Cephalotrichum and related synnematous fungi with notes on species from the built environment

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Abstract: A recent taxonomic revision of Microascaceae with an emphasis on synnematous fungi enabled re-identification of previously isolated indoor strains of Cephalotrichum. All available Cephalotrichum strains from the culture collection of the Westerdijk Institute were studied, 20 originating from the built environment. Phylogenetic relationships were inferred from DNA sequence data from the internal transcribed spacer 1 and 2 and intervening 5.8S nrDNA (ITS), and parts of β-tubulin (tub2) and translation elongation factor 1-α (tef1) genes. Additionally, herbarium material of 14 Cephalotrichum species described from soil in China was studied, and the taxonomy of C. album, not considered in recent revisions, was reevaluated. Sixteen phylogenetic species in Cephalotrichum are distinguished, five described as new species: C. domesticum, C. lignatile, C. longicollum, C. spirale, and C. terricola. Four species are considered nomena dubia (C. cylindrosporum, C. macrosporum, C. ovoideum, and C. robustum), five are placed in synonymy with other Cephalotrichum species (C. acutisporum, C. inflatum, C. longicollum, C. oblongum, C. verrucisporum), and one species, C. verrucipes, is probably a synonym of Penicillium clavigerum. Cephalotrichum columnare, former Doratomyces columnaris, is transferred to Kernia. Cephalotrichum album, formerly known as Doratomyces putredinis, is transferred to Acaulium and redescribed.

Key words: Doratomyces, Herbarium, Microascaceae, Microascales, Sordariomycetes, Synnematous hyphomycetes.

Taxonomic novelties: New combination: Acaulium album (Costantin) Seifert & Woudenh., Kernia columnaris (H.J. Swart) Woudenb. & Samson; New species: Cephalotrichum domesticum Woudenb. & Seifert, C. lignatile Woudenb. & Seifert, C. longicollum Woudenb. & Seifert, C. terricola Woudenb. & Seifert, C. transvaalense Woudenb. & Seifert; Typification: Epitypification (Basionyms): Synpenicillium album Costantin.

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INTRODUCTION

The genus Cephalotrichum is characterised by the formation of dry-spored, indeterminate synnemata and enteroblastic percur rent conidiogenesis. No sexual morph is known. It was first described by Link (1809), for two species, C. rigescens and C. stemonitis. Hughes (1958) chose C. stemonitis as lectotype, anchoring the modern generic concept of Cephalotrichum. Later, Doratomyces was described with D. neesi as its type (Corda 1829, considered a synonym of C. stemonitis by Hughes 1958) and later, Stysanus with S. stemonitis as its type (Corda 1837). Consideration of the type or lectotype species of these three genera, Cephalotrichum, Doratomyces and Stysanus, leads to the conclusion that all are typified by the fungus originally described as Isaria stemonitis (Abbott 2000). A later genus, Trichurus, with T. cylindrical as its type, was distinguished by the presence of sterile setae on the synnema (Clements & Pound 1896). In the unpublished Abbott (2000) thesis on holomorph studies in the Microascaceae, the synonyms of the three genera Doratomyces, Stysanus and Trichurus under Cephalotrichum were proposed, conclusions followed by Seifert et al. (2011). These synonyms were later confirmed based on analyses of the LSU and ITS rDNA subunits (Sandoval-Denis et al. 2016a, b). Within Cephalotrichum Sandoval-Denis et al. (2016b) described two new species, proposed five new combinations, and designated one neotype specimen, two lectotypes and four epitotypes for accepted species. Although this provides a more stable taxonomy for synnematous Microascaceae, the papers also highlighted a large number of taxa that could not be studied because of the absence of living cultures. Their list of uncertain or excluded species included 43 Cephalotrichum spp., and seven Doratomyces spp. These included 14 new Cephalotrichum species described recently from China, mostly based on morphology characters alone (Jiang & Zhang 2008, Jiang et al. 2011). We were fortunate to obtain herbarium material of these latter species for study, allowing us to evaluate them in the broader context of the Cephalotrichum taxonomy established by Sandoval-Denis et al. (2016b).

Most Cephalotrichum species occur on decaying plant material, straw, dung, wood and in soil (Domsch et al. 2007). They are infrequently reported from the indoor or built environment. Cephalotrichum microsporum (previously known as Doratomyces microsporus) is the species most often reported from the indoor environment (Prezant et al. 2008, Samson et al. 2010, Flannigan et al. 2011), where it is mentioned as occurring especially on wet cellulose-containing substrates like wood. Cephalotrichum purpureofuscum has also been reported from indoor air (Abbott 2000, Sandoval-Denis et al. 2016b) as has C. gorgonifer (Abbott 2000, as C. spirale). Cephalotrichum species are not regarded as human pathogens, and not known as producers of...
mycotoxins. Strains have been isolated from clinical origins, mostly human respiratory systems, but are considered passive colonisers or sample contaminants rather than active pathogens (Sandoval-Denis et al. 2016b). Cephalotrichum gorgonifer, for example, has been isolated from human clinical samples and can grow at human body temperatures (Sandoval-Denis et al. 2016b). However such reports are scarce and clinical data is lacking. Given the amount of time we spend indoors, it is important to understand which microorganisms are co-habitants of this environment and what their potential implications may be to human health and to the design of the built environment. For that reason, we re-evaluated the identification of newly isolated strains from house dust and other indoor substrates, and other strains from the built environment in our collections.

The aim of our project was to construct an updated phylogenetic overview of the genus, taking into account the availability of the previously unavailable species described from China, and the strains from the built environment. Cultures and specimens were also examined of an anomalous coprophilous white speckled species, included by Morton & Smith (1963) as Doratomyces putredinis then later renamed as Cephalotrichum album (De Beer et al. 2013), allowing us to complete the phylogenetic analysis of the classical species of this complex that are available in pure culture.

MATERIALS AND METHODS

Isolates and herbarium specimens

Seventy-two strains belonging to the genera Acaulium, Cephalotrichum, Graphium, Kernia and Wardomyces were included in this study (Table 1). They were obtained from the culture collection of the Westerdijk Fungal Biodiversity Institute (CBS), Utrecht, the Netherlands and the working collection of the Applied and Industrial Mycology department (DTO) at the Westerdijk Institute. Strains were grown on oatmeal agar (OA) (Samson et al. 2010).

Portions of fourteen holotype herbarium specimens, originally accessioned in the Plant Pathology Herbarium of the Shandong Agricultural University, China (HSAUP) were recently donated to the herbarium of the Westerdijk Institute (CBS-H) and were re-examined as part of this study (Table 2). For the holotypes of these species, we have indicated the original accession numbers for holotypes from the protologue, and consider the portions deposited in CBS-H to be isotypes, for which new accession numbers are published here with the following form: “holotype HSAUP xxxxx → isotype CBS-H yyyyy.” Additional isotype were listed in the protologues in HMAS; we have not examined these, but include the accession numbers as listed by the authors.

DNA sequences from six strains maintained at the UAMH Centre for Global Microfungal Biodiversity, University of Toronto, Canada were obtained from GenBank (Table 1).

DNA isolation, PCR and sequencing

DNA extractions were performed using the Ultraclean® Microbial DNA Isolation Kit (MoBio laboratories, Carlsbad, CA, USA), following manufacturer’s instructions. The internal transcribed spacer 1 and 2 and intervening 5.8S nrDNA (ITS), and parts of the β-tubulin (tub2) and translation elongation factor 1-α (tef1) genes were amplified and sequenced as described in Woudenberg et al. (2017). Consensus sequences were assembled from forward and reverse sequences using Bionumerics v. 4.61 (Applied Maths, St-Martens-Latem, Belgium). All sequences generated were deposited in GenBank (Table 1).

Alignments and phylogenetic analyses

Individual sequence alignments of the ITS, tub2 and tef1 datasets were generated with MAFFT v. 7.271 (http://mafft.cbrc.jp/alignment/server/index.html) using the L-INS-i method. The best nucleotide substitution models were determined with Findmodel (http://www.hiv.lanl.gov/content/sequence/findmodel/findmodel.html). For both the single gene sequence alignments and the concatenated alignment, Bayesian and Maximum-likelihood analyses were performed as described in Woudenberg et al. (2017). An additional phylogenetic tree was constructed based on the ITS sequences of a broader selection of isolates representing all species recognized by Sandoval-Denis et al. (2016b) and in this study, together with ITS sequences from the Chinese herbarium specimens available in GenBank (Table 2). To demonstrate the placement of two species initially classified in Cephalotrichum outside the genus, an alignment and phylogenetic tree based on the ITS and LSU sequences of representative strains of the genera Acaulium, Cephalotrichum, Kernia and Graphium was assembled based on the sampling of Sandoval-Denis et al. (2016a). The resulting trees were printed with TreeView v. 1.6.6 (Page 1996) and, together with the alignments, deposited in TreeBASE (http://www.treebase.org).

Morphology

Cultures were incubated on oatmeal agar (OA, which favours synnema development), malt extract agar (MEA) and dichloran 18 % glycerol agar (DG18) plates (recipes from Samson et al. 2010) at 25 °C in the dark. After 14 d, growth rates were measured and colony characters noted. Colony colours were rated following the charts of Rayner (1970). Dried herbarium material was rehydrated in sterile water, which was then replaced by Shear’s mounting media for photomicroscopy (Crous et al. 2009). Measurements and descriptions of microscopic structures were made from cultures grown on synthetic nutrient agar (SNA, Samson et al. 2010) at 25 °C in the dark for 14 d, mounted in 85 % lactic acid. Macroscopic photographs were made with a Nikon SMZ25 stereo microscope equipped with a Nikon DS-Ri2 high-definition colour camera head. Photomicrographs of diagnostic structures were made with a Zeiss Axio Imager A2 microscope equipped with a Nikon DS-Ri2 high-definition colour camera head, using differential interference contrast (DIC) optics and the Nikon software NIS-elements D v. 4.50.

RESULTS

Phylogeny

The concatenated, multi-gene Cephalotrichum phylogeny alignment included sequences of 62 strains and was 1 979 bp long, with the partitions being 566 characters for ITS (67 informative or unique), 884 for tef1 (103) and 529 for tub2 (227). The TrN model
Table 1. Isolates used in this study and their GenBank accession numbers. Bold accession numbers were generated in other studies.

| Name                    | CBS Database | Strain number | Substrate/host                          | Location                  | GenBank accession number |
|-------------------------|--------------|---------------|-----------------------------------------|---------------------------|--------------------------|
| **Acaulium acremonium** |              |               | Wheat field soil                        | Germany                   | KY852468 LNS51109 LNS51056 KY852479 |
| **A. albonigrescens**   |              |               | Litter, treated with urea               | Japan                     | KY852469 LNS51111 LNS51058 KY852480 |
| **A. album comb. nov.** |              |               | Queen of bumble-bee                     | Denmark                   |                          |
| **A. caviariforme**     |              |               | Seed                                    | Netherlands               |                          |
| **Cephalotrichum**      |              |               | Soil                                    | Netherlands               |                          |
| **C. brevistipitatum**  |              |               | Soil                                    | Netherlands               |                          |
| **C. cylindricum**      |              |               | Soil                                    | France                    |                          |
| **C. domesticum**       |              |               | Mushroom compost                        | Netherland                |                          |
| **C. gorgonifer**       |              |               | Indoor, plaster                         | Netherlands               |                          |
| **C. terrophilus**      |              |               | Indoor air, house                       | Netherlands               |                          |
| **C. spiralis**         |              |               | Unknown                                 | USA                       |                          |
| **C. stemonitis**       |              |               | Unknown                                 | UK                        |                          |
| **C. terrophilus**      |              |               | Compost ground domestic waste          | Italy                     |                          |
| **D. purpureofuscus**   |              |               | Wheat field soil                        | Germany                   |                          |
| **D. purpureofuscus**   |              |               | Indoor, plaster                         | Netherland                |                          |
| **D. purpureofuscus**   |              |               | Indoor air, house                       | Netherlands               |                          |
| **D. gorgonifer**       |              |               | Unknown                                 | USA                       |                          |
| **D. spiralis**         |              |               | Unknown                                 | UK                        |                          |
| **D. terrophilus**      |              |               | Compost ground domestic waste          | Italy                     |                          |
| **D. spiralis**         |              |               | Wheat field soil                        | Germany                   |                          |
| **D. spiralis**         |              |               | Indoor, plaster                         | Netherland                |                          |
| **D. spiralis**         |              |               | Indoor air, house                       | Netherlands               |                          |
| **D. stemonitis**       |              |               | Indoor, bakery                          | Netherlands               |                          |

(continued on next page)
| Name                  | CBS Database     | Strain number | Substrate/host                      | Location            | GenBank accession number |
|-----------------------|------------------|---------------|-------------------------------------|---------------------|--------------------------|
| **D. microsporus**    | DTO 122.68; DTO 055-I1 | Dug of deer  | Indoor, unknown                     | Netherlands         | KY249270, KY249310, KY249350 |
| **D. stemonitis**     | UAMH 9965; DTO 055-I1 | Soil          | Indoor, unknown                     | Germany             | LN850969, LN851123, LN851070 |
| **D. purpureofuscum** | CBS 174.68; DTO 055-I5 | Zea mays, grain | Unknown, unknown                   | Germany             | KY249275, np, KY249355    |
| **D. stemonitis**     | CBS 179.69; DTO 055-I1 | Seed          | Indoor, unknown                     | Netherlands         | LN850970, LN851124, LN851071 |
| **D. microsporus**    | CBS 127.788; DTO 055-I5 | Soil          | Indoor, unknown                     | Canada              | LN850972, LN851126, LN851073 |
| **D. stemonitis**     | CBS 127.792; DTO 055-I5 | Soil          | Indoor, unknown                     | USA                 | KY249286, KY249323, KY249365 |
| **D. microsporus**    | CBS 128.68; DTO 055-I5 | Soil          | Indoor, unknown                     | Cyprus              | KY249287, KY249325, KY249367 |
| **D. stemonitis**     | CBS 128.69; DTO 055-I5 | Soil          | Indoor, unknown                     | Canada              | KY249288, KY249326, KY249368 |
| **D. microsporus**    | CBS 128.70; DTO 055-I5 | Soil          | Indoor, unknown                     | USA                 | KY249286, KY249324, KY249366 |
| **D. stemonitis**     | CBS 128.71; DTO 055-I5 | Soil          | Indoor, unknown                     | South Africa        | LN850964, LN851118, LN851065 |
| **D. microsporus**    | CBS 128.72; DTO 055-I5 | Soil          | Indoor, unknown                     | Netherlands         | KY249289, KY249327, KY249369 |
| **D. stemonitis**     | CBS 128.73; DTO 055-I5 | Soil          | Indoor, unknown                     | Germany             | KY249290, KY249328, KY249370 |
| **D. microsporus**    | CBS 128.74; DTO 055-I5 | Soil          | Indoor, unknown                     | Greece              | KY852474                 |
| **D. stemonitis**     | CBS 128.75; DTO 055-I5 | Soil          | Indoor, unknown                     | South Africa        | KY852475, KY852477, KY852478 |
| **D. microsporus**    | CBS 128.76; DTO 055-I5 | Soil          | Indoor, unknown                     | France              | KY852476                 |
| **D. stemonitis**     | CBS 128.77; DTO 055-I5 | Soil          | Indoor, unknown                     | Czech Republic      | KY852485, KY852486       |
| **D. microsporus**    | CBS 128.78; DTO 055-I5 | Soil          | Indoor, unknown                     | South Africa        | KY852475, KY852477, KY852478 |
| **D. stemonitis**     | CBS 128.79; DTO 055-I5 | Soil          | Indoor, unknown                     | France              | KY852476                 |

**Note:** The table continues with additional entries for various fungal species, each with detailed information about the strain number, substrate/host, location, and GenBank accession numbers.
Table 1. (Continued).

| Name                  | CBS Database       | Strain number¹ | Substrate/host | Location | GenBank accession number |
|-----------------------|--------------------|----------------|----------------|----------|-------------------------|
| Wardomyces            | CBS 367.62², DTT 170-D2; DAOM 84715; MUCL 669 | - | Greenhouse soil | Belgium | LN850994 LN851153 LN851099 |

¹ First strain number is of the examined isolate. ATCC: American Type Culture Collection, Manassas, VA, USA; CBS: Culture Collection of the Westerdijk Fungal Biodiversity Institute, Utrecht, Netherlands; DAOM: Canadian National Mycological Herbarium, Agriculture and Agri-Food Canada, Ottawa, Canada; DSM: Deutsche Sammlung von Mikroorganismen und Zellkulturen, Braunschweig, Germany; DTO: Working Collection of the Applied and Industrial Mycology Group of the CBS-KNAW Fungal Biodiversity Centre, Utrecht, Netherlands; IFO: Institute for Fermentation Culture Collection, Osaka, Japan; IHEM: Biomedical Fungi and Yeast Collection of the Belgian Co-ordinated Collections of Micro-organisms (BCCM), Brussels, Belgium; IMI: Culture Collection of CABI Europe-UK, Egham, UK; JCM: Japan Collection of Microorganisms, Microbe Division, RIKEN-BioResource Center, Yokohama, Japan; LCP: Laboratory of Cryptogamy, National Museum of Natural History, Paris, France; LSHB: London School of Hygiene and Tropical Medicine, London, UK; MUCL: (Agro)Industrial Fungi and Yeast Collection of the Belgian Co-ordinated Collections of Micro-organisms (BCCM), Louvain-la-Neuve, Belgium; NHL: National Institute of Hygienic Sciences, Tokyo, Japan; RMF: Rocky Mountain Herbarium, University of Wyoming, Laramie, WY, USA; TRTC: Royal Ontario Museum Fungarium, Toronto, Canada; UAMH: University of Toronto, UAMH Centre for Global Microfungal Biodiversity, Toronto, Canada; WSF: Wisconsin Soil Fungi Collection, Madison, WI, USA. Ex-epitype, -isotype, -type, and -neotype isolates are indicated with “ep”, “it”, “ty” and “nt”, respectively.

Table 2. Herbarium specimens studied with their GenBank accession numbers.

| Original name | Collection # | ITS | After examination |
|---------------|--------------|-----|------------------|
| C. acutisporum| HSAUPI072724 | CBS H-22780 | – | C. purpureofuscum |
| C. castaneum  | HSAUPI07034 | CBS H-22781 | FJ914681 | C. castaneum |
| C. cylindrasporum| HSAUPI072414 | CBS H-22782 | FJ914686 | Nomen dubium |
| C. ellipsoideum| HSAUPI07053 | CBS H-22783 | – | C. ellipsoideum |
| C. infatum    | HSAUPI070918 | CBS H-22784 | FJ914676 | C. microsporum |
| C. longicollum| HSAUPI070802 | CBS H-22785 | FJ914672 | C. purpureofuscum |
| C. macrosporum| HSAUPI070878 | CBS H-22786 | FJ914675 | Nomen dubium |
| C. oblongum   | HSAUPI072723 | CBS H-22787 | FJ914667 | C. purpureofuscum |
| C. ovoideum   | HSAUPI070846 | CBS H-22788 | FJ914662 | Nomen dubium |
| C. robustum   | HSAUPI070875 | CBS H-22789 | FJ914674 | Nomen dubium |
| C. spirale    | HSAUPI070433 | CBS H-22790 | FJ914705 | C. spirale |
| C. tenuicola  | HSAUPI070924 | CBS H-22791 | FJ914677 | C. purpureofuscum |
| C. verrucipes | HSAUPI070849 | CBS H-22792 | – | Penicillium clavigerum |
| C. verrucisporum| HSAUPI1029 | CBS H-22793 | FJ914680 | C. verrucisporum |

with a gamma-distributed rate variation was suggested as the best model for the ITS and tub2 alignments, and the GTR model with a gamma-distributed rate variation as the most suitable model for the tef1 alignment. After discarding the burn-in phase trees, the multi-gene Bayesian analysis resulted in 2 020 trees from both runs, from which the majority rule consensus tree and posterior probabilities were calculated.

The multi-gene analysis divided the isolates among 16 species clades (Fig. 1) of which five are proposed as new and described in the **Taxonomy section**: *C. domesticum*, *C. lignatilis*, *C. telluricum*, *C. tenuissimum* and *C. transvaalense*. The 20 strains isolated from indoor environment are distributed among five *Cephalotrichum* species (Fig. 1, blue coloured boxes), namely *C. gorgonifer* (n = 9), *C. microsporum* (n = 4), *C. domesticum* (n = 2), *C. purpureofuscum* (n = 4) and *C. verrucisporum* (n = 1). All 16 species can be identified with either tef1 or tub2 partial gene sequences. The only exception is strain CBS 191.61, which based on its tef1 sequence clusters separately from the other *C. nanum* isolates (data not shown; all single gene phylogenies submitted to TreeBase). Based on ITS barcodes alone, *C. cylindricum* and *C. transvaalenae* sp. nov. cannot be distinguished (Fig. 2).

A second ITS analysis included reference sequences for accepted species combined with sequences obtained from the herbarium specimens received from China, resulting in 28 sequences with a total length of alignment length of 564 bases, with 66 informative or unique sites. The TrN model with a gamma-distributed rate variation was suggested as the best model. After discarding the burn-in phase trees, the multi-gene Bayesian analysis resulted in 1 202 trees from both runs, from which the majority rule consensus tree and posterior probabilities were calculated (Fig. 2). Results of the phylogenetic analyses and data derived from the morphological observations of the herbarium species are discussed in the section, “Additional notes on *Cephalotrichum*” below.

A third phylogeny, based on LSU and ITS sequences, was used to demonstrate the placement of *C. album* and *C. columnare* outside *Cephalotrichum*. The alignment contained sequences from 12 isolates and had a total length of 1 453 characters, with respectively 78 informative or unique characters in the LSU, and 183 in the ITS. The TrN model with a gamma-distributed rate variation was suggested as the best model for the LSU and the GTR model with a gamma-distributed rate variation for the ITS. After discarding burn-in phase trees, the multi-gene Bayesian analysis resulted in 1 502 trees from both runs, from which the majority rule consensus tree and posterior probabilities were calculated.
**Morphology**

In most *Cephalotrichum* species, both mononematous conidiophores and synnemata occur, either in equal abundance or with one more prevalent, with the distinction between them not always clear. Mononematous conidiophores tend to be more highly branched than those in synnemata, but vary from (i) single, lateral conidiogenous cells to, (ii) monoverticillate conidiophores to, (iii) irregularly biverticillate or tertiocerticillate, or reduced to single conidiogenous cells; structures with similar dimensions to those in synnemata. In the branched conidiophores, conidiogenous cells tend to occur in whorls of 3–7 conidiogenous cells. In synnemata, the conidiophores are usually less branched than in the mononematous form, often arising in a palisade directly from the stipe of the hyphae, or more often with 2–3 conidiogenous cells arising from a lateral metula, and rarely with more levels of branching. Although we provide some observations on conidiophores in our descriptions of new species below, we have no evidence that the branching patterns of either mononematous or synnematous conidiophores have diagnostic value for species. As is common with many synnematous hyphomycetes, some strains have a reduced ability to produce well-developed synnema with repeated transfer, and sometimes stop producing them completely.

**Taxonomy**

*Acaulium* album Seifert & Woudenberg, *com. nov*. MycoBank MB821421. Figs 4–5.

*Basionym:* *Synpenicillium album* Costantin, Bull. Soc. Mycol. Fr. 4: 62. 1888.

≡ *Coremium album* (Costantin) Sacc. & Traverso, Syll. fung. 22: 1444. 1913.

≡ *Cephalotrichum album* (Costantin) Seifert, CBS Biodiversity Series 12: 309. 2013.

*Synonym:* *Penicillium* costantinii Bainier, Bull. Soc. Mycol. Fr. 4: 67. 1888. [Non *Penicillium album* Preuss 1851] ≡ *Scopulariopsis costantii* (Bainier) Dale, Ann. Mycol. 12: 57. 1914.

*Styssanus putredinis* Corda, Icon. fung. (Prague) 3: 12. 1839 *fide Morton & Smith 1963* ≡ *Doratomyces putredinis* (Corda) F.J. Morton & G. Sm., Mycol. Pap. 86: 83. 1963. Non *Graphium putredinis* (Corda) S. Hughes, Can. J. Bot. 36: 770. 1958 ≡ *Parascedosporium putredinis* (Corda) Lackner & de Hoog, IMA Fungus 2: 44. 2011.

*Acaulium fulvum* Sopp, Skr. VidenskSelsk. Christiania, Math.-Natur., no. 11: 67. 1912 (*fide Morton & Smith 1963*, but synonymy rejected by Abbott [2000] because of discrepancies in spores sizes, and in the absence of a type specimen).

Conidiophores often mononematous in vitro, aspiltiate, or with a short stipe up to 250 μm tall, then monoverticillate, or irregularly biverticillate or tertiocerticillate, or reduced to single conidiogenous cells; structures with similar dimensions to those in synnema. Synnema on the natural substrate scattered or caespitose, up to 500–700(–1 000) μm tall, stipes white, cream-coloured or eventually very pale brown, 10–45 μm wide, unbranched or with 1–3 side branches, conidial heads hyaline to white, divergent or feathery about 20–65 μm wide and tall. *Hyphae of stipe* hyaline, smooth walled, in two zones: an outer region of parallel hyphae 2.5–4.5 μm wide; surrounding a central broader hypha 7–11 μm wide, with individual cells (10–20)–45 μm long. *Setae* absent.

Conidiophores in synnemata irregularly biverticillate or tertiocerticillate, branches 16–22 × 3–4 μm, metulae 9–13 × 3–3.5 μm. Conidiogenous cells percurrent, ampulliform, hyaline, smooth-walled, 6–8.5 μm long, 2.5–3 μm broad at the widest part, with a distinct shoulder tapering to a cylindrical annellated zone 1.5–2.5 μm wide, up to 6.5 μm long, annellations inconspicuous; in terminal whorls of 3–6. *Conidia* obvoid, ellipsoidal to irregularly fusiform with a truncate base and rounded or bluntly

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**Fig. 1.** Maximum likelihood tree based on the ITS, tub2 and tef1 sequences of 82 isolates. The RAxML bootstrap support values ≥75 % (BS) and Bayesian posterior probabilities ≥0.95 (PP) are given at the nodes. Thickened lines indicate a BS of 100 % and a PP of 1.0. Names in bold face are accepted species names, names in orange are non-accepted species names, names in red are synonyms and names in black are new combinations proposed below for these two species in the “Taxonomy” section.

**Fig. 2.** Maximum likelihood tree based on the ITS sequences of 28 isolates. The RAxML bootstrap support values ≥75 % (BS) and Bayesian posterior probabilities ≥0.95 (PP) are given at the nodes. Thickened lines indicate a BS of 100 % and a PP of 1.0. Ex-type strain numbers are in bold face and indicated with T (or ET, IT, NT, when ex-epitype, ex-isotype or ex-neotype respectively). The blue boxes indicate species which occur in the indoor environment. The tree was rooted to *Wardomyces inflatus* (CBS 367.62).

*Morphology* in most *Cephalotrichum* species, both mononematous conidiophores and synnemata occur, either in equal abundance or with one more prevalent, with the distinction between them not always clear. Mononematous conidiophores tend to be more highly branched than those in synnema, but vary from (i) single, lateral conidiogenous cells to, (ii) monoverticillate conidiophores to, (iii) irregularly biverticillate or tertiocerticillate, or reduced to single conidiogenous cells; structures with similar dimensions to those in synnema. Synnema on the natural substrate scattered or caespitose, up to 500–700(–1 000) μm tall, stipes white, cream-coloured or eventually very pale brown, 10–45 μm wide, unbranched or with 1–3 side branches, conidial heads hyaline to white, divergent or feathery about 20–65 μm wide and tall. *Hyphae of stipe* hyaline, smooth walled, in two zones: an outer region of parallel hyphae 2.5–4.5 μm wide; surrounding a central broader hypha 7–11 μm wide, with individual cells (10–20)–45 μm long. *Setae* absent.

Conidiophores in synnemata irregularly biverticillate or tertiocerticillate, branches 16–22 × 3–4 μm, metulae 9–13 × 3–3.5 μm. Conidiogenous cells percurrent, ampulliform, hyaline, smooth-walled, 6–8.5 μm long, 2.5–3 μm broad at the widest part, with a distinct shoulder tapering to a cylindrical annellated zone 1.5–2.5 μm wide, up to 6.5 μm long, annellations inconspicuous; in terminal whorls of 3–6. *Conidia* obvoid, ellipsoidal to irregularly fusiform with a truncate base and rounded or bluntly
pointed apex, 4.5–6.5(–7) × 2–3(–4) μm, hyaline, smooth and slightly thick-walled, in long, dry, basipetal chains, sometimes sticking laterally and forming columns up to 1 mm long. *Chlamydospores* abundant in culture, sometimes also in the synnema stipe, globose to ellipsoidal, 4–8 × 4–5 μm, single or in pairs, cyanophilous. Sexual morph not observed.

**Culture characteristics:** Colonies on OA 46–47 mm diam after 14 d at 25 °C, planar to low convex, powdery, white to cream-coloured centre with hyaline outer ring, margin discrete, undulate. On MEA 44–45 mm diam, planar to low convex, powdery, white to cream with inconspicuous concentric rings about 1 mm apart, margin undulate.

Specimens and cultures examined: Canada, British Columbia, Vancouver, University of British Columbia (UBC), near University Golf Club, from decaying *Coprinus micaceus*. July 1981, J.A. MacKinnon, CBS 257.82 = ATCC 46569 (DAOM 230530); British Columbia, Vancouver, UBC Campus, 22 Oct. 1980, R.J. Bandoni, CBS H-3873; Same location, UBC chicken coop, 19 Jan. 1980, on chicken droppings, R.J. Bandoni & T. Thompson, CBS H-3874. Same location, UBC Experimental Garden, 2 Feb. 1981, on roting potato, J.A. MacKinnon, CBS H-3872. Ontario, Ottawa-Carleton Twp, Bell’s Corners, 9 May 1998, on bear dung (*Urus americanus*), Keith A. Seifert no. 521 (DAOM 226656). Czech Republic, Prague, on rotting stems of *Echium sp.*, 1938, Fieber (holotype of *Stysanus putredinis*, PR-C 155673). Denmark, from bumble-bee queen, collection date unknown, J.P. Skou, CBS 378.64. Netherlands, Hoogland, near Armesfoort, from hair in dung of pole cat (*Mustela putorius*), March 1984, H.A. van der Aa, (epitype designated here CBS H-12128, MBT376922, culture ex-epitype CBS 539.85); Wageningen, from soil, collection date unknown, J.H. van Emden, CBS 212.73. USA, Maine, Kittery Point, from decaying seaweed, 1918, R. Thaxter (FH).

**Notes:** De Beer et al. (2013, p. 309) briefly reviewed the history of the epithet *putredinis* and its contradictory use in *Graphium* and *Doratomyces*, which need not be repeated in detail here. Because the epithet *putredinis* is now used in *Parascedosporium* but previously was being used for two distinct species (one by Hughes 1958, the other by Morton & Smith 1963), it was necessary to transfer the next available epithet, i.e. from *Synpenicillium album*, to *Cephalotrichum*. The recent treatment by Sandoval-Denis et al. (2016b) noted morphological similarities between this species (as *C. album*) and other asexual species included in the *Acaulium* clade by molecular evidence, but did not redescribe or reclassify this white species. The phylogenetic analysis presented here (Fig. 3) shows that this species does not belong to *Cephalotrichum*, and is best classified as a synnematous species of *Acaulium* as suggested by Sandoval-Denis et al. (2016b).

*Acaulium album* is a relatively infrequently reported asexual fungus, but is broadly distributed in Europe and North America on heavily decayed organic material and various kinds of (often carnivore) dung. Apart from the white synnemata and spores, it is distinctive because of the broad hypha in the centre of the synnema stipe. Developmentally, the synnemata are rather odd. The cells of the broad central hypha produce narrower hyphae growing upward near the top of the cells or hyphae growing downward from the bottom of the same cells, all appressed to the central cylinder to make up the stipe. The downward growing hyphae anchor the conidiomata to the substrate; the upward growing hyphae branch to become the conidiophores. Similar downward growing hyphae, and broader core hyphae, are sometimes seen in the synnema stipes of true *Cephalotrichum* species (lodha 1963, Swart 1964) but are more difficult to see because of the pigmentation of the cells.

Constantin (1888) described his fungus from panther dung from an unreported location, but probably from a zoo in Paris. Morton & Smith (1963) did not locate a type, but considered the identity of the fungus clear from the published illustration. There is a discrepancy in spore sizes, Constantin (1888) reporting dimensions of 7–13 × 3–6 μm, roughly double the size reported here, but given our observations of several specimens of the relatively common species described above, suspect this is probably a measurement error by Constantin (1888). We designate CBS H-12128, isolated from a hair in pole cat dung, as epitype above to further stabilise the species name.

*Synpenicillium* is an older name than *Acaulium* but has rarely been used after its original publication in 1888 (Constantin). *Acaulium* has generally been considered a synonym of *Scopulariopsis* but recently was re-instated as an accepted genus of *Microascaceae* with three species (Sandoval-Denis et al. 2016b). Although both names are relatively obscure, we see no reason to
Fig. 4. Acaulium album DAOMC 226656. A. Four weeks old colony on cornmeal agar. B. Colony surface showing white conidial columns. C. Individual synnemata in side view. D. Synnema with apical conidiophores and broader central hypha. E. Conidia. F. Individual conidiophore on side of synnema. G. Top of synnema showing divergent conidiophores. Scale bars: D. 50 μm, E–G. 10 μm.
resurrect *Synenicillium* for this clade. We will propose protection of *Acaulium* be added to the list of protected generic names now being discussed by the nomenclatural community.

**Cephalotrichum domesticum** Woudenb. & Seifert sp. nov. MycoBank MB819314. Fig. 6.

**Etymology**: The name refers to the usual occurrence of this species in the built environment, or other environments manipulated by humans, such as farms.

*Mononematous conidiophores* abundant among and intergrading with synnemata, hyaline to pale brown, monoverticillate, or irregularly biverticillate to terverticillate, sometimes 3–4- level verticillate, with a short stipe 7–25 μm tall, terminating in 3–5(–7) annellides on cylindrical, clavate or swollen metulae 5–8 × 2.5–3.5 μm; branches appressed or divergent, 10–12 × 2–3 μm. **Synnemata** 130–225(–245) μm tall, stipes pale brown, 7–10 μm wide, composed of rather loosely attached hyphae; conidial heads brown, subglobose to ellipsoidal. **Hyphae** of stipe parallel, 2–4 μm wide, pale-brown, slightly thick-walled. **Setae** absent. **Conidiophores in synnemata** monoverticillate, irregularly biverticillate or conidiogenous cells arising directly from the stipe hyphae, with all elements tightly appressed, metulae 5.5–8.5 × 2–2.5 μm. **Conidiogenous cells** ampulliform, (5.5–)6–7.5(–8) μm long, 2.5–3(–3.5) μm broad at the widest part, tapering gradually to a cylindrical annellate zone 1.5–2 μm wide, hyaline to pale brown, smooth-walled. **Conidia** ellipsoidal to cylindrical with truncate base and rounded or pointed apex, 5.5–6(–6.5) × 3–3.5(–4) μm, pale brown to brown, smooth and thick-walled, in basipetal chains. Sexual morph not observed.

**Culture characteristics**: Colonies on OA 52–55 mm diam after 14 d at 25 °C, low convex, felty, white with olivaceous grey to iron grey centre, margin uneven. On DG18 13–15 mm diam, planar, finely felty, white with iron grey zones, margin undulate.

Specimens examined: **Netherlands**, Limburg, from manure, Mar. 1942, P.J. Bels, CBS 139.42 = IFO 7677 = MUCL 4025; Utrecht, dried culture of strain isolated from indoor air of home (kitchen), 28 Aug. 2008, J. Houbraken, (holotype CBS H-22856, culture ex-type CBS 142035); from plaster, before Sept. 1967, H.J. Hueck, CBS 395.67; from mushroom compost, 1950, H.C. Bels-Koning, CBS 255.50 = MUCL 4037.

**Notes**: Only the ex-type culture CBS 142035 produced synnemata in culture. This phenomenon has also been reported for *C. purpureofuscum*, where several colonial variants can be obtained by spontaneous sectoring (Domsch et al. 2007). Although morphologically *C. domesticum* resembles *C. purpureofuscum*, it can easily be separated from that based on any of the three genes studied here (see Discussion section notes regarding *C. purpureofuscum*). Given the similar morphology, frequently defined by lack of distinctive characters, examination of a larger number of isolates for *C. domesticum* and *C. purpureofuscum* is needed to adequately assess whether any consistent morphological features could be used to identify the species that are clearly distinct based on molecular data. Phylogenetically *C. domesticum* is closely related to *C. tenuissimum*. The smaller synnemata of *C. domesticum* (130–245 μm tall vs. 495–900 μm tall) and faster growth on OA (52–55 mm diam vs. 40 mm) and MEA (45–50 mm diam vs. 30 mm) at 25 °C can be used to distinguish the two species.

**Cephalotrichum lignatile** Woudenb. & Seifert sp. nov. MycoBank MB819309. Fig. 7.

**Etymology**: The name refers to the substrate of isolation, timber.

*Mononematous conidiophores* moderately abundant among synnemata, pale brown, mostly monoverticillate or biverticillate with a
Fig. 6. Cephalotrichum domesticum sp. nov. CBS 142035. A–C. Fourteen day old colonies on OA (A), MEA (B) and DG18 (C). D–G. Synnemata. H–I. Conidiophores, conidiogenous cells and conidia. J. Conidia. Scale bars = 10 μm.
Fig. 7. Cephalotrichum lignatile sp. nov. CBS 209.63. A–C. Fourteen day old colonies on OA (A), MEA (B) and DG18 (C). D–F. Synnemata. G. Detail of the apical portion of a synnema. H–I. Conidiophores, conidiogenous cells and conidia. J. Conidia. Scale bars = 10 μm.
short stipe 4–10(−14) × 2–3 μm, sometimes 2-level verticillate, with (2–)3–5 annellides in compact whorls on slightly divergent, cylindrical to slightly clavate metulae 7–8 × 1.5–2.5 μm. Synnemata (280–)300–445(−465) μm tall, stipes pale brown to brown, (5.5–)6–8.5 μm wide, unbranched, conidial heads hyaline to pale brown, ellipsoidal or cylindrical. Hyphae of stipe parallel, 2–2.5 μm wide, pale-brown, slightly thick-walled. Setae absent. Conidiophores in synnemata irregularly monoverticillate, biverticillate or 2–3(–4)-level verticillate with all elements tightly appressed, metulae 6–8 × 2–3(–3.5) μm. Conidigenous cells ampulliform, hyaline to pale brown, smooth-walled, (5.5–)6–7(−7.5) μm long, 2.5–3 μm broad at the widest part, tapering gradually to a cylindrical annellated zone (1–)1.5(–2) μm wide, annellations inconspicuous. Conidia ovoid to irregularly fusiform with truncate base and rounded or bluntly pointed apex, (4.5–)5–6(–6.5) × (2.5–)3.5–3.5(–4) μm, pale brown to brown, smooth and thick-walled, in basipetal chains. Sexual morph not observed.

**Notes:** The sequences of CBS 209.63, which we describe here as *C. lignatile*, are identical to the sequences previously published for CBS 159.66 as *C. columnare* (Sandoval-Denis et al. 2016b). However, the morphology of CBS 209.63 does not match CBS 159.66. We also sequenced older batches of CBS 159.66 from the CBS collection to exclude the possibility of a mix-up, but all gave identical sequence results, placing *C. columnare* in the genus *Kernia*, where it is transferred below. The sequences associated with this strain by Sandoval-Denis et al. (2016b) seem to contain an error that we can’t explain.

**Cephaliotrichum telluricum** Woudenb. & Seifert sp. nov. MycoBank MB819318. Fig. 8.

**Etymology:** The name refers to the substrate of isolation, soil.

**Monomatus conidiophores** sparse among synnemata, hyaline, unbranched to monoverticillate or irregularly biverticillate, bearing 1–3 annellides on cylindrical or swollen metulae 7–12 × 2.5–3 μm. Synnemata 260–424(−490) μm tall, stipes pale brown to brown, 8.5–11.5(−12.5) μm wide, conidial heads pale brown to brown, subglobose or ellipsoidal. Hyphae of stipe parallel, 2–4 μm wide, pale-brown, slightly thick-walled, wider hyphae in the centre of the stipe near the base, downward growing branches occurring near the base of the synnemata. Setae coiled, simple, septate, pale brown, individually up to about 180 μm long, 3–4.5 μm wide, extending about 70–100 μm beyond the level of the conidiogenous cells with a rounded or acute apex. Conidiophores in synnemata solitary and lateral on stipe hyphae, or monoverticillate, metulae 6–8 × 2–3 μm. Conidigenous cells ampulliform, (5.5–)6–8(−8.5) μm long, 2.5–3.5(–4) μm broad at the widest part, tapering gradually to a cylindrical annellated zone (1–)1.5–2 μm wide, hyaline, smooth-walled. Conidia ovoid to broad fusiform with truncate base, (5.5–)6–7.5(–8) × (3.5–)4–4.5 μm, pale brown, smooth, thick-walled, in basipetal chains. Sexual morph not observed.

**Culture characteristics:** Colonies on OA 65 mm diam after 14 d at 25 °C, planar, thinly felty with tufts of mycelium, grey olivaceous with pale greenish grey mycelium and (pale) olivaceous grey sectors in the centre and a white outer ring, margin entire. On MEA 60–62 mm diam, planar to low convex, floccose, white with pale greenish grey ring and lavender grey to smoke grey regions, margin entire. On DG18 10–12 mm diam, raised, finely felty, cinnamon with olivaceous grey zones and white outer ring, margin undulate.

**Specimens examined:** Canada, Ontario, Vineland, from soil, Sep. 1949, R.F. Cain, CBS 568.50 = TRTC 12269. Cyprus, Nicosia, dried culture of strain isolated from soil, before Jan. 1932, R.M. Natrass (holotype CBS H-22853, culture ex-type CBS 336.32 = MUCL 9829 = UAMH 8882).

**Notes:** Based on morphology and phylogeny, *C. telluricum* is closely related to *C. gorgonifer*. Both species have spirally coiled setae, but the synnemata of *C. telluricum* (<500 μm tall) are shorter than those of *C. gorgonifer* (500–1 000 μm). Based on sequence data *C. telluricum* can be distinguished from *C. gorgonifer* by all three genes, with ITS having 5 nt differences, tub2 15 nt, and rnt 3 nt between *C. telluricum* and the ex-epitype isolate of *C. gorgonifer*, CBS 635.78.
Fig. 8. Cephalotrichum telluricum sp. nov. CBS 336.32. A–C. Fourteen day old colonies on OA (A), MEA (B) and DG18 (C). D–H. Synnemata. I. Detail of the apical portion of a synnema. K. Conidiophores, Conidiogenous cells and conidia. L. Conidia. Scale bars = 10 μm.
Fig. 9. Cephalotrichum tenuissimum sp. nov. CBS 127792. A–C. Fourteen day old colonies on OA (A), MEA (B) and DG18 (C). D–G. Synnemata. H. Detail of the apical portion of a synnema. I–J. Conidiophores, conidiogenous cells and conidia. K. Conidia. Scale bars = 10 μm.
from $C.\ microsorum$ by the size of the conidia, $5–6 \times 3.5–4$ for $C.\ tenuissimum$ vs. $3.5–5 \times 2–3$ μm for $C.\ microsorum$.

**Cephalotrichum transvaalense** Woudenb. & Seifert sp. nov. MycoBank MB819312. Fig. 10.

**Etymology:** The name refers to the Transvaal Province in South Africa, where the ex-type strain was first isolated.

**Mononematous conidiophores** monverticillate to irregularly biverticillate, or 2–3-level verticillate. **Synnemata** 500–1 500 μm tall, stipes brown, 15–35 μm wide, unbranched, conidiial heads pale brown to brown, ellipsoidal; sessile conidiomata lacking a stipe present in some transfers, forming brown to black, sub-globose conidial tufts. **Hyphae** of stipe parallel, 2–4 μm wide, pale-brown, slightly thick-walled. Setae straight, aseptate, brown, (40–)70–110 μm long, 1–1.5 μm wide, base sometimes swollen to 2–2.5 μm wide, unbranched, biserulate (90–120°) or with several layers of basal branching; sometimes arising from the same hyphae or metulae as conidiogenous cells. **Conidiophores in synnemata** mostly biverticillate, sometimes monverticillate, metulae divergent, 5–8 × 2–3 μm. **Conidigenous cells** ampuliform, 6–8(–10) μm long, 2–3 μm broad at the widest part, tapering abruptly to a cylindrical annellate zone 1–1.5 μm wide, pale brown, smooth-walled. **Conidia** ovoid to ellipsoidal with small truncate base and rounded apex, (4.5–)5–6.5 × 3–4.5 μm, pale brown, smooth, thick-walled, in basipetal chains. Sexual morph not observed.

**Culture characteristics:** Colonies on OA 53 mm diam after 14 d at 25 °C, planar, felty, white with olivaceous grey ring and pale olivaceous grey centre, margin uneven. On MEA 48 mm diam, at 25 °C, planar, felty, white with olivaceous grey ring and pale brown, smooth, thick-walled, in basipetal chains. Sexual morph not observed.

**Specimen examined:** South Africa. Transvaal, dried culture of strain isolated from Eucalyptus saligna timber in cellar, 1951, leg. Bekker (holotype CBS H-22854, culture ex-type CBS 448.51 = IFO 7660 = IMI 046251 = LSH B3344 = UAMH 8848).

**Notes:** With the straight setae arising from the conidiial head, C. transvaalense morphologically resembles C. cylindricum and the holotype strain was identified as this species in the past. IMI 46251 was used as the basis for the description of C. cylindricum (as *Trichurus terrophilus*) by Lodha (1963) and Swart (1964); their illustrations and descriptions indicate well-developed synnemata and some aspects of our description are adapted from these sources. Because the strain no longer makes well-developed synnemata, we have adapted measurements and details from these descriptions in our technical description above. *Cephalotrichum transvaalense* and *C. cylindricum* are closely related but distinct based on molecular data. The ITS sequences have no differences, but 20 nt differences in tub2 and 9 nt differences in $tef1$ sequences clearly distinguish the two species.

**Kernia columnaris** (H.J. Swart) Woudenb. & Samson comb. nov. MycoBank MB820690.

**Basionym:** Doratomyces columnaris H.J. Swart, Acta Bot. neerl. 15: 521. 1967 $\equiv$ *Cephalotrichum columnare* (H.J. Swart) S.P. Abbott, Stud. Mycol. 83:206. 2016.

**Descriptions and illustrations:** Swart (1967), Abbott (2000), Sandoval-Denis et al. (2016a, b).

Specimen examined: South Africa, Johannesburg, Melville Koppies Nature Reserve, from dung of hare, 1964, H.J. Swart (culture ex-type CBS 159.66 = IMI 116691).

**Notes:** As noted, sequences previously published for CBS 159.66 (Sandoval-Denis et al. 2016b) match sequences of CBS 209.63, which we describe above as *C. lignatilis*. To exclude the possibility of mislabelling in the CBS collection, we also studied older preservation batches of CBS 159.66 from the CBS collection, which all yielded identical sequence results that convincingly place this species in the genus *Kernia* (Fig. 3). The affinity of this species with the latter genus rather than *Cephalotrichum* was already suggested by Abbott (2000), based on significantly discordant morphological characters recorded from several isolates, including its reduced conidiophores (50–700 μm), mostly mononematous or more rarely synnematos with poorly developed, hyaline stipes, which resemble more to those of the synnematos anamorphs of *Kernia hippocrepida* and *P. pachypleura* (Malloch & Cain 1971). Other relevant features of *K. columnaris* are: annellides subcylindrical to ampulliform, conidia ellipsoid, often slightly asymmetrical, apex rounded or bluntly pointed, smooth, 5–6 × 2.5–4 μm, commonly 5.5 × 3 μm, colonies grey to brown, slowly growing (20–30 mm in 14 d at 25 °C). The mentioned characteristics match with the morphological treatment of the species by Sandoval-Denis et al. (2016a, b), suggesting that their illustrations are based on the actual ex-type strain of *K. columnaris*, while the sequence discrepancy most likely respond to a sequencing overlap.

**ADDITIONAL NOTES ON CEPHALOTRICHUM**

Recently, 14 new *Cephalotrichum* species were described based on isolates from soil from China (Jiang & Zhang 2008, Jiang et al. 2011). The status of those species, only known from their holotypes, could not be thoroughly evaluated by Sandoval-Denis et al. (2016b) because of the unavailability of material. Recently, portions of the holotypes materials were donated to the CBS herbarium collection by the authors of these names, and the species could be re-evaluated in our study. The conclusions derived from the morphological analysis of these specimens, and associated DNA sequences, are as follows:

**Accepted species**

*Cephalotrichum castaneum* (Y.L. Jiang & T.Y. Zhang) Y.L. Jiang & T.Y. Zhang, Mycotaxon 117: 224. 2011. Fig. 11.

**Synonym:** Doratomyces castaneus Y.L. Jiang & T.Y. Zhang, Mycotaxon 104: 131. 2008.

**Notes:** As noted, sequences previously published for CBS 159.66 (Sandoval-Denis et al. 2016b) match sequences of CBS 209.63, which we describe above as *C. lignatilis*. To exclude the possibility of mislabelling in the CBS collection, we also studied older preservation batches of CBS 159.66 from the CBS collection, which all yielded identical sequence results that convincingly place this species in the genus *Kernia* (Fig. 3). The affinity of this species with the latter genus rather than *Cephalotrichum* was already suggested by Abbott (2000), based on significantly discordant morphological characters recorded from several isolates, including its reduced conidiophores (50–700 μm), mostly mononematous or more rarely synnematos with poorly developed, hyaline stipes, which resemble more to those of the synnematos anamorphs of *Kernia hippocrepida* and *P. pachypleura* (Malloch & Cain 1971). Other relevant features of *K. columnaris* are: annellides subcylindrical to ampulliform, conidia ellipsoid, often slightly asymmetrical, apex rounded or bluntly pointed, smooth, 5–6 × 2.5–4 μm, commonly 5.5 × 3 μm, colonies grey to brown, slowly growing (20–30 mm in 14 d at 25 °C). The mentioned characteristics match with the morphological treatment of the species by Sandoval-Denis et al. (2016a, b), suggesting that their illustrations are based on the actual ex-type strain of *K. columnaris*, while the sequence discrepancy most likely respond to a sequencing overlap.
Fig. 10. Cephalotrichum transvaalense sp. nov. CBS 448.51. A–C. Fourteen day old colonies on OA (A), MEA (B) and DG18 (C). D–H. Synnemata. I. Detail of synnema setae. J. conidiophores, conidiogenous cells and conidia. K. Conidia. Scale bars = 10 μm.
C. tenuissimum. However, significant morphological differences exist among these species. The taller synnemata and conidial size and shape distinguish C. castaneum from C. domesticum and C. tenuissimum, while the absence of setae in the synnemata of C. castaneum differentiates it from C. dendrocephalum.

Cephalotrichum ellipsoideum H.Q. Pan & T.Y. Zhang, Mycotaxon 117: 211. 2011. Fig. 12.

Specimen examined: China, Qinghai Province, Maduo, dried culture isolated from grassland soil, Jun. 8, 2007, H.Q. Pan (holotype HSAUPII074053/isotype CBS H-22783, additional isotype HMAS196224).

Notes: The dimensions of synnemata given in the protologue do not correlate with those observed in the type material. The length and robustness of the synnematal stipe and the shape of the conidial head are the main characters that distinguish this species from other Cephalotrichum spp. In C. ellipsoideum, the
synnemata are much more robust (<2500 μm tall, with stipes <125 μm wide) with an obclavate and elongated conidial head, often tapering towards the apex. Other *Cephalotrichum* spp. with synnemata of similar size are *C. stemonitis* and *C. verrucisporum*; *C. ellipsoideum* differs from *C. stemonitis* by the absence of echinobotryum-like morph, and *C. verrucisporum* by its smooth conidia, in contrast to the markedly verrucose and pointed conidia of *C. verrucisporum*.

**Cephalotrichum ellipsoideum** H.M. Liu, H.Q. Pan & T.Y. Zhang, Mycotaxon 117: 220. 2011. Fig. 13.

Specimen examined: China, Qinghai Province, Dari County, dried culture isolated from grassland soil, Jun. 12. 2007, H.Q. Pan (holotype HSAUPII074033/ isotype CBS H-22790, additional isotype HMAS196233).

Notes: The type material contains two fungi, the synnematous *C. spirale* and a *Cladosporium* spp., the second probably a culture contaminant judging from its sparse presence.

**Cephalotrichum spirale** H.M. Liu, H.Q. Pan & T.Y. Zhang, Mycotaxon 117: 220. 2011. Fig. 13.

Specimen examined: China, Qinghai Province, Dari County, dried culture isolated from grassland soil, Jun. 12. 2007, H.Q. Pan (holotype HSAUPII074033/ isotype CBS H-22790, additional isotype HMAS196233).

Notes: The type material contains two fungi, the synnematous *C. spirale* and a *Cladosporium* spp., the second probably a culture contaminant judging from its sparse presence.
Morphologically, *C. spirale* resembles *C. asperulum* and *C. nanum*, and all species have distinctly verrucose conidia. *Cephalotrichum spirale* differs from *C. asperulum* mainly by the conidial shape, with rounded apices in *C. spirale* vs. pointed apices in *C. asperulum*, and the degree of conidial roughness, which is not as pronounced in *C. asperulum*, which sometimes has conidia that are smooth. *Cephalotrichum spirale* differs from *C. nanum* by the size of its synnemata (<850 μm tall in *C. spirale* vs. <2000 μm tall in *C. nanum*) as well as by conidial size and shape (5–7 × 3–4.5 μm, broadly ovoid to broadly ellipsoidal in *C. spirale* vs. 6–8 × 4.5–7.5 μm, subspherical to oval in *C. nanum*). *Cephalotrichum verrucisporum* is the closest relative genetically (ITS 2 nt difference, Fig. 2) but the two species are easily differentiated morphologically (see note under *C. verrucisporum* below). Note that this species is different from the well-known fungus described as *Trichurus spiralis*, but the coincidental epithets in *Cephalotrichum* led to the adoption of the later species name *C. gorgonifer* for the latter fungus.
Cephalotrichum verrucisporum (Y.L. Jiang & T.Y. Zhang) Y.L. Jiang & T.Y. Zhang, Mycotaxon 117: 223. 2011.
Synonym: Doratomyces verrucisporus Y.L. Jiang & T.Y. Zhang, Mycotaxon 104: 133. 2008.

Specimens examined: China, Guizhou Province, Guiyang, Huaxi Park, dried culture isolated from mountain soil, Oct. 6. 2005, Y.L. Jiang (holotype of D. verrucisporum HSAUPII051029 → isotype CBS H-22793); Germany, from indoor environment, 2007, DTO 055-D7; Netherlands, Katwijk, from sand dune (50 cm depth), Mar. 1978, W. Gams, CBS 187.78; Wageningen, from agricultural soil, Jul. 1972, J.W. Veenbaas-Rijks, CBS 512.72.

Notes: This species was recently accepted as distinct and was illustrated by Sandoval-Denis et al. (2016b) on the basis of the identity of an ITS derived from the type with an available culture (CBS 187.78). Our study of type material confirms that application of this name (Fig. 2), showing this species to be a closely related lineage to C. spirale. Both species produce verrucosia conidia. Cephalotrichum verrucisporum can be differentiated by its taller synnemata (<3,000 μm tall vs. <850 μm tall in C. spirale) and its somewhat larger and pointed conidia (6–9 × 3–5.5 μm vs. 5–7 × 3–4.5 μm, with a rounded apex in C. spirale). Cephalotrichum verrucisporum has ovoid conidia that are a bit darker than the oval to ellipsoidal pale brown conidia of C. asperulum, and synnemata that are longer than those of C. asperulum, which are usually ~1,000 μm tall (Sandoval-Denis et al. 2016b).

Doubtful and excluded species

Cephalotrichum acutisporum J.J. Xu & T.Y. Zhang, Mycotaxon 117: 208. 2011.

Specimen examined: China, Fujian Province, Zhangping, dried culture isolated from soil of a park, Oct. 22. 2004, J.J. Xu (holotype HSAUPII042724 → isotype CBS H-22785, additional isotype HMAS196226).

Notes: This species is a synonym of C. purpureofuscum. The original description is inaccurate, according to our observations, with conidiogenous cells 8–11 (–12.5) × (2.5–)3–4 μm, and conidia (4–)5–6 × 3–3.5 (–4) μm. The isotype material contains only short synnemata 475–500 μm tall; however, synnemata of this stature are not uncommon in C. purpureofuscum. Morton & Smith (1963) examined isolates of C. purpureofuscum with reduced synnemata, as little as 50 μm tall. The morphological identity with C. purpureofuscum is confirmed by DNA data. The ITS sequence from the ex-type of C. longicollum has 1 nt difference from the reference strain of C. purpureofuscum (CBS 174.68, Fig. 2), but is identical to the ITS sequences of the other C. purpureofuscum isolates included in this study (data not shown).

Cephalotrichum macrosorum Y.L. Jiang & T.Y. Zhang, Mycotaxon 117: 214. 2011.

Specimen examined: China, Sichuan Province, Jiuzhaigou, dried culture isolated from forest soil, Aug. 18. 2005, Y.L. Jiang (holotype HSAUPII052414 → isotype CBS H-22786, additional isotype HMAS196229).

Notes: The isotype is in poor condition. Only fragments of synnema stipes and conidia can be seen, and the fungus is untangleable. Synnemata and conidiogenous cells in the isotype material are much larger than indicated in the protologue. According to our observations synnemata are (600–)640–955 μm tall, with conidiogenous cells (8.5–)9.5–10.5 × (2.5–)3–4 μm. Also, the conidial shape, originally described and illustrated as markedly pointed is not a consistent character; nearly half of the conidia observed in the isotype have rounded apices, a pattern commonly observed in C. purpureofuscum.

Cephalotrichum cylindrosorum Y.L. Zhang & T.Y. Zhang, Mycotaxon 117: 209. 2011.

Specimen examined: China, Hainan Province, Turchang, dried culture isolated from rice field soil, Nov. 1. 2005, Y.L. Jiang (holotype HSAUPII052414 → isotype CBS H-22782, additional isotype HMAS196223).

Notes: The fungus on the isotype is morphologically indistinguishable from C. purpureofuscum. As noted by Sandoval-Denis et al. (2016b), this is a serious discrepancy from the ITS sequence derived from the ex-type (FJ914686), which matches the epitope of C. stemonitis, and hence cannot represent C. purpureofuscum (Fig. 2). It is probable that mislabelling or cross contamination of the original culture occurred, and the name must be regarded as a nomen dubium.

Cephalotrichum inflatum Y.L. Jiang & T.Y. Zhang, Mycotaxon 117: 213. 2011.

Specimen examined: China, Sichuan Province, Mianyang, dried culture isolated from mountain soil, Aug. 8. 2005, Y.L. Jiang (holotype HSAUPII050918 → isotype CBS H-22784, additional isotype HMAS196226).

Notes: This species is a synonym of C. microsporum. The main distinctive feature of C. inflatum was the presence of distinctly swollen cells at the top of the synnemata, from which the conidiogenous cells arise. When cultures were grown on PDA, this feature was also observed in our C. microsporum isolates. Although the ITS sequence of C. inflatum has 1 nt difference from the ex-type strain of C. microsporum (CBS 523.63), it is identical to that of C. microsporum strain DTO 207-C6.

Cephalotrichum longicollum Y.L. Jiang & T.Y. Zhang, Mycotaxon 117: 213. 2011.

Specimen examined: China, Sichuan Province, Emei Mountain, dried culture isolated from soil, Aug. 9. 2005, Y.L. Jiang (holotype HSAUPII052414 → isotype CBS H-22785, additional isotype HMAS196228).

Notes: This species is a synonym of C. purpureofuscum. The original description is inaccurate, according to our observations, with conidiogenous cells 8–11 (–12.5) × (2.5–)3–4 μm, and conidia (4–)5–6 × 3–3.5 (–4) μm. The isotype material contains only short synnemata 475–500 μm tall; however, synnemata of this stature are not uncommon in C. purpureofuscum. Morton & Smith (1963) examined isolates of C. purpureofuscum with reduced synnemata, as little as 50 μm tall. The morphological identity with C. purpureofuscum is confirmed by DNA data. The ITS sequence from the ex-type of C. longicollum has 1 nt difference from the reference strain of C. purpureofuscum (CBS 174.68, Fig. 2), but is identical to the ITS sequences of the other C. purpureofuscum isolates included in this study (data not shown).

Cephalotrichum microsporum Y.L. Jiang & T.Y. Zhang, Mycotaxon 117: 216. 2011.

Specimen examined: China, Yunnan Province, Pingbian County, dried culture isolated from forest soil, Oct. 11. 2004, J.J. Xu (holotype HSAUPII052414 → isotype CBS H-22787, additional isotype HMAS196230).

Notes: This is a synonym of C. purpureofuscum. The isotype material contains elements of two fungi, synnemata of C. purpureofuscum and numerous mesocoidia and macroconidia of a Fusarium spp. The original description deviates from our observations of the synnemata on the type material. Synnemata are taller than reported, (305–)325–650 μm tall, the conidiogenous cells are shorter and wider, 5.5–8 × 3–4 μm, and the conidia are larger, (4.5–)5–6 (–6.5) × (2.5–)3–3.5 (–4) μm,
all dimensions that fit well with \textit{C. purpureofuscum}. The ITS sequence has 1 nt difference from the reference strain of \textit{C. purpureofuscum} (CBS 174.68, Fig. 2), but is identical to the ITS sequences of the other \textit{C. purpureofuscum} isolates included in this study (data not shown).

**Cephalotrichum ovoidum** Y.L. Jiang & T.Y. Zhang, Mycotaxon 117: 217. 2011.

Specimen examined: \textit{China}, Sichuan Province, Jiuzhaigou, dried culture isolated from forest soil, Aug. 18. 2005, Y.L. Jiang (holotype HSAUPi370846 → isotype CBS H-22789, additional isotype HMAS196231).

*Notes*: Based on the original publication, this species could be synonymised with \textit{C. microsporum}. However, the isotype material is in poor condition. Only conidia were observed, while synnema stipes and conidial heads were not well preserved. The ITS phylogeny suggests a close affinity with both \textit{C. microsporum} and \textit{C. robustum}. Until the remainder of the holotype can be examined, or a fresh isolate obtained, \textit{C. ovoidum} should be considered a provisional synonym of \textit{C. microsporum}.

**Cephalotrichum robustum** Y.L. Jiang & T.Y. Zhang, Mycotaxon 117: 218. 2011.

Specimen examined: \textit{China}, Sichuan Province, Jiuzhaigou, dried culture isolated from forest soil, Aug. 18. 2005, Y.L. Jiang (holotype HSAUPi370875 → isotype CBS H-22789, additional isotype HMAS196232).

*Notes*: This fungus morphologically resembles \textit{C. microsporum}, \textit{C. purpureofuscum} and \textit{C. ovoidum}, but conclusive comparisons are impossible because of the poor condition of the isotype material (see notes on \textit{C. ovoidum} above). The ITS phylogeny shows a relationship with \textit{C. microsporum}, from which \textit{C. robustum} differs morphologically by its shorter synnemata and longer conidia. This species is provisionally synonymised with \textit{C. microsporum} until the holotype material of fresh isolations can be examined.

**Cephalotrichum terricola** Y.L. Jiang & T.Y. Zhang, Mycotaxon 117: 221. 2011.

Specimen examined: \textit{China}, Sichuan Province, Panzhihua, dried culture isolated from mountain soil, Aug. 13. 2005, Y.L. Jiang (holotype HSAUPi370924 → isotype CBS H-22791, additional isotype HMAS196227).

*Notes*: This is a synonym of \textit{C. purpureofuscum}. The isotype contains two fungi, synnemata of \textit{Cephalotrichum} and second hyaline fungus, probably an \textit{Aspergillus} sp. The synnemata show some differences from the original description. The conidial surface is not smooth as reported but presents some fine roughness. Most conidia are finely pointed, but conidia with rounded apices were also commonly observed. The synonymy is supported by sequence data. The ITS sequence from the ex-type of \textit{C. terricola} has 1 nt difference with the reference strain of \textit{C. purpureofuscum} (CBS 174.68), but is identical to ITS sequences of other \textit{C. purpureofuscum} isolates included in this study (data not shown).

**Cephalotrichum verrucipes** Y.L. Jiang & T.Y. Zhang, Mycotaxon 117: 223. 2011.

Specimen examined: \textit{China}, Sichuan Province, Jiuzhaigou, dried culture isolated from forest soil, Aug. 19. 2005, Y.L. Jiang (holotype HSAUPi370849 → isotype CBS H-22792, additional isotype HMAS196234).

*Note*: This is a synonymous \textit{Penicillium} species closely matching morphologically with \textit{P. clavigerum}. Apart from the reported percurrent rather than phialidic conidiogenesis, the protologue of \textit{C. verrucipes} is more or less consistent with this synonymy.

**DISCUSSION**

This study presents a molecular phylogenetic study of species of the genus \textit{Cephalotrichum}, clarifying the identity of species recently described from China, reclassifying the white synnematosus species as \textit{Acaulium album}, and confirming the identity of the species occurring in the built environment.

\textit{Cephalotrichum purpureofuscum} has a worldwide distribution and is mainly isolated from soil, dung and wood (Domsch et al. 2007) and as noted below is also common indoors. The absence of clear diagnostic morphological characters (e.g. smooth conidia, absence of setae) can be used to identify an isolated as belonging to the \textit{C. purpureofuscum} species complex (Sandoval-Denis et al. 2016a, b). The newly described \textit{C. domesticum} morphologically resembles \textit{C. purpureofuscum}, but molecular data can easily separate the two species, using any of the three genes studied here. All \textit{C. domesticum} isolates were initially identified as \textit{C. purpureofuscum} at CBS based on their morphology. Several of the recently described species from China fall into the broad concept of \textit{C. purpureofuscum}, and are synonymised here (\textit{C. acutisporum}, \textit{C. longicillum}, \textit{C. oblongum} and \textit{C. terricola}, with \textit{C. cylindrosporum} and \textit{C. macrosporum} possible synonyms). \textit{Cephalotrichum microsporum} also resembles \textit{C. purpureofuscum} and \textit{C. domesticum}, with smooth conidia and the lack of setae, but can be distinguished but its smaller conidia and synnemata. Morphologically, the group of species that would previously have been included in \textit{Trichurus} are easily recognized, with two species with coiled setae being distinguished by the length of the synnemata, 500–1000 μm for \textit{C. gorgonifer} and <500 μm for the newly described \textit{C. telluricum}. The two species with straight setae, \textit{C. cylindricum} and the newly described \textit{C. transvaalense}, are morphologically very similar but easily distinguished by DNA sequences.

All 16 phylogenetic species of \textit{Cephalotrichum} recognised can be identified with \textit{tef1} and \textit{tub2} partial gene sequences. One anomaly is the strain \textit{C. nanum} CBS 191.61, which does not group with other \textit{C. nanum} isolates based on \textit{tef1} (data not shown, all single gene phylogenies are submitted to TreeBase). Based on ITS alone, \textit{C. cylindricum} and \textit{C. transvaalense} cannot be distinguished (Fig. 2), but morphology and \textit{tub2} and \textit{tef1} sequences clearly differentiate them. The lack of discriminating power of ITS barcodes, in combination with the poor quality of some of the isotype herbarium specimens examined here, prevented us from conclusively characterizing four of the recently described Chinese species, leaving them as nomena dubia. This highlights the importance of depositing living material in internationally accessible culture collections for taxonomic and biodiversity studies.

In this study, five \textit{Cephalotrichum} spp. were confirmed for the built environment, the newly described \textit{C. domesticum}, \textit{C. gorgonifer} (previously reported by Abbott 2000), \textit{C. microsporum} (Prezant et al. 2008, Samson et al. 2010, Flannigan et al. 2011), \textit{C. purpureofuscum} (Abbott 2000, Sandoval-Denis et al. 2016b), and newly reported \textit{C. verrucisporum}. \textit{Cephalotrichum gorgonifer} (formerly mainly known as \textit{Trichurus spiralis}) seems to be the most common species in the indoor environment, with \textit{C. purpureofuscum} and \textit{C. microsporum} as other commonly
isolated species. *Cephalotrichum gorgonifer* and *C. microsporum* both have a worldwide distribution, and have mostly been isolated from cultivated soils (Domsch et al. 2007). They both degrade cellulose (Domsch et al. 2007), and the latter may decay wood (Nilsson 1973). Some isolates of *C. microsporum* also decompose xylan (Domsch & Gams 1969), and may produce extracellular keratinase capable of hydrolysing keratinous materials such as wool, hair, nails and skin (Gradszlar et al. 2000).

Only one indoor strain of *C. verrucisporum* was isolated (DTS 055-D7), for which we unfortunately do not have more information other than that it was isolated from the indoor environment in Germany. The species is morphologically similar to *C. asperulum* and *C. spirale*, as all have rough-walled conidia. Both *C. verrucisporum* isolates were originally identified as *Doratomyces asperulus* (*C. asperulum*) at CBS. Additional isolates are necessary to determine whether *C. verrucisporum* actually occurs consistently in the indoor environment, or whether this was just an incidental, single isolation.

During the publication process of this manuscript, three new *Cephalotrichum* species are described from a carbonate cave in China (Jiang et al. 2017). Phylogenetic comparison places the new species *C. oligotrophicum* and *C. laeve* as sister species of *C. verrucisporum*. The new species *C. guizhouense* is closely related to *C. dendrocephalum* and our newly described species *C. domesticum* and *C. tenuissimum* and *C. domesticum*. With the now up-to-date phylogeny of the genus *Cephalotrichum*, identification of (new) *Cephalotrichum* species is made much easier. We expect more *Cephalotrichum* species to be discovered and described.

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