.74	HQ232175		Ex-type of <i>Acremonium obclavatum</i>
<i>Trichothecium crotocinigenum</i> T	CBS 129.64	HQ232018		Ex-type of <i>Acremonium crotocinigenum</i>
" <i>Trichothecium indicum</i> "/ <i>Leucosphaerina indica</i> T	CBS 123.78	AF096194		Ex-type of ' <i>Leucosphaera</i> ' <i>indica</i>
<i>Trichothecium roseum</i>	DAOM 208997	U69891		
<i>Trichothecium sympodiale</i>	ATCC 36477	U69889		In CBS as <i>Spicellum roseum</i>
<i>Verticillium alboatrum</i>	CBS 130.51	HQ231976	–	Ex-type of <i>Cephalosporium apii</i> , in CBS as <i>Acremonium apii</i>
<i>Verticillium insectorum</i>	CBS 101239	HQ248107		
<i>Verticillium leptobactrum</i>	CBS 109351	HQ231993		In CBS as <i>Acremonium cf. bacillisporum</i>

Nine of the named *Acremonium* species in this analysis belong to the *Plectosphaerellaceae*. The *Sordariales* are represented in Fig. 1 only by *Acremonium alabamense*, the only named *Acremonium* species in *Acremonium* section *Chaetomioidea*. Outside these groups *Acremonium atrogriseum*, represented by numerous conspecific isolates, belongs to the family *Cephalothecaceae* (Fig. 1C), along with *Albertiniella polyporicola* and *Cephalotheca sulfurea*; this family is sister to the *Coniochaetales*. Another *Acremonium* species, *A. thermophilum*, falls into the *Cephalothecaceae* clade grouping with *Albertiniella polyporicola*. An isolate provisionally identified as *Acremonium alternatum*, CBS 109043 is a member of the *Cephalothecaceae*. The complex status of *A. alternatum* is discussed below.

The *Acremonium* species in the *Hypocreales* form an array of poorly to well distinguished clades, most of which do not correspond to previously recognised genera or suprageneric taxa. Included within the *Hypocreales* in the *Sarocladium* clade labeled the "strictum-clade"

is the well known soil fungus long known as *Acremonium strictum* (Fig. 1A). The soil fungus and human opportunistic pathogen traditionally called *A. kiliense* is also included as is the maize corn endophyte known as *A. zaeae*. The corresponding clade in Fig. 2C based on LSU reveals that this group of fungi includes the rice pathogen *Sarocladium oryzae* as a saltatory morphological apomorph. No teleomorphs are known to be associated with this group. This clade consists of fungi forming conidia in mucoid heads; it is closely related to a clade of species forming catenulate conidia, namely the *Acremonium bacillisporum* clade including *A. bacillisporum*, *A. glaucum*, *A. implicatum* pro parte, and, in a separate subclade, *A. ochraceum* (Figs 1A, 2C). The "bacillisporum-clade" and "strictum-clade" grouped together in an overall *Sarocladium* clade (Figs 1, 2). Two catenulate-conidial isolates labeled *A. alternatum* are also loosely associated with the *A. bacillisporum* clade in Fig. 2C. In Fig. 1A, one isolate CBS 406.66 is connected to the *Sarocladium* and *A. breve/curvulum* clades with a 96 % bootstrap value.

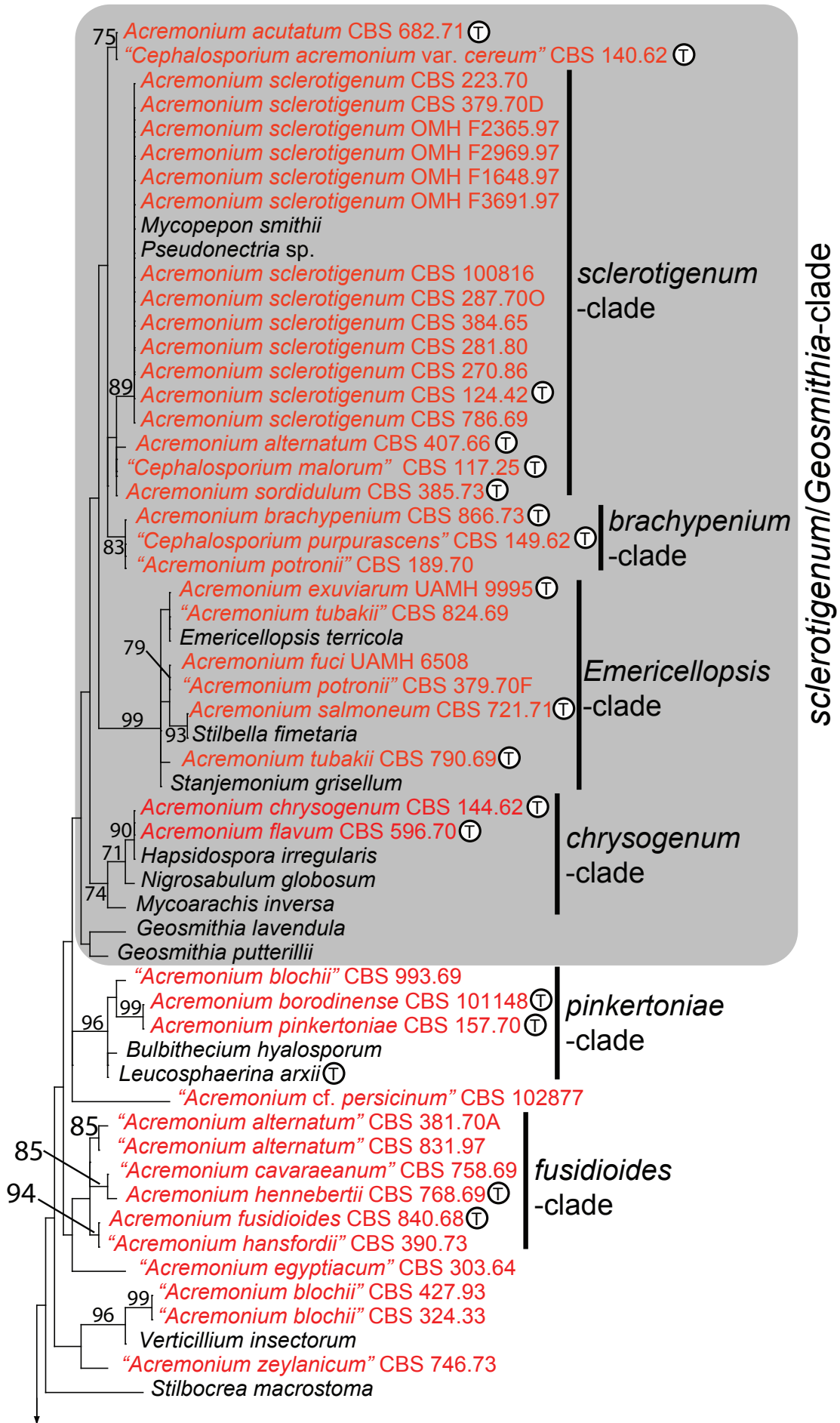


Fig. 2.A–E. The phylogenetic position of *Acremonium* and related fungi within the *Hypocreales*, as seen in nuLSU analysed by maximum likelihood via RAxML VI-HPC following a GTRMIX model applied to a single partition. 100 % bootstrap values are indicated by a black dot on the relevant internode.

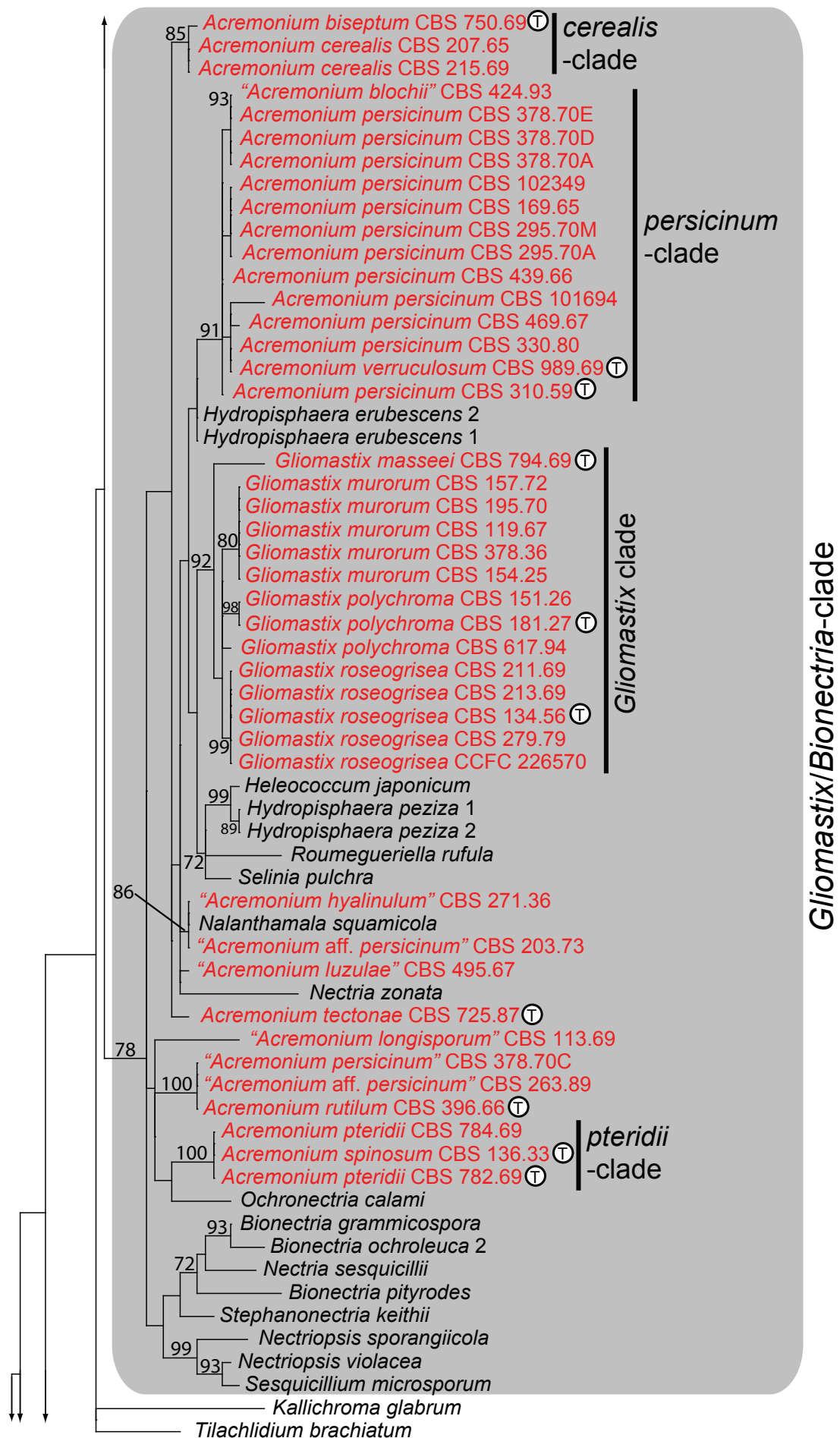


Fig. 2. (Continued).

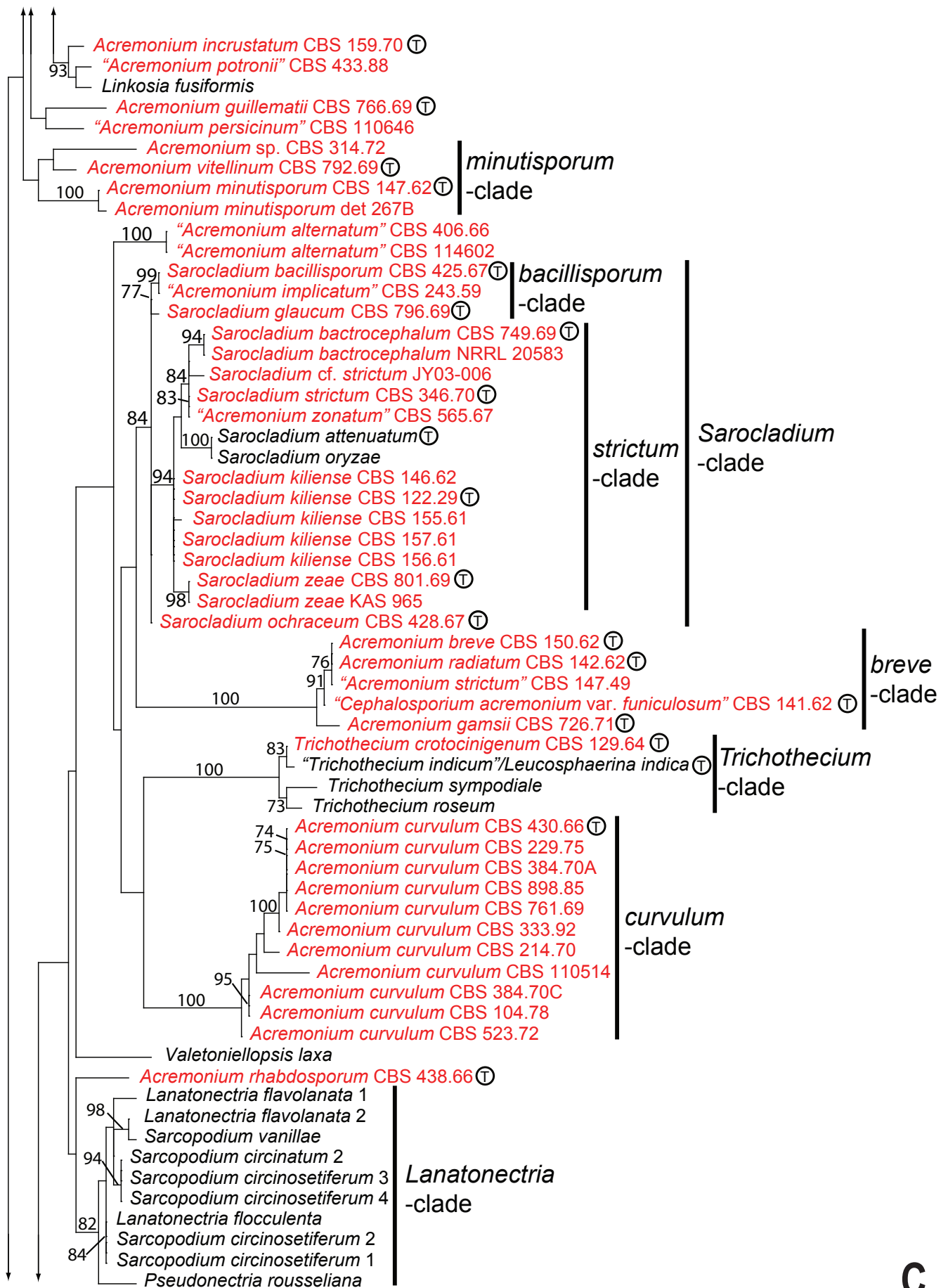
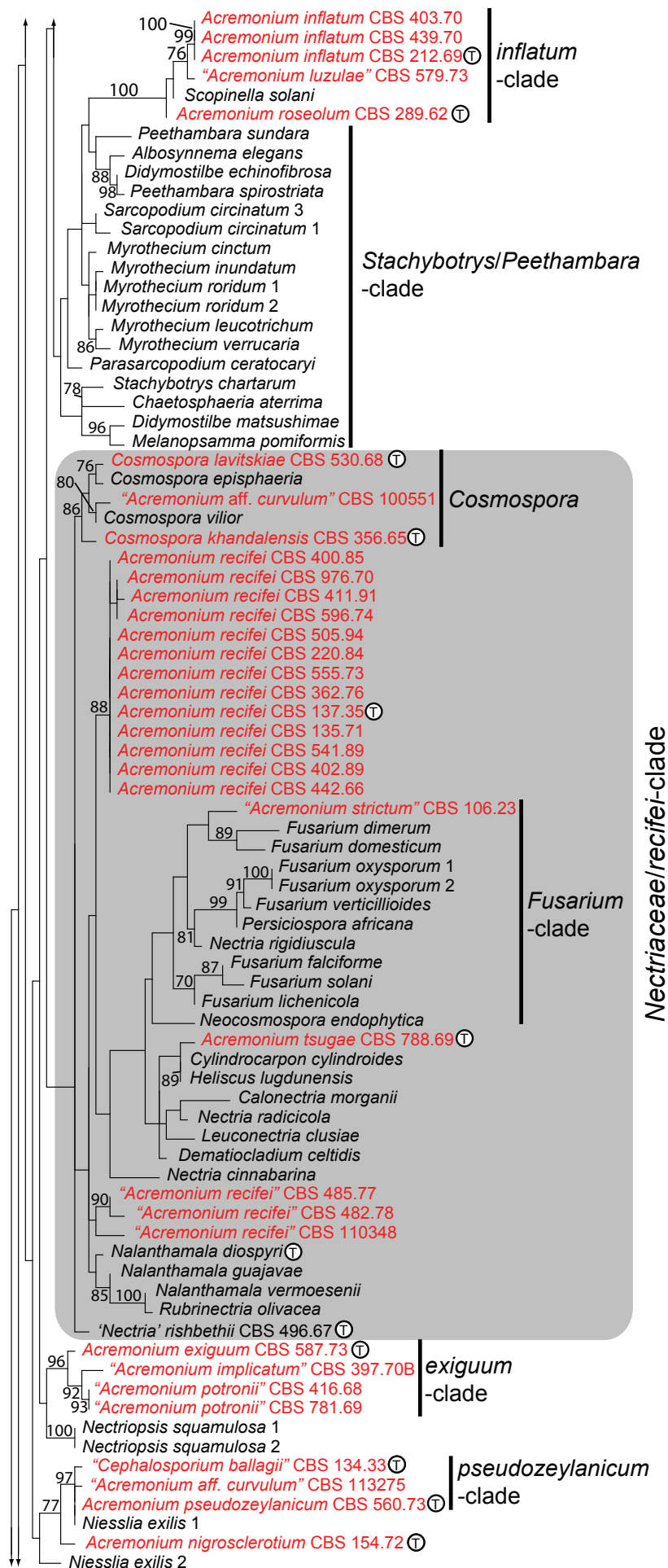


Fig. 2. (Continued).

C



D

Fig. 2. (Continued).

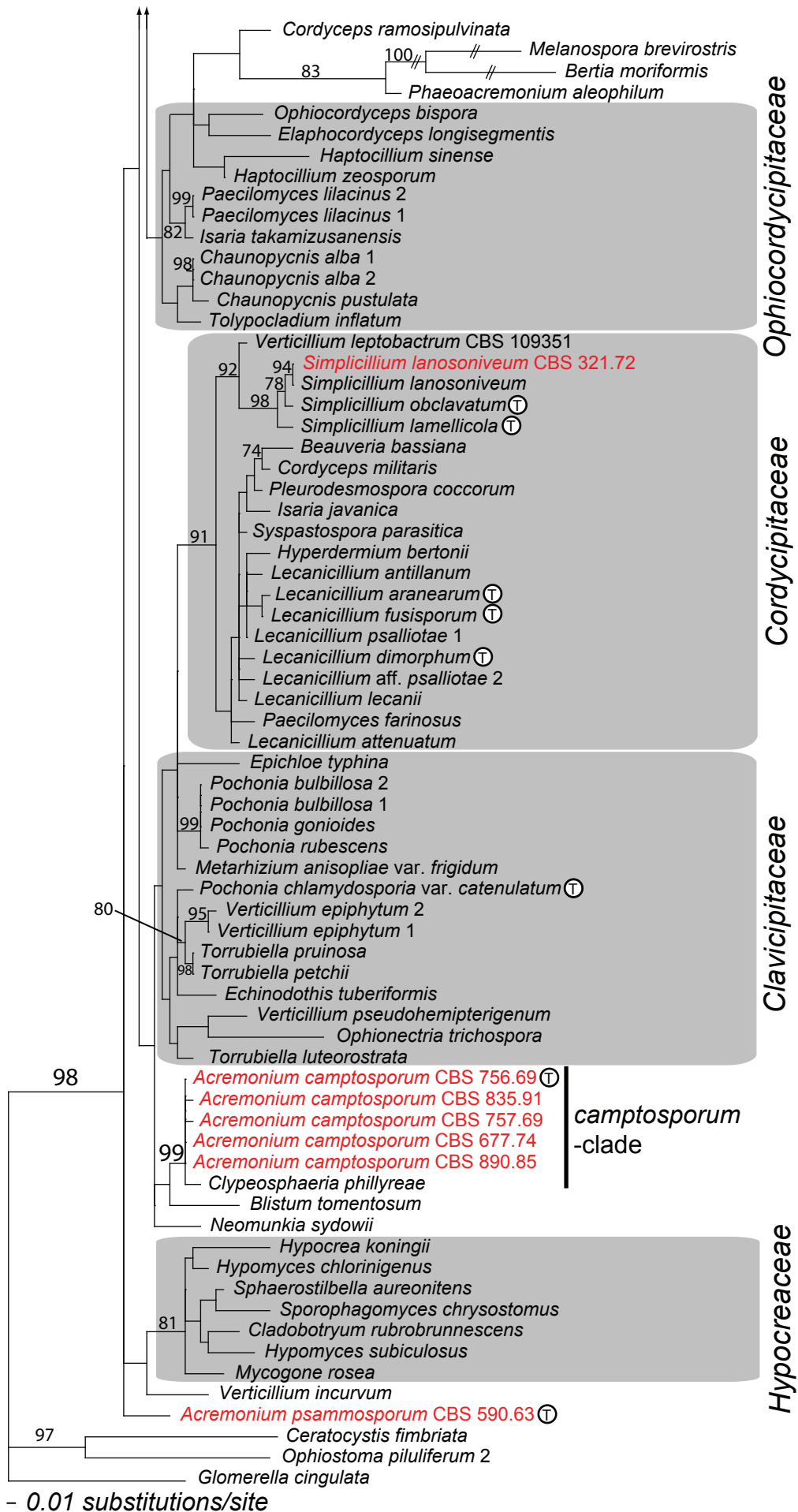


Fig. 2. (Continued).

Another major hypocrealean *Acremonium* clade in Fig. 1A contains *A. breve*, *A. radiatum*, *A. gamsii* and, more distantly, with 96 % bootstrap support, *A. curvulum*. In Fig. 2C where phylogenetic signal is lower, *A. curvulum* loses its tight association with *A. breve* and its relatives and appears in unsupported juxtaposition with the genus *Trichothecium* and the corresponding teleomorph genus, *Leucosphaerina*. The clade containing *Trichothecium roseum* and *Leucosphaerina indica* (see taxonomic comments below) also contains two anamorph species that were long placed in different genera based on conidiogenesis, namely, *Acremonium crocacinigenum* and *Spicellum roseum*, here recombined into *Trichothecium*.

The next clade in Fig. 1A is a loosely structured assemblage consisting of members of *Acremonium* subgenus *Gliomastix*, some of which are delineated below as members of a phylogenetically delineated genus *Gliomastix*, plus the teleomorphic genera *Bionectria*, linked to the well known penicillate hyphomycete anamorph genus *Clonostachys* (Schroers 2001), *Hydropisphaera*, and *Roumegueriella*. As Fig. 2B shows in more detail, the type species of the genus *Gliomastix*, originally named *Gliomastix chartarum* but currently called *G. murorum*, is in a relatively well supported clade (92 % bootstrap support) along with *G. masseei*, *G. polychroma*, and *G. roseogrisa*, three other species with melanised conidia that were placed in *Acremonium* subg. *Gliomastix* by Gams (1971). Related to *Gliomastix* are two clades of non-melanised *Acremonium* species placed in *A. subg. Gliomastix*, the *A. persicinum* clade, and *A. pteridii* clade. Smaller clades containing species in *A. subg. Gliomastix* such as *A. biseptum*, *A. cerealis*, *A. luzulae*, and *A. rutilum* (= *A. roseum*) are included in the large *Gliomastix/Bionectria* clade, which has 78 % bootstrap support. This clade includes additional teleomorphic fungi such as *Heleococcum*, *Hydropisphaera*, *Nectriopsis*, *Ochronectria*, *Selinia*, and *Stephanonectria*, along with the anamorph *Sesquicillium microsporum*.

The *Gliomastix/Bionectria* clade, the *sclerotigenum/Geosmithia* clade, and other members of the *Bionectriaceae* form a weakly supported clade with 74 % bootstrap value as shown in Fig. 1A. Included in the *sclerotigenum/Geosmithia* clade is the penicillate anamorph genus *Geosmithia sensu stricto* and the ex-type isolates of *Acremonium pinkertoniae* and *A. sclerotigenum* as well as the cephalosporin-producer *Acremonium chrysogenum* and its close relative, the thermophilic *A. flavum*. It also includes non-type isolates identified as *A. blochii* and *A. egyptiacum*. In the LSU-tree (Fig. 2A) the *sclerotigenum/Geosmithia* clade includes an extensive group of *Acremonium* species and cleistothecial *Bionectriaceae* with *Acremonium*-like anamorphs, namely, *Emericellopsis*, *Hapsidospora*, *Mycoarachis*, and *Nigrosabulum*. Among the anamorphic species in this group are most of the phylogenetically disparate isolates identified as the type species of *Acremonium*, *A. alternatum*. One of these, CBS 407.66, is designated below as epitype of *A. alternatum*. Prominent subclades include the *Acremonium sclerotigenum* clade containing the ex-type isolates of *A. sclerotigenum* and *A. sordidulum*.

Another major, well supported bionectriaceous subclade associated with the *sclerotigenum* clade is the *Emericellopsis* clade (Fig. 2A). It includes the type species of the synnematal hyphomycete genus *Stilbella*, *S. fimetaria* (Seifert 1985) as well as the type of *Stanjemonium* (Gams *et al.* 1998) and the marine *Acremonium tubakii sensu stricto* and *A. fuci* (Zuccaro *et al.* 2004). *Stilbella fimetaria* is closely related to the ex-type isolate of *Acremonium salmoneum* isolated from dung, also a typical habitat for *S. fimetaria* (Seifert 1985). An adjacent weakly

supported clade includes *Hapsidospora*, *Mycoarachis*, and *Nigrosabulum*, and the two *Acremonium* species named for yellow pigmentation, *A. chrysogenum* and *A. flavum*. Although associated with *A. chrysogenum* and *A. flavum* in Fig. 1B, *A. pinkertoniae* and *A. borodinense* form a distinct clade in Fig. 2A along with an isolate included in the polyphyletic *A. blochii* (CBS 993.69), plus the cleistothecial teleomorphs *Bulbithecium hyalosporum* and *Leucosphaerina arxii*, both of which have unnamed *Acremonium* anamorphs. In Fig. 2A, the *A. chrysogenum* subclade appears to be distinct from the other clades containing *A. sclerotigenum*, *Emericellopsis*, and *Geosmithia*. The other clades within the overall *sclerotigenum/Geosmithia* clade include the *A. fusidioides* clade containing several *acremonia* forming similar conidial chains (*A. cavaraeanum*, *A. fusidioides*, *A. hansfordii*, *A. hennebertii*, one of the isolates labeled *A. alternatum*). A small *A. brachypenium* clade associated with the *A. sclerotigenum* clade includes *A. brachypenium* plus the ex-type strain of *Cephalosporium purpurascens* placed by Gams (1971) in *A. persicinum*. There is also an isolate of the polyphyletic, untypified species *A. potronii*. Basal to these clades is another small clade that links an entomogenous isolate identified as *Verticillium insectorum* with two isolates from human sources identified as *A. blochii*; these conidial chain-forming isolates are sister to an isolate of the chain-forming entomogenous species *Acremonium zeylanicum*. The “*A. blochii*” isolate CBS 427.93, linked with a 99 % bootstrap value to *A. pinkertoniae* in Fig. 1B, is one of the two isolates associated with *Acremonium zeylanicum* in Fig. 2A.

Adjacent and loosely linked to the bionectriaceous clades in Fig. 2B is a small clade in Fig. 2C containing the ex-type isolate of *Acremonium incrustatum* plus an isolate labeled *A. potronii*, and a sequence attributed to *Linkosia fusiformis*, although this sequence most likely represents a contaminant.

Below the *sclerotigenum/Geosmithia* clade in Fig. 1A and above the *Hypocreaceae* in Fig. 2E fall clades representing the *Clavicipitaceae sensu lato*. These clades include the families *Clavicipitaceae sensu stricto*, *Ophiocordycipitaceae*, and *Cordycipitaceae*. Although many species in this group of three families have *Acremonium*-like anamorphic states, only two described *Acremonium* species are associated here. In Fig. 2E *A. camptosporum* sits basally in a clade adjacent to the *Clavicipitaceae* and is close to the poorly understood teleomorphic species *Clypeosphaeria phillyrae*, assuming the latter is correctly associated with the sequence attributed to it. *Simplicillium obclavatum*, originally described as *Acremonium obclavatum*, provides the only other clavicipitaceous species in Fig. 2 representing a named species of *Acremonium*.

Below the *Clavicipitaceae* in Fig. 1B is a clade of ambiguous affinities containing *Acremonium guillematii*, *A. minutisporum* and *A. vitellinum*. This group also appears as two to three unaffiliated clades in Fig. 2C. An insignificant branch in Fig. 1B subtends *Acremonium exiguum*, *A. psammosporum*, and an isolate identified as *A. potronii*. In Fig. 2D, just *A. exiguum* and the *A. potronii* entity remain associated while *Acremonium psammosporum* segregates into a basal hypocrealean clade of its own in Fig. 2E.

The *Nectriaceae* is represented by *Nectria cinnabarina* in Fig. 1B along with the ex-type isolate of the tropical opportunistic pathogen of humans, *Acremonium recifei*. Fig. 2D shows *A. recifei* subtending multiple taxa with three non-type isolates splitting off as a separate clade. These clades have approximately the same status in the *Nectriaceae* as the genus *Nalanthamala*, including *N. diospyri*, the former *Acremonium diospyri*. Another nectriaceous *Acremonium* in Fig. 2D is *A. tsugae*, which is closely related

to *Cylindrocarpon cylindroides*. The broad morphotaxonomic concept of *Acremonium berkeleyanum* is polyphyletic consisting of isolates placed in the nectriaceous genus *Cosmospora* (Fig. 2D). *Acremonium berkeleyanum sensu lato* is represented in Fig. 2D by the newly recombined *Cosmospora* species, *C. lavitskiae* and *C. khandalensis* based on the ex-type isolates of *Gliomastix lavitskiae* and *Cephalosporium khandalense* (Gräfenhan *et al.* 2011). Another purported synonym of *A. berkeleyanum*, a *Cadophora* isolate received as *A. butyri* CBS 301.38, falls outside the *Hypocreales* (Fig. 1C).

Basally in the *Hypocreales* in Fig. 1B, *Acremonium roseolum* appears in loose association with *Stachybotrys* species. In Fig. 2D, it appears in a clade along with the teleomorph *Scopinella solani* and three *Acremonium inflatum* isolates, including CBS 403.70, an atypical, catenate-conidial isolate identified at CBS as *A. atrogriseum*. Nearby but statistically unlinked clades include *Stachybotrys* and allied fungi such as *Peethambara spirostriata* and *Didymostilbe echinofibrosa* (Castlebury *et al.* 2004).

Acremonium nigrosclerotium represents an isolated *Acremonium* near the families *Hypocreaceae* and *Niessliaceae* (Fig. 1B). In Fig. 2D, *A. nigrosclerotium* is intercalated among two genotypes ascribed to *N. exilis*, and loosely associated (77 % bootstrap) with *Acremonium pseudozeylanicum* and the type culture of *Cephalosporium ballagii*, currently in synonymy with *Acremonium charticola* (Gams 1971).

A distant outlier is *Acremonium lichenicola* at the bottom of Fig. 1C. This isolate, CBS 425.66, chosen to represent this species in lieu of ex-type material, blasts as a pezizalean fungus with affinities to another hyaline, phialidic fungus, *Phialophora alba*.

A number of genera in addition to *Acremonium* were investigated for possible affinity with *Acremonium* clades as shown in Fig. 2. The sporodochial genus *Sarcopodium* was investigated and found to split into two groups (Fig. 2C, D). One isolate identified as *S. circinatum* grouped with *Sarcopodium circinoseiferum* and *S. vanillae* in a widely separated clade along with *Lanatonectria* teleomorphs and a sequence identified as *Pseudonectria rousseiliana* (Fig. 2C). This clade appeared in LSU sequencing to be independently situated within the *Hypocreales*. *Acremonium rhabdosporum* appeared as a statistically unsupported, possible distant relative. The other two isolates of *S. circinatum* formed a clade near *Myrothecium* in the *Stachybotrys/Peethambara* clade (Fig. 2D). Also appearing in this clade was *Parasarcopodium ceratocaryi*, a monotypic genus recently described by Mel'nik *et al.* (2004).

DISCUSSION

The main morphotaxonomic groundwork for *Acremonium* as conceived in the late 20th century was laid by Gams (1971) in his monograph *Cephalosporium-artige Schimmelpilze (Hyphomycetes)*. This monograph was radically more comprehensive than previous treatments of the species and was followed by several key adjunct studies, including but not limited to Gams & Lacey (1972), Gams (1975), and Ito *et al.* (2000). Gams' studies were based on a meticulous morphological observation scheme that involved growing species on appropriate media, *e.g.*, oatmeal agar, and then making camera lucida drawings that could be directly compared with subsequent isolates. The comparison was done by superimposing the virtual image of the new isolate directly over the camera lucida drawings of previous isolates drawn

at the same scale. This highly rigorous approach was necessary for a group of hyphomycetous fungi so morphologically simplified as *Acremonium*.

Gams (1971, 1975) also discovered a subtle character that allowed him to associate dark-conidial species, monographed by Dickinson (1968) as the genus *Gliomastix*, with numerous biologically related hyaline-conidial species. This character was "chondroid hyphae," which could be seen under the microscope as hyphae with wall thickenings, and which makes colonies somewhat resistant to being cut with a scalpel. The species Gams (1971) united using this character are, for the most part, grouped in the *Gliomastix/Bionectria* clade referred to earlier in this study.

Despite the rigorous approach and the discovery of new, useful characters, a number of the morphotaxonomic species names ultimately were applied in the CBS collection to phylogenetically divergent organisms. Six distinct taxa from CBS investigated in this study were identified as *A. persicinum*; three are now seen phylogenetically to fall within the *Gliomastix* clade and three sort elsewhere. These taxa are mostly directly visible as *A. persicinum* isolates in Fig. 2. Names without quotation marks are consistent with the type, while names in quotation marks sort into other phylogenetic groups. An exception is represented by CBS 149.62. This isolate, the ex-type of *Cephalosporium purpurascens*, was listed by Gams (1971) as a synonym of *A. persicinum*. Five taxa in Fig. 2 were labeled *A. potronii* in CBS, and four were called *A. strictum*. Within both *A. potronii* and *A. strictum*, as conceived morphologically, some isolates fall within *A. sclerotigenum*. The name *A. alternatum* was applied to four species, three of them visible in Fig. 2, plus isolates of *A. sclerotigenum* with catenulate conidia. "*Acremonium blochii*" was applied to three different species.

Phylogenetic analysis compared to the morphological treatment of *Acremonium*

Gams (1971, 1975) divided *Acremonium* into three major sections, *Simplex*, a name later updated as the type section *Acremonium*, *Gliomastix*, and *Nectrioidea*. Of these sections, only *Gliomastix* withstands phylogenetic scrutiny as a unit, albeit a loosely associated one.

The type section *Acremonium* contained four widely phylogenetically scattered major clades (Fig. 2), specifically the *A. sclerotigenum* clade, *Sarcocladium* clade, *A. curvulum* clade, and *A. breve* clade. As seen best in Fig. 1, the *Sarcocladium* clade and the *A. breve* and *A. curvulum* clades comprise a distinct group that falls within the *Hypocreales* but outside any currently recognised family. *Acremonium sclerotigenum* falls into a distinct clade within the *Bionectriaceae* that also contains *Emericellopsis* and *Geosmithia*. This clade also includes about half the investigated CBS isolates identified as the type species of *Acremonium*, *A. alternatum*, including CBS 407.66 as well as some isolates such as CBS 223.70 revealed as morphological variants of *A. sclerotigenum*. Despite the substantial phylogenetic distance between *A. sclerotigenum* and *A. strictum*, relatively glabrous, cylindrical-conidial isolates of *A. sclerotigenum* not producing sclerotia on special media (lupine stem agar according to Gams, 1971, later replaced at CBS by nettle stem agar) are essentially micromorphologically indistinguishable from *A. strictum*. Table 1 shows CBS 287.70 O as an *A. sclerotigenum* isolate identified in CBS as *A. strictum*; ITS sequencing studies of additional strains (data not shown) have found two more such isolates, CBS 319.70 D and CBS 474.67.

The convergence among isolates of phylogenetically remote species is remarkable. An unknown proportion of the literature on *A. strictum* is based on studies of *A. sclerotigenum*. For example, in a study influential in medical mycology, Novicki *et al.* (2003) labeled ITS-sequenced isolates of *A. sclerotigenum* in GenBank as "*Acremonium strictum* genogroup II." The complexity of *A. sclerotigenum*, not its earliest valid name, goes beyond the scope of this paper. Perdomo *et al.* (2010) have recently investigated the diversity of medically important isolates within this species.

Besides the four clades mentioned above, *Acremonium* sect. *Acremonium* species also make up the non-synnematal anamorphs of the *Emericellopsis* clade, most of the *A. fusidioides* clade, and most of the small *A. camptosporum*, *A. exiguum*, *A. minutisporum*, *A. pinkertoniae*, and *A. pseudozeylanicum* clades. Gams (1975) accommodated *A. byssoides*, now known to belong in *Simplicillium lanosoniveum* (Zare & Gams 2001), in *Acremonium* sect. *Acremonium*, while commenting that it was suggestive of *Verticillium* sect. *Prostrata*, later recognised as *Simplicillium* (Zare & Gams 2001). He withheld *A. byssoides* from *Verticillium* because the colony margin was relatively flat and slightly fasciculate, rather than cottony. To some extent *Acremonium* sect. *Acremonium* was based on keying out all the relatively flat or fasciculate *Acremonium*-like species together provided that they lacked the dark conidia or chondroid hyphae of *Gliomastix*.

Acremonium sect. *Nectrioidea* as delineated by Gams (1971) included many *Nectria sensu lato* anamorphs. Some of these species are now placed in the genus *Cosmospora* by Gräfenhan *et al.* (2011). These include members of the *A. berkeleyanum* complex as well as *A. arxii* and *A. cymosum*. *Acremonium falciforme* in *A. sect. Nectrioidea* had already been recognised as a member of the *Fusarium solani* complex (Summerbell & Schroers 2002) and *A. diospyri* had been transferred into *Nalanthamala* along with other nectriaceous species (Schroers *et al.* 2005). *Acremonium tsugae* appears to be a microconidial *Cylindrocarpon* species. The *Acremonium recifei* complex still remains as an undisposed major group of nectriaceous *Acremonium* species originally included in *A. sect. Nectrioidea*. The placement of *A. sect. Nectrioidea* species *A. alcalophilum*, *A. brunnescens*, *A. furcatum*, *A. nepalense*, *A. restrictum*, and *A. stromaticum* in the *Plectosphaerellaceae* has already been shown by Zare *et al.* (2007). *Acremonium apii* also has been shown to belong to this family as a synonym of *Verticillium alboatrum*, and its ex-type strain, CBS 130.51, was used as the representative isolate of that species by Zare *et al.* (2007).

Other anomalous elements of *A. sect. Nectrioidea* include *A. crotocinigenum* in the *Trichothecium* clade, *A. radiatum* in the phylogenetically isolated *A. breve* clade, *A. biseptum* in the *A. cerealis* clade near *Gliomastix*, *A. salmoneum* in the *Emericellopsis* clade near *Stilbella fimetaria*, *A. chrysogenum* in a bionectriaceous clade containing cleistothecial teleomorphs such as *Nigrosabulum*, *A. rutilum* in a clade otherwise containing isolates identified as *A. persicinum*, and a non-type *A. hyalinulum* isolate in another clade peripheral to *Gliomastix*. When *Sarocladium zeae* as *A. zeae* in *A. sect. Nectrioidea* was compared to the phylogenetically related *S. kiliense* as *A. kiliense* in *A. sect. Acremonium* by Gams (1971, p. 16), he noted that the latter species may sometimes also be strongly branched and thus resemble the former. The exigencies of dichotomous morphological keying tended to sort closely related species into widely separated Sections of the genus.

The main heterogeneous element included in Gams' (1971) original concept of sect. *Gliomastix* was the "*Striatosporium* series." These were later distinguished as the separate genus *Sagenomella* (Gams 1978). Both *Sagenomella* and the recently described genus

Phialosimplex are members of the *Eurotiales* (Sigler *et al.* 2010). Another anomalous element in sect. *Gliomastix*, *Acremonium atrogriseum*, is here removed to the *Cephalothecaceae*.

Other species included by Gams (1971, 1975) in *A. sect. Gliomastix* that can now be seen to be separated from the *Gliomastix/Bionectria* clade include "*Cephalosporium purpurascens*," synonymised by Gams (1971) with *A. persicinum* as well as *A. brachyphenium*, *A. hennebertii*, *A. incrustatum*, and *A. inflatum*. Species outside the *Gliomastix/Bionectria* clade that have well developed chondroid hyphae include *A. hennebertii* and *A. incrustatum*.

TAXONOMY

The main purpose of this study is to provide a phylogenetic overview of *Acremonium* plus distinctive LSU sequences to render the described species recognisable in molecular studies. In addition, some taxonomic changes are undertaken.

What is *Acremonium*?

The first task at hand is to establish what *Acremonium* is. The lectotype species of *Acremonium* is *A. alternatum* as designated by Gams (1968). Gams (1968) studied and illustrated the type material used by Link (1809) in describing *A. alternatum*. This material consists of a thin fungal mycelium colonising a birch leaf. In choosing living cultures that best approximated this specimen, Gams (1968) listed four isolates. From among these, one is chosen with a dried culture to be designated here as the epitype with an ex-epitype culture. This is CBS 407.66, which groups with the ex-type isolate of *Cephalosporium malorum*, synonymised by Gams (1971) with *A. charticola*, as well as with *A. sordidulum* and *A. charticola* in the poorly defined *A. sclerotigenum/Geosmithia* clade. Use of the corresponding dried culture CBS H-20525 as an epitype specimen serves nomenclatural stability because the genus name *Acremonium* is then used to designate a large group of species currently accepted in *Acremonium*.

Other candidate isolates included CBS 308.70 (called "Kultur 1127"), which died out and was replenished from its degenerated, nonsporulating subculture MUCL 8432, now also called CBS 114602. As a degenerated isolate, it makes poor potential epitype material. Another isolate mentioned by Gams (1968), CBS 406.66, is conspecific with CBS 114602 and in good condition. Both isolates are included in a clade relatively distant from any other *Acremonium* group but deeply basal to the *Sarocladium* and *A. breve* clades, as seen in Fig. 1A. If *Acremonium* were epitypified with one of these isolates, the generic name might be restricted to this single species. The final isolate is CBS 223.70, an isolate that, despite its catenate conidia, is conspecific with the type of *A. sclerotigenum* (100 % ITS sequence identity; GenBank AJ621772 for CBS 124.42 is essentially identical to *A. sclerotigenum*, U57674, CBS 223.70). Isolate CBS 223.70 strongly resembles pale greenish grey coloured, sclerotium-forming isolates identified as *A. egyptiacum* (e.g., CBS 734.69), which are also conspecific with *A. sclerotigenum*. It differs by not forming sclerotia. Catenate conidia may or may not be produced in this group and the greenish grey colonies produced by chain-forming isolates have explicitly been connected with *A. egyptiacum*, not *A. alternatum*. One other taxon that Gams (1971, 1975) consistently identified as *A. alternatum*, a species in the *A. fusidioides* clade, is represented by CBS 831.97

and 381.70A. These isolates have the disadvantage of not having been explicitly compared with the type material. In addition, this clade is related to several clades with known teleomorphs, e.g., *Emericellopsis* and *Nigrosabulum*, and anamorphs, e.g., *Stilbella* and *Geosmithia*. In a revised nomenclatural system, it would root *Acremonium* as a broad unitary genus name encompassing the teleomorphs and complex anamorphs. Ultimately, it might epitypify *Acremonium* strictly as a genus name for the *A. fusidioides* clade.

Acremonium alternatum Link : Fr., Mag. Ges. naturf. Fr. Berlin 3: 15. 1809 : Fries, Syst. Mycol. 3: 425. 1832.

Holotype: Germany, Rostock, on leaf litter of *Betula*, collected by Ditmar, B-type specimen labeled in Link's handwriting.

Epitype designated here: Austria, Stangensteig near Innsbruck, ex *Ustulina deusta*, W. Gams, Dec. 1965, CBS-H 20525 dried culture of CBS 407.66, ex-epitype living culture CBS 407.66.

Additional genera recognised here

Based on these analyses, three genera are represented in sufficient detail and with high bootstrap support to be formally recognised here. In most cases, the genera and clades are not sufficiently populated with their constituent members without analysis of additional sequences. For example, the *Emericellopsis* clade is missing 12 of its 13 species including two identified as *E. minima* (Zuccaro *et al.* 2004) as well as one of its two *Stanjemonium* species.

Gliomastix

The core clade of *Gliomastix* including the type species is well delimited with a 92 % bootstrap value even in the very conservative LSU analysis. Although Gams (1971) placed this genus into *Acremonium*, several authors have recognised *Gliomastix*. Most notably, Matsushima (1975) placed *Acremonium maseei* and *A. polychromum* into *Gliomastix* and Lechat *et al.* (2010) linked *G. fusigera* with *Hydropisphaera bambusicola*. As circumscribed in this paper, the phylogenetically supported *Gliomastix* differs from previous morphological concepts by excluding several distantly related species such as *Acremonium cerealis* and *A. inflatum*. The closely related *A. persicinum* clade may also be included as suggested by Supplemental fig. 6E in Schoch *et al.* (2009) and discussed above. At the moment, we recognise only four species from the present study in *Gliomastix*. An additional species, published while the present manuscript was in preparation, *Acremonium tumulicola* (Kiyuna *et al.* 2010), should also be included in this concept of *Gliomastix*.

The generic characters do not differ significantly from those summarised in the generic diagnosis of Dickinson (1968).

1. Type species. *Gliomastix murorum* (Corda) S. Hughes, Canad. J. Bot. 36: 769. 1958.

Basionym: *Torula murorum* Corda, Icon. Fung. 2: 9. 1838.

- ≡ *Sagrahamala murorum* (Corda) Subram., Curr. Sci. 41: 49. 1972.
- ≡ *Acremonium murorum* (Corda) W. Gams, *Cephalosporium*-artige Schimmelpilze (Stuttgart): 84. 1971.
- = *Torula chartarum* Corda, Icon. Fung. 2: 9. 1839.
- ≡ *Gliomastix chartarum* (Corda) Guég. Bull. Soc. Mycol. France 21: 240. 1905.

For additional synonyms, see Gams (1971). The type species of *Gliomastix*, *G. chartarum*, is a synonym of *G. murorum* (Hughes

1958). The distinction between *G. murorum* var. *murorum* having conidia in chains and *G. murorum* var. *felina* having conidia in mucoid heads does not appear to be supported by phylogenetic analysis. *Gliomastix murorum* var. *felina* isolates originally described as *Graphium malorum* (ex-type CBS 154.25) and *Torula cephalosporioides* (ex-type CBS 378.36) are molecularly confirmed as synonyms of *G. murorum* (Fig. 2B). Recently, Kiyuna *et al.* (2010) neotypified *Gliomastix felina* (Marchal) Hammill, recombined as *Acremonium felinum* (Marchal) Kiyuna, An, Kigawa & Sugiy., with CBS 147.81. The sequences deposited in GenBank, e.g., AB540562, suggest that this isolate represents *G. roseogrisea*. The new combination is reduced to synonymy with that species below.

2. *Gliomastix maseei* (Sacc.) Matsush., Icon. microfung. Matsush. lect. (Kobe): 76. 1975.

Basionym: *Trichosporium maseei* Sacc., Syll. Fung. 22: 1356. 1913

- [= *Trichosporium aterrimum* Masee, Bull. Misc. Inform. 1899: 167 non (Corda) Sacc. 1886]
- ≡ *Acremonium maseei* (Sacc.) W. Gams, *Cephalosporium*-artige Schimmelpilze (Stuttgart): 83. 1971.

The name lacks an ex-type isolate. Although the isolate (CBS 794.69) sequenced is basal to the *Gliomastix* clade (Fig. 2B), it appears to be a suitable to serve as the basis for epitypification.

Holotype of *Trichosporium maseei*: India, Punjab, Changa Manga, on *Morus indica*, Jan. 1898, J. Gleadow, ex Herb. Masee, K; isotypes IMI 49,214 = IMI 87,346.

Epitype designated here: Italy, Turin, isolated from rabbit dung, A. Fontana, CBS H-8244, ex-epitype culture CBS 794.69.

3. *Gliomastix polychroma* (J.F.H. Beyma) Matsush., Icon. microfung. Matsush. lect. (Kobe): 77. 1975.

Basionym: *Oospora polychroma* J.F.H. Beyma, Verh. K. Ned. Akad. Wetensch., Sect. 2, 26 (2): 5. 1928.

- ≡ *Sagrahamala polychroma* (J.F.H. Beyma) Subram., Curr. Sci. 41: 49. 1972.
- ≡ *Acremonium polychromum* (J.F.H. Beyma) W. Gams, *Cephalosporium*-artige Schimmelpilze (Stuttgart): 81. 1971.

Additional synonyms are given by Gams (1971). This clade includes the ex-type isolate of *Oospora polychroma*, basionym of *G. polychroma*, CBS 181.27 (Fig. 2B). *Periconia tenuissima* var. *nigra* is confirmed as a synonym via inclusion of its ex-type isolate CBS 151.26 (Fig. 2B). The status of the different isolate, CBS 617.94, from banana, requires further clarification. This isolate may be related to *Acremonium musicola*, a species not represented in CBS.

4. *Gliomastix roseogrisea* (S.B. Saksena) Summerbell, **comb. nov.** MycoBank MB519588.

Basionym: *Cephalosporium roseogriseum* S.B. Saksena, Mycologia 47: 895. 1956 [1955].

- ≡ *Acremonium roseogriseum* (S.B. Saksena) W. Gams [as 'roseogriseum'], *Cephalosporium*-artige Schimmelpilze (Stuttgart): 87. 1971.
- = *Acremonium felinum* (Marchal) Kiyuna, An, Kigawa & Sugiy., Mycoscience 52: 13. 2010.

Gliomastix roseogrisea, like *G. murorum*, has a variety of conidial forms including conidia in chains and conidia of various shapes in mucoid heads. This plasticity of form recalls the situation mentioned

above for *A. sclerotigenum* and may represent a relatively common situation in acremonioid species. As another example Gams (1971) lists "*Gliomastix murorum* var. *felina pro parte* in Dickinson in Mycol Pap. 115: 16, 1968" as an additional synonym of this taxon.

As mentioned above in the discussion of the genus, Kiyuna *et al.* (2010) recently neotypified *Gliomastix felina* (basonym *Periconia felina* Marchal, Bull. Soc. R. Bot. Belg. 34:141. 1895) with CBS 147.81, an isolate collected by Hammill (1981). This isolate is a typical *G. roseogrisea*, a taxon not studied by Kiyuna *et al.* (2010).

5. *Gliomastix tumulicola* (Kiyuna, An, Kigawa & Sugiy.) Summerbell, **comb. nov.** MycoBank MB519599.

Basonym: *Acremonium tumulicola* Kiyuna, An, Kigawa & Sugiy., Mycoscience 52: 13. 2010.

This newly described species is phylogenetically placed by its original authors (Kiyuna *et al.* 2010) in the *Gliomastix* clade and comparison of sequences confirms that placement. Although this information was received too late to include this species in our phylogenetic analyses, the species is placed in *Gliomastix*.

Sarocladium

The genus *Sarocladium* was described for two pinkish coloured fungal pathogens causing sheath blast of rice (Gams & Hawksworth 1976). The drawings in that paper and the photographs in Bills *et al.* (2004) show structures that overlap with those produced by the phylogenetically related *A. kiliense*, *A. strictum*, and *A. zeae*. As in *Fusarium*, plant pathogenic fungi that sporulate on above-ground plant parts are likely to produce upright, branching sporulating structures with mucoid conidia suggesting dispersal by insects that fly from plant to plant. Species with habitats where water flux or microarthropod movement may be important in dispersal, e.g., various *Acremonia* occurring in soil or *Fusarium domesticum* growing on cheese, may have simplified conidiogenous structures. Bills *et al.* (2004) suggested that the generic placement of *Acremonium kiliense* and *A. strictum* should be re-examined in light of their close relationship with *Sarocladium oryzae*.

The genus *Sarocladium* is delineated here to include several species previously recognised in *Acremonium*, as seen in Figs 1 and 2. In Fig. 2, where phylogenetic signal is relatively low, *Sarocladium* tepidly (84 % bootstrap) links to the *A. bacillisporum* clade. In Fig. 1, it links with a 99 % bootstrap value. Phylogenetic clustering algorithms often insert the *A. bacillisporum* clade between *A. strictum* and *A. kiliense* due to certain apo- or plesiomorphies shared with one or the other of these two members of the *A. strictum* clade (data not shown). On the other hand, the next most closely related clade in Fig. 1, the *A. breve/A. curvulum* clade, has ITS sequences with substantial sections that are difficult to align with those of the *A. bacillisporum* and *A. strictum* clades, indicating considerable evolutionary distance.

The genus *Sarocladium* is emended here to include those species that belong to the *A. strictum* and *A. bacillisporum* clades. The generic name *Sagrahamala* is not a contender for this group because the type species is the unrelated *Acremonium luzulae*. In addition *Acremonium luzulae* is a species in need of epitypification, because, as shown in the present study, more than one phylogenetic species is encompassed under the name.

Sarocladium W. Gams & D. Hawksw., Kavaka 3: 57. 1976 [1975].

Colonies on 2 % malt extract agar slimy-glabrous to moderately floccose to deeply dusty, sometimes ropy; with, in Gams' terminology (Gams 1971), phalacrogenous, nematogenous, to plectonematogenous conidiation; growing 13–25 mm in 10 d at 20 °C, whitish to pinkish to salmonaceous or, when conidia are formed in chains, sometimes acquiring vivid conidial mass colouration such as ochraceous or greenish glaucous; reverse pale to pinkish orange to pale grey-brown, rarely greenish-blue. Conidiogenous apparatus ranging from adelophialides, solitary orthotropic phialides to conidiophore structures with one or a few branches, or with cymose branching or occasionally with one or two ranks of loosely structured verticils, sometimes with repeated branching extending to 90 µm long. Phialides subulate, aculeate to acerose, straight, slightly curved, or undulate, thin- and smooth-walled, 15–60(–75) µm long, tapering from a basal width of 1.2–2.5 µm, with minimal collarette; conidia borne in mucoid heads or dry chains, notably longer than broad, l/w mostly 2.2–7.0, cylindrical to fusiform to bacilliform, aseptate, smooth-walled, with rounded or tapered-truncate ends, 3.5–8(–14) × 0.5–2 µm. Chlamydospores present or absent, when present relatively thick-walled, smooth or slightly roughened, globose to ellipsoidal, intercalary or terminal, mostly solitary, occasionally in short chains, 4–8 µm. *Internal transcribed spacer sequence* mostly with distinctive CGGTGCGGCC motif in mid-ITS2 region.

Several species of *Sarocladium* are noted for melanogenesis yielding ochre-brown to dark grey-brown colony reverse colours on Sabouraud agar: *S. glaucum*, *S. kiliense*, and *S. zeae* (Gams 1971). In the case of *S. kiliense*, this melanogenesis has the result that most mycetoma cases feature black "grains" or sclerotium-like balls of compacted fungal hyphae (Summerbell 2003); melanogenesis is a well known pathogenicity factor in fungal diseases of humans and animals (Gómez & Nosanchuk 2003). As recognised here *Sarocladium* yields a remarkable unity of species with elongated conidia and phialides. Several species including *S. kiliense*, *S. oryzae*, and *S. strictum* form adelophialides prominently, at least in some isolates; acremonioid species outside *Sarocladium* usually lack this character.

The recognised species are given below. *Acremonium implicatum* may belong here, but the species lacks living ex-type or representative material. The "*A. implicatum*" isolate that grouped in *Sarocladium*, CBS 243.59, is noted by Gams (1971) as an authentic isolate of *Fusidium terricola* J.H. Mill., Giddens & A.A. Foster and this name could be used if *A. implicatum sensu* Gams is revealed as polyphyletic. The other "*A. implicatum*" isolate, CBS 397.70B, included in this study is not a *Sarocladium*; rather it is a member of the *A. exiguum* clade.

1. Type species. *Sarocladium oryzae* (Sawada) W. Gams & D. Hawksw., Kavaka 3: 58. 1976 [1975].

A description and synonymy are given by Gams & Hawksworth (1975). Bills *et al.* (2004) synonymised *Sarocladium attenuatum* with *S. oryzae* based on the reported identity of the ITS sequence of its ex-type isolate, CBS 399.73, with that of representative isolates of *S. oryzae*. We resequenced the ITS region of CBS 399.73 and obtained a sequence differing from Bills *et al.* (AY566995) by 6 base-pairs and 2 gaps. Some of the base pairs in our sequence appeared to be symplesiomorphies shared with *A. kiliense* or *A. strictum* but not *S. oryzae*, rather than random mutations or possible miscalls. Our resequencing of unequivocal *S. oryzae* isolates CBS 180.74 and CBS 361.75 yielded results consistent with those of Bills *et al.* (2004). The status of *S. attenuatum* thus requires further study.

2. *Sarocladium bacillisporum* (Onions & Barron) Summerbell, **comb. nov.** MycoBank MB519589.

Basionym: *Paecilomyces bacillisporus* Onions & G.L. Barron, *Mycol. Pap.* 107: 11. 1967.

≡ *Acremonium bacillisporum* (Onions & G.L. Barron) W. Gams, *Cephalosporium*-artige Schimmelpilze (Stuttgart): 72. 1971.

≡ *Sagrahamala bacillispora* (Onions & G.L. Barron) Subram., *Curr. Sci.* 41: 49. 1972.

This species was described by Gams (1971). It is easily confused with *Verticillium leptobactrum*, which can be relatively floccose and loosely structured although some isolates are very dense and slow-growing (Gams, 1971). In addition colonies of *S. bacillisporum* at maturity have a pinkish colouration.

3. *Sarocladium bactrocephalum* (W. Gams) Summerbell, **comb. nov.** MycoBank MB519590.

Basionym: *Acremonium bactrocephalum* W. Gams, *Cephalosporium*-artige Schimmelpilze (Stuttgart): 44. 1971.

As indicated by Gams (1971) this uncommon species is closely related to *S. strictum*, but is distinguished morphologically by its long, narrow conidia. It is molecularly distinguishable by LSU sequences.

4. *Sarocladium glaucum* (W. Gams) Summerbell, **comb. nov.** MycoBank MB519591.

Basionym: *Acremonium glaucum* W. Gams, *Cephalosporium*-artige Schimmelpilze (Stuttgart): 68. 1971.

This species was described by Gams (1971). The ex-type culture CBS 796.69 indicates that this species belongs in *Sarocladium*.

5. *Sarocladium kiliense* (Grütz) Summerbell **comb. nov.** MycoBank MB519592.

Basionym: *Acremonium kiliense* Grütz, *Dermatol. Wochenschr.* 80: 774. 1925.

= *Cephalosporium incoloratum* Sukapure & Thirum., *Sydowia* 19: 171. 1966 [1965].

= *Acremonium incoloratum* (Sukapure & Thirum.) W. Gams, *Cephalosporium*-artige Schimmelpilze (Stuttgart): 50. 1971.

Additional synonyms and a description of *S. kiliense* are given by Gams (1971) and Domsch *et al.* (2007); the species is also extensively illustrated by de Hoog *et al.* (2000). The ITS sequence of the ex-type strain of *Acremonium incoloratum*, CBS 146.62, is identical to that of the ex-type of *S. kiliense*, CBS 122.29 (data not shown). Though isolate CBS 146.62 is unusual in colour and lacks well differentiated chlamydospores that generally occur in *S. kiliense*, there is no phenetic difference profound enough to suggest that additional genes must be examined to be certain of their synonymy.

The sequences deposited in GenBank by Novicki *et al.* (2003) for their "*Acremonium strictum* genogroup III" (ITS: AY138846; LSU: AY138484) are actually of *S. kiliense*.

6. *Sarocladium ochraceum* (Onions & Barron) Summerbell, **comb. nov.** MycoBank MB519593.

Basionym: *Paecilomyces ochraceus* Onions & G.L. Barron, *Mycol. Pap.* 107: 15. 1967.

≡ *Acremonium ochraceum* (Onions & G.L. Barron) W. Gams, *Cephalosporium*-artige Schimmelpilze (Stuttgart): 67. 1971.

≡ *Sagrahamala ochracea* (Onions & G.L. Barron) Subram. & Pushkaran, *Kavaka* 3: 89. 1975 [1976].

This species was described by Gams (1971). We analysed the ex-type culture, CBS 428.67.

7. *Sarocladium strictum* (W. Gams) Summerbell, **comb. nov.** MycoBank MB519594.

Basionym: *Acremonium strictum* W. Gams, *Cephalosporium*-artige Schimmelpilze (Stuttgart): 42. 1971.

Descriptions of *S. strictum* are given by Gams (1971) and Domsch *et al.* (2007). The type isolate of *S. strictum* was confirmed in this genus (Fig. 2C). Of the three isolates illustrated by Gams (1971) under *A. strictum*, CBS 287.70 D, is confirmed by sequencing as *S. strictum*. The only isolate of *Acremonium zonatum* in this study, CBS 565.67, turned out to have an ITS sequence identical to that of *S. strictum*. This is one of three isolates examined by Gams (1971) as *A. zonatum*. He stated that another isolate, CBS 145.62, appeared to be *A. kiliense*, but that examination of herbarium material suggested that this species had been growing on the natural substrate mixed with the real *A. zonatum* and had been isolated accidentally. One herbarium specimen examined by Gams (1971) showed septate conidia, something not otherwise seen in *Sarocladium*, so there may indeed be a real *A. zonatum*. It is not clear if *A. zonatum sensu* Gams is a unified concept or a designation of various acremonioid fungi forming leaf spots on tropical plants. In any case, the known connection of the genus *Sarocladium* with phytopathogenesis and endophytism as in *S. zeae* makes it plausible that species such as *S. strictum* and *S. kiliense* may play a role in plant disease.

8. *Sarocladium zeae* (W. Gams & D.R. Sumner) Summerbell, **comb. nov.** MycoBank MB519595.

Basionym: *Acremonium zeae* W. Gams & D.R. Sumner, in Gams, *Cephalosporium*-artige Schimmelpilze (Stuttgart): 121. 1971.

This economically important maize endophyte species fits the description given by Gams (1971) as a fungus with felty to shaggy colonies. Two *S. zeae* isolates with more flattened colonies were accessed in CBS as *A. strictum*. Both CBS 646.75 and 226.84 were from maize and found to be producers of pyrrocidine metabolites as well as dihydroresorcylide, characteristic of *S. zeae* (Wicklow *et al.* 2008). Pyrrocidines are antagonistic to *Aspergillus flavus* and *Fusarium verticillioides* in maize inflorescences and are thus important in the ecology and economic significance of *S. zeae*. An additional *A. strictum* isolate, CBS 310.85, is also *S. zeae* as evidenced by pyrrocidine production, but has not yet been sequenced (Wicklow *et al.* 2008).

Trichothecium

A significant theme of the current volume is the pioneering of a new approach to dikaryomycete nomenclature: the unitary naming of genus-level clades based on the oldest valid generic name, whether originally anamorphic or teleomorphic in nature (see discussion in Gräfenhan *et al.* 2011). Because the first named fungi were often species prominently in contact with humans and their environs and because the first names usually were attached to the most frequently seen reproductive state, there is considerable wisdom to using the oldest name applied to either aspect of the holomorph in constructing a unitary nomenclature.

The genus *Trichothecium* makes an excellent example, since the system used here preserves the best known species name in the group. A unitary system giving teleomorphs primacy

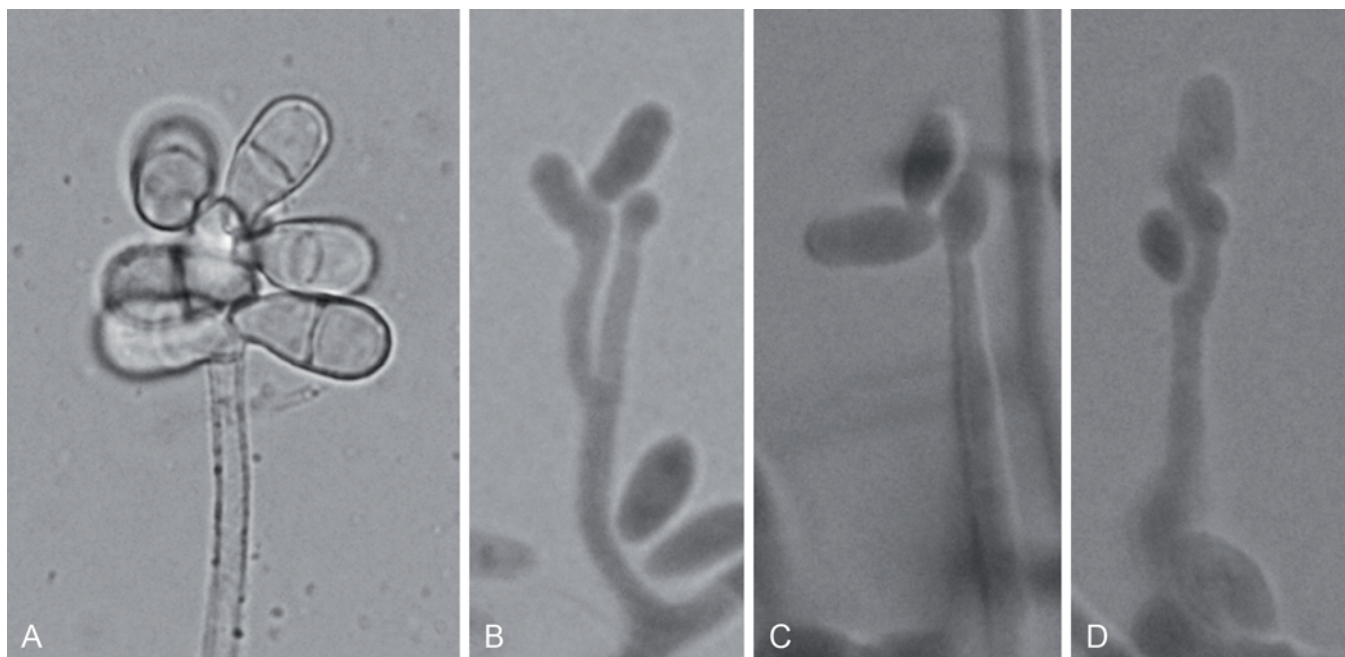


Fig. 3. A. *Trichothecium roseum* CBS 113334 showing retrogressive conidiation. B-D. conidiogenesis in "*Trichothecium indicum*"/*Leucosphaerina indica* CBS 123.78 showing retrogressive development (B), phialidic development (C) and sympodial development (D).

would replace the familiar "*T. roseum*" with a *Leucosphaerina* name. A system that retains primacy for morphology, which is the only reasonable basis for dual nomenclature in the molecular era, would divide the *Trichothecium* clade into four genera, as is the case today. One of those genera, *Acremonium*, would be quintessentially artificial and almost completely divorced from evolutionary biological relationships. With increased emphasis on genomes, proteomes, and metabolomes, a focus on polyphyletic elements of microscopic shape seems counterproductive. Every new system of nomenclatural change will entail both fortunate and infelicitous changes and will receive some resistance in scientific communities. A nomenclatural system based on phylogeny will be considerably more stable than any previous system. The interests of all would be best served if it bridged gracefully out of pre-phylogenetic taxonomy, preserving as many familiar elements as possible. *Trichothecium roseum*, a constant from 1809 to today, is one of those elements that is worthy of being preserved.

The small, tightly unified clade of *Trichothecium* includes isolates with three different anamorphic forms, currently classified as *Acremonium* (phialoconidia), *Spicellum* (sympodial blastoconidia), and *Trichothecium* (retrogressive blastoconidia). The associated teleomorph, *Leucosphaerina indica*, produces anamorphic forms described as "*Acremonium* or *Sporothrix*" (Suh & Blackwell 1999). These morphs are illustrated by von Arx *et al.* (1978). The range of anamorphic forms produced by *L. indica* overlaps those produced by all the anamorphic species in the clade (Fig. 3).

The four species studied here, *Trichothecium roseum*, *Acremonium crocacinigenum*, *Leucosphaerina indica*, and *Spicellum roseum*, have recently been associated with a fifth, newly described species, *Spicellum ovalisporum*. The dendrogram produced by Seifert *et al.* (2008) makes it clear that *S. ovalisporum* is related to *S. roseum* and is certainly a member of the *Trichothecium* clade. In parallel with the revision of the genus *Microcera* by Gräfenhan *et al.* (2011), this clade is redefined here as a genus with the oldest valid generic name, *Trichothecium*.

As Fig. 2 shows, the second described *Leucosphaerina* species, *L. arxii*, is in the distant *Acremonium pinkertoniae* clade and is closely related to *Bulbithecium hyalosporum*. Malloch (1989)

commented that it differed from *L. indica* by lacking sheathing gel around the ascospores and by having an *Acremonium* anamorph.

Trichothecium Link : Fr., Mag. Gesell. naturf. Freunde, Berlin 3: 18. 1809.

= *Spicellum* Nicot & Roquebert, Revue Mycol., Paris 39: 272. 1976 [1975].

= *Leucosphaerina* Arx, Persoonia 13: 294. 1987.

Older synonymy for the genus is given by Rifai & Cooke (1966).

Colonies on malt extract agar 20–40 µm after 7 d at 24 °C, white to salmon orange or salmon pink (Methuen 6-7A2, 4-5A2-3), felty, floccose or lanose, sometimes appearing powdery with heavy conidiation. Ascomatal initials, if present, produced on aerial mycelium, irregularly coiled. *Ascospores* spherical or nearly so, non-ostiolate, colourless or slightly pink, 150–300 µm; ascospore wall persistent, nearly colourless, 10–13 µm thick, of indistinct hyphal cells; *asci* uniformly distributed in centrum, clavate to spherical, with thin, evanescent walls, 8-spored, 10–13 µm wide; ascospores ellipsoidal or reniform, with refractile walls and a 1–1.5 µm broad gelatinous sheath, smooth or finely striate, hyaline, yellow to pink *en masse*, without germ pore, 6–7 × 3–4 µm. *Conidiogenous apparatus* varying by species, featuring one or more of: conidiophores up to 125 µm long × 2–3.5 µm wide, septate, unbranched, with terminal phialides 10–65 µm long, producing unicellular, hyaline, smooth-walled phialoconidia, obovate, oblong or cylindrical 4.4–7.4 µm; or conidiophores up to 175 µm long, unbranched or uncommonly with one or more branches, retrogressive, shortening with production of each conidium, with each conidial base subsuming a portion of conidiophore apex; conidia 0–1-septate, ellipsoidal or ovate, with a decurved, abruptly narrowed basal hilum terminating in a distinct truncate end, 5–12 × 3–6.5 µm; or conidiophores ranging from unicellular conidiogenous cells to multicellular, multiply rebranched apparati extending indefinitely to beyond 200 µm long; terminal cells 9–37 µm long with a cylindrical basal part and a narrowing, apically extending conidiogenous rachis sympodially proliferating and producing oval to ellipsoidal to cylindrical or allantoid conidia 3.5–11 × 1.5–3.5 µm, with truncate bases. *Chlamydospores* absent

or present, when present mostly in intercalary chains, hyaline, smooth or finely warted, 5–8(–12) μm wide. *Internal transcribed spacer sequence* generally with distinct CACAAACCTCGCG motif in ITS2 region. The numerical position varies by species and isolate, cf. position 476 in GenBank record EU445372, ITS for *Spicellum ovalisporum* ex-type isolate DAOM 186447.

Various taxa described as *Trichothecium* need to be investigated to determine their relationship to this phylogenetic genus. For example, *Trichothecium luteum* and *T. parvum*, not represented by living cultures, should be investigated, as should *T. campaniforme* and *T. plasmoparae*, which are represented by one isolate each in CBS. *Trichothecium domesticum* was recently redisposed as *Fusarium domesticum* (Bachmann *et al.* 2005). Of teleomorphs reported to have *Trichothecium* anamorphs, *Heleococcum japonense* is unrelated to the *Trichothecium* clade (Fig. 2; the sequence is erroneously listed as *H. japonicum* in GenBank); rather it is related to *Gliomastix* and *Hydropisphaera*. A *Trichothecium* state of *Hypomyces subiculosus* (syn. *H. trichothecoides*) was described, but *Hypomyces*, a member of the *Hypocreaceae*, is a remote relative of the *Trichothecium* clade within the *Hypocreales* (Fig. 2).

1. Type species. *Trichothecium roseum* (Pers.) Link, Mag. Gesell. naturf. Freunde, Berlin 3: 18. 1809.
Synonymy is given in MycoBank record MB164181.

2. *Trichothecium crotocinigenum* (Schol-Schwarz) Summerbell, Seifert, & Schroers, comb. nov. MycoBank MB519596.

Basionym: *Cephalosporium crotocinigenum* Schol-Schwarz, Trans. Brit. Mycol. Soc. 48: 53. 1965.

\equiv *Acremonium crotocinigenum* (Schol-Schwarz) W. Gams, *Cephalosporium*-artige Schimmelpilze (Stuttgart): 112. 1971.

As pointed out by Seifert *et al.* (2008, supplement), *T. crotocinigenum* has long been known to produce crotocin mycotoxins that are similar to the trichothecenes produced by *T. roseum* and *T. sympodiale*. The production of similar mycotoxins reinforces the argument for phylogenetic nomenclature such that scientific names reflect true relationships.

3. *Trichothecium indicum* (Arx, Mukerji & N. Singh) Summerbell, Seifert, & Schroers, comb. nov. MycoBank MB519597.

Basionym: *Leucosphaerina indica* (Arx, Mukerji & N. Singh) Arx, *Persoonia* 13: 294. 1987.

With phylogenetic hindsight, the photographs of this species' anamorph in the original description by von Arx *et al.* (1978) can be seen to suggest *Acremonium*, *Spicellum*, and *Trichothecium*.

4. *Trichothecium ovalisporum* (Seifert & Rehner) Seifert & Rehner, comb. nov. MycoBank MB519598.

Basionym: *Spicellum ovalisporum* Seifert & S.A. Rehner, *Fungal Planet*: no. 28. 2008.

The relationship of the recently described *Spicellum ovalisporum* to *T. sympodiale* is not clear. The ex-type of *T. sympodiale* (CBS 227.76) was resequenced for the ITS region; the resulting sequence differed from the GenBank record AB019365 by 7 gaps and one C \leftrightarrow T transition. The sequence had 100 % identity

with ITS sequence record EU445372 for the ex-type isolate of *S. ovalisporum*, DAOM 186447. Two more CBS isolates accessed as *S. roseum*, CBS 119.77 and CBS 146.78, also gave ITS sequences identical to EU445372. A recent partial ITS sequence made by K.A. Seifert for CBS 227.76 agreed with our sequence (data not shown). No one has thus been able to replicate the sequence given for *S. roseum* in AB019365 and we are uncertain of its significance, even though a similar sequence (GenBank AB019364) has been attributed to two other *S. roseum* isolates in the JCM collection by the same depositor, G. Okada. If the fallibilities of earlier sequencing chemistries are involved in these discrepancies, *S. ovalisporum* may be more closely related to *T. sympodiale* than is evident in the literature. Preliminary results have shown at least one substitution distinguishing the translation elongation factor α sequence of *S. ovalisporum* from that of *T. sympodiale* (Rehner, data not shown). Based on comparative morphology and habitat, the authors of *S. ovalisporum* are confident that their species is distinct, and thus the new combination is included here with their sanction.

5. *Trichothecium sympodiale* Summerbell, Seifert, & Schroers, nom. nov. MycoBank MB 519600.

Basionym: *Spicellum roseum* Nicot & Roquebert, *Revue Mycol.*, Paris 39: 272. 1976 [1975].

If recombined into *Trichothecium*, *Spicellum roseum* would result in a homonym of the type species, thus a new name is needed.

***Acremonium atrogriseum* and *Acremonium cf. alternatum* CBS 109043 in the *Cephalothecaceae*: a study in comparative morphology vs. phylogeny**

Acremonium atrogriseum and an isolate identified as *Acremonium cf. alternatum* CBS 109043 belong in the *Cephalothecaceae* (Fig. 1C). This isolate is a white coloured acremonioid fungus forming fusoid conidia in long chains. It also forms small, dark structures that may be aborted ascumata initials. Sequencing of the ITS region (data not shown) reveals it to be a representative of *Phialemonium obovatum*. It is identical in all bases but one to the ITS sequence of ex-type strain CBS 279.76 (AB278187) and in all but two bases to another isolate of this species, CBS 116.74. *Phialemonium obovatum* was described as having conidia in slimy heads (Gams & McGinnis 1983). CBS 109043 shows that either mucoid heads or chains may be formed in this species, as in *Acremonium persicinum*, *A. sclerotigenum*, and *Gliomastix murorum*. Gams (1971) mentions an isolate of *Sarocladium bacillisporum* that tends to produce mucoid heads. Colonies producing conidia in chains often have a different look from their head-forming conspecifics; the mass colour of the chains may give the colony colours not found in the species descriptions, such as the chalk white colour of CBS 109043 in contrast to the normally pale greenish brown of *P. obovatum* or the greenish grey of *A. sclerotigenum* isolate 223.70, in contrast to the normal pale salmon pink of non-catenate *A. sclerotigenum*.

Existing morphological keys and descriptions not just in *Acremonium* but in all the acremonioid fungi need to be cautiously and skeptically interpreted. At the very least, identifications for publication should be tested by sequencing. We hope that the LSU sequences in this paper will provide the foundation for a phylogenetically sound approach to the systematics and ecology of acremonioid fungi.

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