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 the genus Acremonium acrogenatum, the genus Emericellopsis and Acremonium and relatives. The second clade contains the genera Gliomastix sensu stricto and Biometria. 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 brevis and related species plus Acremonium curvulum and related species. This sequence information allows the revision of these genera. Gliomastix is revived for five species, G. murorum, G. polychroma, G. roseogrisea, and G. masseei. Sarocladium is extended to include all members of the phylogenetically distinct A. strictum clade including the medically important A. kilimani and the protective maize endophyte A. zeae. Also included in Sarocladium are members of the phylogenetically delimited Acremonium bacillicarpum 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 crotocinigenum, Sclerotium roseum, and teleomorph Leuconosphaeria indica. Outside the Hypocreales, numerous Acremonium-like species fall into the Plectosphaerellaceae, and A. aegyptium falls into the Cephalothecaceae.

Key words: Acremonium, Cephalothecaceae, Gliomastix, holomorph concept, Leuconosphaeria, nomenclature, Sarco podium, Sarocladium, Trichothecium.

Taxonomic novelties: Trichothecium symподиálе Summerbell, Seifert, & Schroers, nom. nov.; Gliomastix roseogrisea (S.B. Saksena) Summerbell, comb. nov., Gliomastix tumulicola (Kyuno, An, Kigawa & Sugiy.) Summerbell, comb. nov., Sarocladium bacillicarpum (Onions & Barron) Summerbell, comb. nov., Sarocladium bactrocephalum (W. Gams) Summerbell, comb. nov., Sarocladium kilimani (Grütz) Summerbell, comb. nov., Sarocladium ochraceum (Onions & Barron) Summerbell, comb. nov., Sarocladium strictum (W. Gams) Summerbell, comb. nov., Sarocladium zeae (W. Gams & D.R. Summerbell) comb. nov., Trichothecium crotocinigenum (Schof-Schwarz) Summerbell, Seifert, & Schroers, comb. nov., Trichothecium indicum (Arc, Muerj & 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. cucbitacearum 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 Sordariales 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 Gabarmania (Microascales), Lecythophora (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 neotyphoidaeic 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 vilior, 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 strains of (nucLSU and nucSSU, respectively) and 166 taxa, including 56 of the large and small subunits of the nuclear ribosomal RNA gene.

The second is a one-gene analysis focusing on the strains of (nucLSU and nucSSU, respectively) and 166 taxa, including 56 of the large and small subunits of the nuclear ribosomal RNA gene.

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, nucLSU 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 nucLSU and 36 nucSSU (Table 1). For the two-gene dataset, one nucLSU and 41 nucSSU sequences were missing. After exclusion of ambiguous regions and introns, the two-gene dataset included 2 955 characters (1 250 nucLSU 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.
Fig. 1A–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.
Simplicillium lanosoniveum CBS 321.72
Cordyceps cardinalis
Acremonium camptosporum CBS 756.69
Paecilomyces lilacinus 2
Elaphocordyceps capitata
Elaphocordyceps ophioglossoides
Balansia henningsiana
Epichloe typhina
Claviceps purpurea
Acremonium guillenatii CBS 766.68
Acremonium minutisporum CBS 147.62
Acremonium vitellinum CBS 792.69
Acremonium exiguum CBS 587.73
"Acremonium potronii" CBS 416.68
Acremonium psammosporum CBS 590.63
Acremonium recifei CBS 137.35
Nectria cinnabarina
Acremonium roseolum CBS 289.62
Stachybotrys chartarum
Stachybotrys subsimplex
Myrothecium roridum 1
Peethambara spirostriata
Pseudonecklace rousselliana
Acremonium nigrosclerotium CBS 154.72
Hypocrea americana
Hypocrea lutea
Sphaerostilbella berkeleyana
Niesslia exilis
Nectria haematococca
Chaetosphaerella phaeostroma
Melanospora tiffanii
Melanospora zamiae
Lindra thalassiae
Lulworthia grandispora
"Acremonium alabamense" CBS 456.75
Cercophora terricola
Apiosordaria verruculosa
Cercophora striata
Podospora decipiens
Bombardia bombarda
Lasiosphaeria ovina
Cercophora newfieldiana
Gelasinospora tetrasperma
Neurospora crassa
Immersiella immersa
Lasiosphaeria hispida
Podospora fibrinocaudata
Strattonia carbonaria
Camarops amorpha
Camarops microspora
Camarops tubulina
Camarops ustulinoides
Chaetosphaeria ovoidea
Menispora tortuosa
Melanochaeta hemipsila
Lasiosphaeria nitida
Linocarpon appendiculatum

Fig. 1. (Continued).
“Acremonium cf. alternatum” CBS 109043
Acremonium atrogriseum CBS 544.79
Acremonium atrogriseum CBS 981.70
Acremonium atrogriseum CBS 774.97
Acremonium atrogriseum CBS 507.82
Acremonium atrogriseum CBS 733.70
Acremonium atrogriseum CBS 252.68
Acremonium atrogriseum CBS 604.67
Acremonium atrogriseum CBS 306.85
Coniochaeta ostrea
Coniochaeta savoyi
Coniochaeta discoidea
Annulatascus triseptatus
Fragosphaeria purpurea
Ophiostoma piliferum 1
Ophiostoma stenoceras
Papulosa amerospora

Ophiostomales

Apiognomonia errabunda
Plagiostoma euphorbiae
Cryptodiaporthe aesculi
Gnomonia gnomon
Cryptosporella hypodermia
Melanconis aini
Melanconis stibostoma
Melanconis marginalis
Chromendothia citrina
Endothia gyrosa
Chrysoporthe cubensis
Diaporthe eres
Diaporthe phaseolorum
Mazzantia napelli
Leucostoma niveum
Valsella salicis
Valsaambiens
Cryphonectria parasitica

Diaporthales

Anthostomella torosa
Apiospora montagnei
Diatrype disciformis
Eutypa lata
Graphostroma platystoma
Xylaria acuta
Xylaria hypoxylon
Seynesia erumpens

Xylariales

Leotia lubrica
Microglossum rufum
Pseudeurotium zonatum
Chalara aurea
Acremonium butyri (?) CBS 301.38
Acremonium lichenicola CBS 425.66

Leotiomycetes (outgroup)

0.01 substitutions/site
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 |
|---------------------------------|--------------------|--------|--------|-------|
| *Acremoniella lutzi* T          | CBS 103.48         | HQ231971 | –      | Ex-type of *Acremoniella lutzi* |
| *Acremonium acutatum* T         | CBS 682.71         | HQ231965 |        |       |
| *Acremonium alabamense*         | CBS 456.75         | HQ231972 | –      | Ex-type of *Acremonium alcalophilum* |
| *Acremonium alcalophilum* T     | CBS 114.92         | HQ231973 | –      | Ex-type of *Acremonium alcalophilum* |
| *Acremonium alternatum* T      | CBS 407.66         | HQ231988 |        |       |
| “*Acremonium alternatum*”       | CBS 381.70A        | HQ231986 |        |       |
|                                | CBS 408.66         | HQ231987 | HQ232178 |       |
|                                | CBS 831.97         | HQ231989 |        |       |
|                                | CBS 114602         | HQ231990 |        |       |
| “*Acremonium cf. alternatum*”   | CBS 109043         | HQ231974 | –      |       |
| *Acremonium antarcticum*       | CBS 987.87         | HQ231975 | –      |       |
| *Acremonium atrogriseum* T     | CBS 604.67         | HQ231981 | –      | Ex-type of *Phaeoscopulariopsis atrogrisea* |
|                                | 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 | –      |       |
| *Acremonium biseptum* T        | CBS 750.69         | HQ231998 |        | Ex-type of *Acremonium biseptum* |
| “*Acremonium blochii*”          | CBS 324.33         | HQ231999 |        |       |
|                                | CBS 424.93         | HQ232000 | HQ232181 |       |
|                                | CBS 427.93         | HQ232001 | HQ232182 |       |
|                                | CBS 993.69         | HQ232002 |        |       |
| *Acremonium borodinense* T     | CBS 101148         | HQ232003 |        | Ex-type of *Acremonium borodinense* |
| *Acremonium brachypenium* T    | CBS 866.73         | HQ232004 |        |       |
| *Acremonium breve* T           | CBS 150.62         | HQ232005 | HQ232183 | Ex-type of *Cephalosporium roseum var. breve* |
| *Acremonium brunnescens* T     | CBS 559.73         | HQ231966 | HQ232184 | Ex-type of *Acremonium brunnescens* |
| *Acremonium butyri* T          | CBS 301.38         | HQ231967 | –      | Ex-type of *Tilachlidium butyri*; synonym of *Cadophora malorum* |
| *Acremonium camptosporum* T    | CBS 756.69         | HQ232008 | HQ232186 | Ex-type of *Acremonium camptosporum* |
|                                | CBS 677.74         | HQ232007 |        |       |
|                                | CBS 757.69         | HQ232009 |        |       |
|                                | CBS 835.91         | HQ232010 |        |       |
|                                | CBS 890.85         | HQ232011 |        |       |
| *Acremonium cavaareanum*       | CBS 758.69         | HQ232012 |        |       |
| *Acremonium cerealis*          | CBS 207.65         | HQ232013 |        | Ex-type of *Gliomastix guttuliformis* |
|                                | CBS 215.69         | HQ232014 |        |       |
| *Acremonium chrysogenum* T     | CBS 144.62         | HQ232017 | HQ232187 | Ex-type of *Cephalosporium chrysogenum* |
| *Acremonium cucurbitacearum* T | CBS 683.88         | HQ231968 | –      | Ex-type of *Acremonium cucurbitacearum* |
| *Acremonium curvulum* T        | CBS 430.66         | HQ232026 | HQ232188 | Ex-type of *Acremonium curvulum* |
|                                | 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 |        |       |
| “*Acremonium aff. curvulum*”   | CBS 100551         | HQ232031 |        |       |
|                                | CBS 113275         | HQ232033 |        |       |
| *Acremonium egyptiacum*        | CBS 303.64         | HQ232034 | HQ232189 |       |
| *Acremonium exiguum* T         | CBS 587.73         | HQ232035 | HQ232190 | Ex-type of *Acremonium exiguum* |
| *Acremonium exuvium* T         | UAMH 9995          | HQ232036 |        |       |
| *Acremonium flavum* T          | CBS 596.70         | HQ232037 | HQ232191 | Ex-type of *Acremonium flavum* |
| *Acremonium fuci*              | UAMH 6508          | HQ232038 |        |       |
| *Acremonium furcatum* T        | CBS 122.42         | AY378154 | HQ232192 | Ex-type of *Acremonium furcatum* |
Table 1. (Continued).

| Currently assigned species name | Collection numbers | nuclLSU   | nuclSSU   | Notes                                                                 |
|---------------------------------|--------------------|-----------|-----------|----------------------------------------------------------------------|
| *Acremonium fusidioides* T      | CBS 840.68         | HQ232039  |           | Ex-type of *Paecilomyces fusidioides*                               |
| *Acremonium gamsii* T           | CBS 726.71         | HQ232040  | HQ232193  | Ex-type of *Acremonium gamsii*                                      |
| *Acremonium guillematii* T      | CBS 766.69         | HQ232042  | HQ232194  | Ex-type of *Acremonium guillematii*                                 |
| *Acremonium hansfordii* T       | CBS 390.73         | HQ232043  |           |                                                                       |
| *Acremonium hennebertii* T      | CBS 768.69         | HQ232044  | HQ232195  | Ex-type of *Acremonium hennebertii*                                 |
| "Acremonium implicatum"         | CBS 271.36         | HQ232045  | HQ232196  | Authentic strain of *Fusarium tenuicola*                             |
| *Acremonium incrustatum* T      | CBS 397.70B        | HQ232047  |           |                                                                       |
| *Acremonium inflatum* T         | CBS 159.70         | HQ232049  |           |                                                                       |
| *Acremonium guillematii* T      | CBS 766.69         | HQ232042  | HQ232194  | Ex-type of *Acremonium guillematii*                                 |
| *Acremonium gamsii* T           | CBS 391.70         | HQ232043  |           |                                                                       |
| *Acremonium guillematii* T      | CBS 243.59         | HQ232046  | HQ232196  |                                                                       |
| "Acremonium implicatum"         | CBS 379.70B        | HQ232047  |           |                                                                       |
| "Acremonium impeditum"          | CBS 157.70         | HQ232049  |           |                                                                       |
| "Acremonium inflatum" T         | CBS 212.69         | HQ232050  |           | Ex-type of *Glomastix inflata*                                       |
| "Acremonium luzulae"            | CBS 113.69         | HQ232057  |           |                                                                       |
| "Acremonium minisporum" T       | CBS 113.69         | HQ232057  |           |                                                                       |
| "Acremonium pseudopergamentum"  | CBS 243.59         | HQ232050  |           | Ex-type of *Glomastix inflata*                                       |
| *Acremonium persicinum* T       | CBS 169.65         | HQ232072  |           |                                                                       |
| "Acremonium persicinum*"        | CBS 147.62         | HQ232069  | HQ232199  | Ex-type of *Cephalosporium minutisporum*                             |
| "Acremonium persicinum*"        | CBS 295.70A        | HQ232075  |           |                                                                       |
| "Acremonium persicinum*"        | CBS 295.70M        | HQ232076  |           |                                                                       |
| "Acremonium persicinum*"        | CBS 330.80         | HQ232078  |           |                                                                       |
| "Acremonium persicinum*"        | CBS 378.70A        | HQ232079  |           |                                                                       |
| "Acremonium persicinum*"        | CBS 378.70D        | HQ232081  |           |                                                                       |
| "Acremonium persicinum*"        | CBS 378.70 E       | HQ232082  |           |                                                                       |
| "Acremonium persicinum*"        | CBS 439.66         | HQ232083  |           |                                                                       |
| "Acremonium persicinum*"        | CBS 469.67         | HQ232084  |           |                                                                       |
| "Acremonium persicinum*"        | CBS 101649         | HQ232085  |           |                                                                       |
| "Acremonium persicinum*"        | CBS 102349         | HQ232086  |           |                                                                       |
| "Acremonium persicinum*"        | CBS 243.59         | HQ232050  |           | Ex-type of *Paecilomyces persicinus*                                 |
| "Acremonium persicinum*"        | CBS 169.65         | HQ232072  |           |                                                                       |
| "Acremonium persicinum*"        | CBS 295.70A        | HQ232075  |           |                                                                       |
| "Acremonium persicinum*"        | CBS 295.70M        | HQ232076  |           |                                                                       |
| "Acremonium persicinum*"        | CBS 330.80         | HQ232078  |           |                                                                       |
| "Acremonium persicinum*"        | CBS 378.70A        | HQ232079  |           |                                                                       |
| "Acremonium persicinum*"        | CBS 378.70D        | HQ232081  |           |                                                                       |
| "Acremonium persicinum*"        | CBS 378.70 E       | HQ232082  |           |                                                                       |
| "Acremonium persicinum*"        | CBS 439.66         | HQ232083  |           |                                                                       |
| "Acremonium persicinum*"        | CBS 469.67         | HQ232084  |           |                                                                       |
| "Acremonium persicinum*"        | CBS 101649         | HQ232085  |           |                                                                       |
| "Acremonium persicinum*"        | CBS 102349         | HQ232086  |           |                                                                       |
| "Acremonium persicinum*"        | CBS 243.59         | HQ232050  |           | Ex-type of *Paecilomyces persicinus*                                 |
| "Acremonium pseudopusiozeylanicum* T | CBS 590.63      | HQ232100  | HQ232204  | Ex-type of *Acremonium psammosporum*                                |
| "Acremonium psammosporum* T     | CBS 590.63         | HQ232100  | HQ232204  | Ex-type of *Acremonium psammosporum*                                |
| "Acremonium psammosporum* T     | CBS 560.73         | HQ232101  |           | Ex-type of *Acremonium psammosporum*                                |
| "Acremonium psammosporum* T     | CBS 789.69         | HQ232103  |           |                                                                       |
| "Acremonium psamycolatum* T     | CBS 432.62         | HQ232104  | HQ232205  | Ex-type of *Cephalosporium acremonium var. radiatum*                |
| "Acremonium psamycolatum* T     | CBS 137.35         | HQ232106  | HQ232206  | Ex-type of *Cephalosporium recifei*                                  |
| "Acremonium psamycolatum* T     | CBS 135.71         | HQ232105  |           |                                                                       |
| "Acremonium psamycolatum* T     | CBS 220.84         | HQ232107  |           |                                                                       |
| "Acremonium psamycolatum* T     | CBS 362.76         | HQ232108  |           |                                                                       |
| "Acremonium psamycolatum* T     | CBS 402.89         | HQ232109  |           |                                                                       |
| "Acremonium psamycolatum* T     | CBS 411.91         | HQ232110  |           |                                                                       |
| "Acremonium psamycolatum* T     | CBS 442.66         | HQ232111  |           |                                                                       |
| "Acremonium psamycolatum* T     | CBS 541.89         | HQ232114  |           |                                                                       |
| "Acremonium psamycolatum* T     | CBS 555.73         | HQ232115  |           |                                                                       |
| "Acremonium psamycolatum* T     | CBS 596.74         | HQ232116  |           |                                                                       |
| "Acremonium psamycolatum* T     | CBS 976.70         | HQ232117  |           |                                                                       |
| "Acremonium psamycolatum* T     | CBS 400.85         | HQ232025  |           |                                                                       |
| "Acremonium psamycolatum* T     | CBS 505.94         | HQ232027  |           |                                                                       |
| "Acremonium psamycolatum* T     | CBS 465.77         | HQ232113  |           |                                                                       |
| "Acremonium psamycolatum* T     | CBS 482.78         | HQ232112  |           |                                                                       |
| Currently assigned species name | Collection numbers | nucLSU    | nucSSU    | Notes                                      |
|--------------------------------|--------------------|-----------|-----------|--------------------------------------------|
| Acremonium restrictum T        | CBS 110348         | HQ232118  |           |                                            |
| Acremonium rhabdosporum T      | CBS 178.40         | HQ232119  |           |                                            |
| Acremonium roseolum T          | CBS 438.66         | HQ232120  |           | Ex-type of Acremonium rhabdosporum         |
| Acremonium rutulum T           | CBS 289.62         | HQ232123  | HQ232207  | Ex-type of Paecilomyces roseolus           |
| Acremonium salmonaneum T       | CBS 396.66         | HQ232124  | HQ232208  | Ex-type of Acremonium rutulum              |
| Acremonium sclerotigenum T     | CBS 721.71         | HQ232125  |           | Ex-type of Acremonium salmonineum         |
| Acremonium polychroma          | CBS 124.42         | HQ232126  | HQ232209  | Ex-type of Cephalosporium sclerotigenum    |
| Acremonium roseogriseum        | CBS 270.86         | HQ232127  |           |                                            |
| Acremonium murorum             | CBS 281.80         | HQ232128  |           |                                            |
| Acremonium roseogriseum        | CBS 384.65         | HQ232129  |           |                                            |
| Acremonium roseogriseum        | CBS 786.69         | HQ232130  |           |                                            |
| Acremonium roseogriseum        | CBS 100816         | HQ232131  |           |                                            |
| Acremonium roseogriseum        | OMH F1646.97       | HQ232132  |           |                                            |
| Acremonium roseogriseum        | OMH F2365.97       | HQ232133  |           |                                            |
| Acremonium roseogriseum        | OMH F2969.97       | HQ232134  |           |                                            |
| Acremonium roseogriseum        | OMH F3961.97       | HQ232135  |           |                                            |
| Acremonium roseogriseum        | CBS 287.7O         | HQ232140  |           | In CBS as Acremonium restrictum            |
| Acremonium roseogriseum        | CBS 379.7O         | HQ232095  |           | In CBS as Acremonium polychroma           |
| Acremonium roseogriseum        | CBS 223.70         | HQ231985  |           | In CBS as Acremonium alternatum            |
| Acremonium roseogriseum        | CBS 385.73         | HQ231336  |           | Ex-type of Acremonium sordidulum           |
| Acremonium roseogriseum        | CBS 314.72         | HQ23156   |           |                                            |
| Acremonium roseogriseum        | CBS 136.33         | HQ23137   | HQ232210  | Ex-type of Cephalosporium spinosum         |
| “Acremonium strictum”          | CBS 106.23         | HQ23138   |           |                                            |
| “Acremonium strictum”          | CBS 147.49         | HQ23139   |           |                                            |
| Acremonium sordidulum T        | CBS 863.73         | HQ23143   |           | Ex-type of Acremonium sordidulum           |
| Acremonium tectonae T          | CBS 725.87         | HQ23144   |           | Ex-type of Acremonium tectonae             |
| Acremonium thermophilum T      | CBS 734.71         | HQ23145   |           | Ex-type of Acremonium thermophilum         |
| Acremonium tsuga T             | CBS 788.69         | HQ23146   |           | Ex-type of Acremonium tsuga                |
| Acremonium tubakii T           | CBS 790.69         | HQ23148   |           | Ex-type of Acremonium tubakii              |
| “Acremonium tubakii”           | CBS 824.69         | HQ23149   |           |                                            |
| Acremonium verruculosum T      | CBS 989.69         | HQ23150   |           | Ex-type of Acremonium verruculosum         |
| Acremonium zeylanicum          | CBS 792.69         | HQ23151   | HQ232212  | Ex-type of Acremonium zeylanicum           |
| Acremonium zonatum             | CBS 746.73         | HQ23154   |           |                                            |
| Acremonium zonatum             | CBS 565.67         | HQ23155   |           |                                            |
| “Cephalosporium acremonium var. cereum” T | CBS 140.62         | HQ23147   |           | Ex-type of Cephalosporium acremonium var. cereum. In CBS as Acremonium tubakii |
| “Cephalosporium acremonium var. funiculorum” T | CBS 141.62         | HQ232053  |           | Ex-type of Cephalosporium acremonium var. funiculorum. In CBS as Acremonium kilerense |
| “Cephalosporium ballagii” T    | CBS 134.33         | HQ232016  |           | Ex-type of Cephalosporium ballagii. In CBS as Acremonium charticola |
| “Cephalosporium malorum” T     | CBS 117.25         | HQ232015  |           | Ex-type of Cephalosporium malorum. In CBS as Acremonium charticola |
| “Cephalosporium purpurascens” T | CBS 149.62         | HQ232071  |           | Ex-type of Cephalosporium purpurascens. In CBS as Acremonium periscinum |
| Cosmospora khandalensis T      | CBS 356.65         | HQ231996  |           | Ex-type of Cephalosporium khandalensis. In CBS as Acremonium berkeleyanum |
| Cosmospora lavitskiae T        | CBS 530.68         | HQ231997  |           | Ex-type of Gilomasix lavitskiae. In CBS as Acremonium berkeleyanum |
| Gilomasix masseei             | CBS 794.69         | HQ232060  |           | In CBS as Acremonium masseei               |
| Gilomasix murorum             | CBS 154.25         | HQ232063  |           | Ex-type of Graphium malorum. In CBS as Acremonium murorum var. felina |
| Gilomasix murorum             | CBS 195.70         | HQ232064  |           | In CBS as Acremonium murorum var. felina   |
| Gilomasix murorum             | CBS 119.67         | HQ232066  |           | In CBS as Acremonium murorum var. murorum  |
| Gilomasix murorum             | CBS 157.72         | HQ232067  |           | In CBS as Acremonium murorum var. murorum  |
| Gilomasix murorum             | CBS 378.36         | HQ232068  |           | Ex-type of Torula cephalosporoides. In CBS as Acremonium murorum var. murorum |
| Gilomasix polychroma T        | CBS 181.27         | HQ232091  |           | Ex-type of Oospora polychroma. In CBS as Acremonium polychromum |
| Gilomasix polychroma T        | CBS 151.26         | HQ232090  |           | Ex-type of Periconia tenuissima var. nigra. In CBS as Acremonium polychromum |
| Gilomasix polychroma T        | CBS 617.94         | HQ232093  |           | In CBS as Acremonium polychromum           |
| “G. roseogrisea” T            | CBS 134.56         | HQ232121  |           | Ex-type of Cephalosporium roseogriseum. In CBS as Acremonium roseogriseum |
| “G. roseogrisea” T            | CBS 279.79         | HQ232122  |           | In CBS as Acremonium roseogriseum          |
| “G. roseogrisea” T            | CBS 213.69         | HQ232092  |           | In CBS as Acremonium polychromum           |
| “G. roseogrisea” T            | CCF CC 226570      | AV283559  |           | Identified as Acremonium murorum var. felina |
| “G. roseogrisea” T            | CBS 211.69         | HQ232065  |           | In CBS as Acremonium murorum var. felina   |
| Lanatospora flavolana          | CBS 230.31         | HQ232157  |           |                                            |
Table 1. (Continued).

| Currently assigned species name | Collection numbers | nucLSU | nucSSU | Notes |
|---------------------------------|--------------------|--------|--------|-------|
| Lanatonecra filocentans CBS 113461 | HZQ2158            |        |        | Ex-type of Leucosphaerina arxii |
| Leucosphaeria arxii T CBS 737.84 | HZQ2159            |        |        | Ex-type of Cephalosporum d雅思y = Acremonium d雅思y |
| Nalanthamala d雅思y CBS 560.89 | HZQ2160            |        |        | Ex-type of Cephalosporum d雅思y |
| Nectria breithii T CBS 496.67 | HZQ2162            |        |        | Ex-type of Nectria richthii |
| Neocosmospora endophytica AR 2674 | U17411             |        |        | Anamorph is Acremonium fungicola |
| Paeclomyces ilacinus CBS 101068 | HZQ2163            | HZQ2214 |        | Atypical monophalidic isolate, Acremonium+E402-like |
| Pochonia rubbiaCBS 102853 | HZQ2164            |        |        | Atypical isolate |
| Sarocladium cincinatum CBS 376.81 | HZQ2167            |        |        | |
| Sarocladium cincinatum CBS 587.92 | HZQ2168            |        |        | |
| Sarocladium cincinatum CBS 114068 | HZQ2169            |        |        | |
| Sarocladium cincinisetifer CBS 100251 | HZQ2170         |        |        | |
| Sarocladium cincinisetifer CBS 100252 | HZQ2171            |        |        | |
| Sarocladium cincinisetifer CBS 100998 | HZQ2172            |        |        | |
| Sarocladium cincinisetifer CBS 101116 | HZQ2173            |        |        | |
| Sarocladium vaniliae CBS 100582 | HZQ2174            |        |        | |
| Sarocladium attenuatum T CBS 399.73 | HZQ2165            |        |        | Ex-type of Sarocladium attenuatum |
| Sarocladium bacillusporum T CBS 425.67 | HZQ2192            | HZQ2179 |        | Ex-type of Acremonium bacillusporum |
| Sarocladium bactrocephalum T CBS 749.69 | HZQ2194            | HZQ2180 |        | Ex-type of Acremonium bactrocephalum |
| Sarocladium glaucum CBS 796.69 | HZQ2195            |        |        | |
| Sarocladium kiliense T CBS 122.29 | HZQ2198            |        |        | Ex-type of Acremonium kiliense |
| Sarocladium kiliense T CBS 146.62 | HZQ2197            |        |        | Ex-type of Cephalosporum incoloratum. In CBS as Acremonium incoloratum |
| Sarocladium ochraceum T CBS 428.67 | HZQ2156            |        |        | Ex-type of Cephalosporum incarnatum. In CBS as Acremonium ochraceum |
| Sarocladium oryzae CBS 180.74 | HZQ2166            |        |        | |
| Sarocladium strictum T CBS 346.70 | HZQ2141            | HZQ2211 |        | Ex-type of Acremonium strictum |
| "Sarocladium cf. strictum" JY03-006 | HZQ2142            |        |        | |
| Sarocladium zeae T CBS 801.69 | HZQ2152            | HZQ2213 |        | Ex-type of Acremonium zeae |
| Simplicillium lansonivium CBS 321.72 | HZQ2167            |        |        | Ex-type of Acremonium byssoides |
| Simplicillium obclavatum CBS 311.74 | HZQ2175            |        |        | Ex-type of Acremonium obclavatum |
| Trichothecium crocinigerum T CBS 129.64 | HZQ2108            |        |        | Ex-type of Acremonium crocinigerum |
| "Trichothecium indicum"/ Leucosphaerina indica CBS 123.78 | AF096194 |        |        | Ex-type of ‘Leucosphaera’ indica |
| Trichothecium roseum DAOM 209997 | U89991             |        |        | |
| Trichothecium symподiala ATCC 36477 | U68889             |        |        | In CBS as Spegicillum roseum |
| Verticillium alboamum CBS 130.51 | HZQ2197            | –      |        | Ex-type of Cephalosporum api, in CBS as Acremonium api |
| Verticillium aplcubica CBS 102139 | HZQ248107          |        |        | |
| Verticillium leptobactrum CBS 103951 | HZQ2193            |        |        | In CBS as Acremonium cf. bacillisporum |

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 Chaelomomoidea. Outside these groups Acremonium atrigospernum, represented by numerous conspecific isolates, belongs to the family Cephalothecaceae (Fig. 1C), along with Albertiniella polyrhilica and Cephalothecis sulphurea; this family is sister to the Coniochaetales. Another Acremonium species, A. thermophilum, falls into the Cephalothecaceae clade grouping with Albertiniella polyrhilica. 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. zeae. 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 telemorphs 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 nucLSU 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.
Acremonium biseptum CBS 750.69
Acremonium cerealis CBS 207.65
Acremonium cerealis CBS 215.69
“Acremonium blochii” CBS 424.93
Acremonium persicinum CBS 378.70E
Acremonium persicinum CBS 378.70D
Acremonium persicinum CBS 378.70A
Acremonium persicinum CBS 102349
Acremonium persicinum CBS 169.65
Acremonium persicinum CBS 295.70M
Acremonium persicinum CBS 295.70A
Acremonium persicinum CBS 439.66
Acremonium persicinum CBS 101694
Acremonium persicinum CBS 469.67
Acremonium persicinum CBS 330.80
Acremonium verruculosum CBS 989.69
Hydropisphaera erubescens 2
Hydropisphaera erubescens 1
Gliomastix masseei CBS 794.69
Gliomastix murorum CBS 157.72
Gliomastix murorum CBS 195.70
Gliomastix murorum CBS 378.36
Gliomastix murorum CBS 154.25
Gliomastix polychroma CBS 151.26
Gliomastix polychroma CBS 181.27
Gliomastix polychroma CBS 617.94
Gliomastix roseogrisea CBS 211.69
Gliomastix roseogrisea CBS 213.69
Gliomastix roseogrisea CBS 134.56
Gliomastix roseogrisea CBS 279.79
Gliomastix roseogrisea CCFC 226570
Heleococcum japonicum
Hydropisphaera peziza 2
Hydropisphaera peziza 1
Roumegueriella rufula
Selinia pulchra
“Acremonium hyalinulum” CBS 271.36
“Nalanthamala squamulosa” CBS 203.73
Nedria zonata
“Acremonium ledeaneae” CBS 725.87
“Acremonium persicinum” CBS 113.69
“Acremonium rufum” CBS 366.66
“Acremonium spinosum” CBS 263.89
Nedria sesquicillii
Bionectria ochroleuca 2
Bionectria ochroleuca 1
Ochronecrotia clemensi CBS 782.68
“Acremonium spinosum” CBS 136.33
“Nalanthamala squamulosa” CBS 203.73
Nedria zonata
“Acremonium persicinum” CBS 295.70B
“Acremonium persicinum” CBS 295.70A
“Acremonium persicinum” CBS 305.58
“Acremonium persicinum” CBS 310.59
“Ironomonectria japonica” CBS 505.67
Gliomastix/Bionectria-clade
“Ironomonectria japonica” CBS 505.67
Gliomastix/Bionectria-clade
Fig. 2. (Continued).
Fig. 2. (Continued).
Fig. 2. (Continued).
Fig. 2. (Continued).

- 0.01 substitutions/site
Another major hypocreaean Acremonium clade in Fig. 1A contains A. breve, A. radatum, A. gamsi 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, Leucohspaira. The clade containing Trichothecium roseum and Leucohspaira indica (see taxonomic comments below) also contains two anamorph species that were long placed in different genera based on conidiogenesis, namely, Acremonium lactocigenum and Spicellum roseum, here recombined into Trichothecium.

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

The Giomastix/Bionectria clade, the sclerotigenum/Geosmithia clade, and other members of the Nectriaceae 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 Bionectiaceae with Acremonium-like anamorphs, namely, Emericellopsis, Hapsidospora, Mycorachis, 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 synnemetal 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 salmonae isolated from dung, also a typical habitat for S. fimetaria (Seifert 1985). An adjacent weakly supported clade includes Hapsidospora, Mycorachis, 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 Leucohspaira 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. fusidioidei clade containing several acremonium forming similar conidial chains (A. cavaraneanum, A. fusidioidei, A. hansfordii, A. hennbetti, 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 Verticillum 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 incarnatum 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. camptosporium sits basally in a clade adjacent to the Clavicipitaceae and is close to the poorly understood teleomorphic species Clypeosphaeria philyaea, 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 guilliermit, 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 hypocreaean clade of its own in Fig. 2E.

The Nectriaceae is represented by Nectria cinnaabarina 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. khandelensis* based on the ex-type isolates of *Gliomastix lavitskiae* and *Cephalosporium khandelense* (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 infulatum* 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 spirosiatria* and *Didymostilbe echinofibrosa* (Castlebury et al. 2004).

*Acremonium nigriscerotium* represents an isolated *Acremonium* near the families Hypocreaceae and *Niessliaceae* (Fig. 1B). In Fig. 2D, *A. nigriscerotium* is intercalated among two genotypes ascribed to *N. exilis*, and loosely associated (77 % bootstrap) with *Acremonium pseudezylanicum* 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 *Sarcodiplas* was investigated and found to split into two groups (Fig. 2C, D). One isolate identified as *S. circinatum* grouped with *Sarcodiplas cincinosetiferum* and *S. vanilli* in a widely separated clade along with *Lanatonecridia* teleomorphs and a sequence identified as *Pseudonecridia rouseliana* (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 Stachybrotys/Peethambara clade (Fig. 2D). Also appearing in this clade was *Parasarcodiplas ceratocarya*, 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-condial species, monographed by Dickinson (1968) as the genus *Gliomastix*, with numerous biologically related hyaline-condial 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 blochi*” 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 *Nectriidea*. 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, *Sarocladium* clade, *A. curvulum* clade, and *A. breve* clade. As seen best in Fig. 1, the *Sarocladium* 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-condial 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 genopig 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-synamorophic anamorphs of the Emericellopsis clade, most of the A. fusidioides clade, and most of the small A. campiflorum, A. exiguum, A. minutisporum, A. pinkertoniae, and A. pseudozelanicum clades. Gams (1975) accommodated A. byssoides, now known to be Acremonium sect. Acremonium, while commenting that it was suggestive of Verticillum sect. Prostrata, later recognised as Simplicillium (Zare & Gams 2001). He withheld A. byssoides from Verticillum 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 Glomastix.

Acremonium sect. Nectriidea 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 falsicolori in A. sect. Nectriidea had already been recognised as a member of the Fusarium solani complex (Summerbell & Schroers 2002) and A. diospyri had been transferred into Nalantamala together 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 undesignated major group of nectriaceous Acremonium species, originally included in A. sect. Nectriidea. The placement of A. sect. Nectriidea species A. alcaphilum, A. brunnescens, A. fuscum, A. nepalense, A. restrictum, and A. stromaticum in the Plecostosphaeriaceae has already been shown by Zare et al. (2007). Acremonium apii also has been shown to belong to this family as a synonym of Verticillum 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. Nectriidea include A. crotoctigenum in the Trichotheceum clade, A. radiatum in the phylogenetically isolated A. breve clade, A. biseptum in the A. cerealis clade near Glomastix, A. salmonum in the Emericelopsis clade near Stilbella fimetaria, A. chrysogenum in a bionectriacean clade containing cleistothecial teleomorphs such as Nigrosabulum, A. rutulum in a clade otherwise containing isolates identified as A. persicinum, and a non-type A. hyalinulum isolate in another clade peripheral to Glomastix. When Sarocladium zeae as A. zeae in A. sect. Nectriidea was compared to the phylogenetically related S. kilense as A. kilense 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. Glomastix was the "Striatisporum 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. Glomastix, Acremonium atrogriseum, is here removed to the Cephalothecaceae.

Other species included by Gams (1971, 1975) in A. sect. Glomastix that can now be seen to be separated from the Glomastix/Bionecltia clade include "Cephalosporium purpurascens," synonymised by Gams (1971) with A. persicinum as well as A. brachypenium, A. hennibertii, A. incrustatum, and A. inflatum. Species outside the Glomastix/Bionecltia clade that have well developed chondroid hyphae include A. hennibertii 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 conidium 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 telemorphs, 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 telemorphs and complex anamorphs. Ultimately, it might epitypify *Acremonium* strictly as a genus name for the *A. fusídioidei* 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 *Stachyromonos* 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 masseei* 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. infatuat*.

The closely related *A. persicum* clade may also be included as such suggested by Supplemental fig. 8E 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 tumulicolata* (Kiyuna et al. 2010), should also be included in this concept of *Gliomastix*.

The generic characters do not significantly differ 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 polychroma* (J.F.H. Beyma) 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) Gugl., 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 masseei** (Sacc.) Matsush., Icon. microfung. Matsush. lect. (Kobe): 76. 1975.

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

≡ *Acremonium masseei* (Sacc.) W. Gams, Cephalosporium-artige Schimmelpilze (Stuttgart): 83. 1971.

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

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.

3. **Gliomastix polychroma** (J.F.H. Beyma) S.B. Saksena, *MycoBank* MB519588. 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 acroemionioid 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* (basionym *Periconia felina* Marchal, Bull. Soc. R. Bot. Belg. 34:141. 1895) with *Periconia felina* Gliomastix *murorum* var. *felina* Gams & Hawksworth 

5. *Gliomastix tumulicola* (Kiyuna, An, Kigawa & Sugiy.) Summerbell, **comb. nov.** MycoBank MB519599. **Basionym:** *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 *Acremonium* 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 *Sagaramala* 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, sometimesropy; with, in Gams’ terminology (Gams 1971), phalacrographous, 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 adelophialidial, solitary orthotrophic 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, aculate to aceroso, 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. Chlamydothecia 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 CGGTCGGCCG 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 adelophialidial prominently, at least in some isolates; acroemionioid 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 baccilisporum* (Onions & Barron) *Summerbell, comb. nov.* MycoBank MB519589.  
*Basionym: Paeclomyces baccilisporus* Onions & G.L. Barron, Mycol. Pap. 107: 11. 1967.  
≡ *Acremonium baccilisporum* (Onions & G.L. Barron) W. Gams, *Cephalosporium-artige Schimmelpilze* (Stuttgart): 67. 1971.  
≡ *Sagarahamala baccilispora* (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. baccilisporum* 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: 1925.  
≡ *Cephalosporium incoloratum* Sukapure & Thirum., *Sydowia* 19: 171. 1966  
≡ *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 Domsh 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 chlamydoconidia 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* genroup III" (ITS: AY138846; LSU: AY138484) are actually of *S. kiliense*.

6. *Sarocladium ochraceum* (Onions & Barron) *Summerbell, comb. nov.* MycoBank MB519593.  
*Basionym: Paeclomyces 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, *Kavakia* 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 Domsh 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 acroemion 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
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 polyphylectic 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 crotocinigenum, 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), floccose or lanose, sometimes appearing powdery with heavy conidiation. Ascomatal initials, if present, produced on aerial mycelium, irregularly coiled. Ascomata spherical or nearly so, non-ostiolate, colourless or slightly pink, 150–300 μm; ascomatal wall persistent, nearly colourless, 10–13 μm thick, of indistinct hyphal cells; ascii 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 in massae, 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 branched apparatus 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, 5–9(–12) μm wide. Internal transcribed spacer sequence generally with distinct CACACACCTCGCG 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. plasmaporae, which are represented by one isolate each in CBS. Trichothecium domesticum was recently redispersed 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. trichothecides) 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.
   ≡ Acremonium crotoycinigenum (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 crotoycin mycotoxins that are similar to the trichochenes 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 ↔ 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 a 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 ascornatal 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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