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pg. 110

110

A taxonomic re-evaluation of *Phialocephala* phycomyces

K. Jacobs, M.J. Wingfield, A. Jacobs, and B.D. Wingfield

Abstract: Phialocephala was established for species that produce their conidia from phialides at the apex of dark mononematous conidiophores. Phialocephala phycomyces (Auersw.) Kendrick was described more than a century ago as the only species of the genus Hantzschia. The phialides of P. phycomyces are not as deep-seated as those found in Phialocephala dimorphospora Kendrick, the type of Phialocephala, and conidium development occurs near the apex of the conidiogenous cell. Furthermore, P. phycomyces is characterized by reddish-brown conidiophores and is cycloheximide resistant. Based on morphological, as well as molecular comparisons, we concluded that P. phycomyces is a distinct genus, Kendrickiella gen.nov.

Key words: Leptographium complex, morphology, phylogeny, Phialocephala, Kendrickiella.

Résumé: Le genre Phialocephala a été établi pour regrouper les espèces qui produisent leurs conidies à partir de phialides à l'apex de conidiophores mononèmes foncés. On a décrit le Phialocephala phycomyces (Auersw.) Kendrick, il y a plus de cent ans, comme seule espèce du genre Hantzschia. Les phialides du P. phycomyces ne sont pas aussi fortement ancrées que celles qu'on retrouve chez le Phialocephala dimorphospora, le type du genre Phialocephala, et le développement de la conidie se fait près de l'apex de la cellule conidiogène. De plus, le P. phycomyces est caractérisé par des conidiophores brun-rougeâtre et n'est pas résistant à la cycloheximide. En se basant sur la morphologie ainsi que les comparaisons moléculaires, les auteurs concluent que le P. phycomyces appartient à un genre distinct, le Kendrickiella gen.nov.

Mots clés: complexe Leptographium, morphologie, phylogénie, Phialocephala, Kendrickiella.

[Traduit par la Rédaction]

Introduction

Phialocephala Kendrick, together with Leptographium Lundberg & Melin, forms part of the Leptographium complex, which also originally included Verticicladiella Hughes. Phialocephala can be distinguished from Leptographium and Verticicladiella based on differences in conidium development (Kendrick 1961, 1962, 1963, 1964a, 1964b). Phialocephala species are characterized by phialidic conidium ontogeny, in contrast to the annellidic and sympodial development of Leptographium and Verticicladiella spp., respectively (Kendrick 1961, 1962). Wingfield (1985) reduced Verticicladiella to synonymy with Leptographium, because species in these genera have indistinguishable conidium development when viewed by electron microscopy.

Leptographium spp. are anamorphs of Ophiostoma spp. (Harrington 1987, 1988) and display the taxonomically useful character of being able to tolerate high concentrations of cycloheximide. In contrast, Phialocephala spp. are sensitive

to low concentrations of cycloheximide (Harrington 1988). *Phialocephala* and *Leptographium* spp. can be distinguished also based on differences in their host relationships. *Leptographium* spp. generally occur on conifers and living woody tissue (Lagerberg et al. 1927; Harrington 1988), whereas *Phialocephala* spp. are generally associated with dead or decaying material and soil (Kendrick 1961, 1963; Siegfried et al. 1992).

Phialocephala phycomyces (Auersw.) Kendrick was described as the single species of Hantzschia by Auerswald in 1862 (Kendrick 1964) and was later transferred to Graphium (Saccardo 1886). This species was revisited after Grosmann (1932) described several species of fungi causing blue-stain on spruce in Europe. After considering both Scopularia Preuss as well as Hantzschia as possible genera for H. phycomyces, she found that the descriptions and illustrations of both Scopularia and Hantzschia were unclear. Grosmann, therefore, synonomized Hantzschia with the newly described genus, Leptographium (Grosmann 1932;

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K. Jacobs, ^{1,2} M.J. Wingfield, and A. Jacobs. Tree Pathology Co-operative Programme (TPCP), Forestry and Agricultural Biotechnology Institute (FABI), Department of Microbiology and Plant Pathology, University of Pretoria, Pretoria, 0002, Republic of South Africa.

B.D. Wingfield. Department of Genetics, University of Pretoria, Pretoria, 0002, Republic of South Africa.

¹Corresponding author (e-mail: jacobsk@em.agr.ca).

²Present address: Eastern Cereal and Oilseed Research Centre (ECORC), Agriculture & Agri-Food Canada, K.W. Neatby Building, 960 Carling Avenue, Ottawa, ON K1A 0C6, Canada.

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Jacobs et al. 111

Shaw and Hubert 1952) and H. phycomyces became Leptographium phycomyces (Auersw.) Grosm.

Kendrick (1961) established *Phialocephala* for species of the *Leptographium* complex with phialidic conidium development. *Leptographium phycomyces* was consequently transferred to *Phialocephala* as *P. phycomyces*. However, from the type material as well as the description (Kendrick 1961) of *P. phycomyces*, it is clear that this fungus has poorly developed collarettes on the phialides. Compared with the type of *Phialocephala*, *P. dimorphospora* Kendrick, it is atypical of this genus. *Phialocephala dimorphospora* has deep-seated phialides, which are characterized by distinct, well-developed collarettes. In addition, the ecology of *P. phycomyces* is unlike other species in *Phialocephala*. It appears to be tropical and has been described as a contaminant of a culture of a basidiomycete (Kendrick 1964b).

Myxocephala albida Weber, Spaaij & Oberwinkler, bears a resemblance to Phialocephala phycomyces. This is evident from the poorly developed phialides with conidia in slimy drops. The habitat of M. albida, which is soil, is also similar to that of P. phycomyces (Weber et al. 1989). Recently, a single isolate of P. phycomyces has become available to us. This enabled us to restudy the species in detail.

The aim of this study was to reconsider the taxonomic placement of *P. phycomyces* based on morphology, physiology, and molecular data.

Materials and methods

Molecular comparison

Isolates used for molecular comparisons, and their corresponding GENBANK accession numbers, included Leptographium Wingfield (CMW 2817, (Peck) L. penicillatum (Grosmann) Siemaszko (CMW453 = CBS 441.69, AF269214), Ophiostoma piceaperdum (Rumbold) Von Arx (CMW 2811, AF269215), O. francke-grosmanniae (Davidson) De Hoog & Scheffer (CMW 445 = CBS 356.77, AF269213), P. phycomyces (CMW 2556 = MUCL 38565, AF269216), P. dimorphospora (CMW 168 = ATCC 44606, AF269218), P. fortinii Wang & Wilcox (CMW 815, AF269219), P. xalapensis Persiani & Maggi (CMW 807, AF269217), and Myxocephala albida Weber, Spaaij, & Oberwinkler (CMW 2212, CMW 2239 = CBS 962.87, AF269220, AF269221). Isolates used in this study are maintained in the culture collection (CMW) of the Forestry and Agricultural Biotechnology Institute (FABI), University of Pretoria.

A basic local alignment search tool (BLAST) search with the sequence of P. phycomyces was done in GENBANK and the closest related genera were used for comparison. Sequences for closely related genera were obtained from GENBANK and the accession numbers are as follows: Aspergillus fumigatus (AF109336), Aspergillus parasiticus (AB008418), Ajellomyces dermatitidis (AF038358, AF038356), Ceratocystis albofundus (AF043605), laricicola (AF043600), Colletotrichum capsici (Z18982), (Z18978), Emericella nidulans Colletotrichum truncatum (AF109338, AF109337), Emmonsia crescens (AF038351, AF038350), Epichloe glyceriae (L07137), Epichloe typhina (L07132), Eupenicillium hirayamae (AF033418), Eupenicillium katangense (AF033458), Glomerella cingulata Monascus purpureus (AF222496, AF033394), Ophiostoma querci (AF128931), Penicillium raperi (AF033433), P. implicatum Peziza cerea (AF133164), Peziza (AF033428). (AF133171), Xylaria curta (U47840), X. hypoxylon (U47841).

Genomic DNA was extracted from 2-week-old cultures grown in ME broth (2% malt extract). This was done by grinding a small

amount of mycelium in liquid nitrogen to a fine powder and adding 1.0 μL extraction buffer (1% cetyltrimethylammonium bromide, 200mM Tris-HCl (pH 8.0), 25mM EDTA, 250 mM NaCl, 1.5% SDS]. This was then incubated in a 60°C water bath for 1 h. Proteins were removed with phenol and chloroform (1:1), followed by a series of chloroform extractions, until the interface was clean. The DNA was precipitated with 0.1 volume NaAc and 0.6 volume isopropanol and left overnight at $-20^{\circ} C$. This was then centrifuged at 13 000 rpm for 30 min; the resulting pellet was washed with cold 70% ethanol and dissolved in 100–200 μL sterile water. The presence of DNA was checked by agarose electrophoresis.

The ITS2 (internal transcribed spacer) region and part of the large subunit of the ribosomal DNA gene were amplified using the polymerase chain reaction (PCR) (Saiki et al. 1988) on a HybaidTM Touchdown thermo cycling system (Life Sciences International, U.K.). The primers ITS3 (5'-GCATAGATGAAGAAGCAGC-3') and LR3 (5'-CCGTGTTTCAAGACGGG-3') were used in these reactions. Each reaction was done in 100 μL containing 10 μL 10x PCR buffer, 20 μL of 25 mM MgCl₂, 10 mM dNTPs, 20 pmol of each primer, 0.5 μL DNA, and 1.75 U Expand *Taq* polymerase (Boehringer Mannheim, Germany). The PCR conditions were as follows: 2 min at 94°C, annealing at 48°C for 1 min, 10 s at 62°C, 2 min at 72°C with an increase of 5°C/s. This was repeated for 40 cycles, and a final elongation reaction was done at 72°C for 8 min. The resulting products were purified with the High Pure PCR product purification kit (Boehringer Mannheim) and used in the sequence reactions.

Sequencing was done on both strands using the primers ITS3, LR3, and 404X (5'-CCCTTTCAACAATTTCAC-3'). Sequencing was performed on an ABI 377 automated sequencer using the Thermo Sequenase dye terminator cycle sequencing premix kit (Perkin Elmer Applied Biosystems). Sequence data were edited in Sequence Navigator (Perkin Elmer Applied Biosystems) and manually aligned in PAUP, version 4.0 (phylogenetic analysis using parsimony) (Swofford 1993). Confidence intervals were determined by 1000 bootstrap replicates.

Morphology

Material examined included the herbarium type specimens (DAOM 34098; DAOM 64734; 63899) as well as a single live isolate (MUCL 38565) of *P. phycomyces*. These were compared with the herbarium type specimens of *Leptographium* (*L. lundbergii* Lagerberg & Melin, PREM 50548, CMW 30) and *Phialocephala* (*P. dimorphospora*, DAOM 71465(c), ATCC 24087). Fungal structures produced on 2% malt extract agar (MEA, 20 g Biolab malt extract, 20 g Biolab agar, and 1000 mL distilled water) were used for light as well as scanning and transmission electron microscopic study. For light microscopy, relevant structures from the cultures, as well as herbarium specimens, were mounted in lactophenol on glass slides. Fifty measurements of each relevant morphological structure were made and ranges and averages computed. Colours of structures and colonies were determined using the charts of Rayner (1970).

For scanning electron microscopy (SEM), small blocks of agar cut from sporulating colonies were fixed in 3% glutaraldehyde and 0.5% osmium tetroxide in a 0.1 M phosphate buffer, dehydrated in a graded acetone series and critical-point dried. Specimens were mounted and coated with gold palladium alloy and examined using a JSM 6400 scanning electron microscope.

For ultrastructural examination, the isolate of *P. phycomyces* (MUCL 38565) was grown on 2% MEA in Petri dishes at 25°C. Small blocks of agar were cut from the colony and fixed in the same manner as described for scanning electron microscopy. The material was then embedded in epoxy resin (Spurr 1969) and ultrathin sections (60 nm) were cut with glass knives, using an LKB Ultratome III. Sections were stained for 20 min with 6% ura-

112 Can. J. Bot. Vol. 79, 2001

Fig. 1. One of the three most parsimonious trees derived from analysis of a partial sequence of the large subunit of the ribosomal gene. Tree length = 640. The number of base substitutions are indicated below the tree by the scale and the bootstrap values are indicated above the branches.

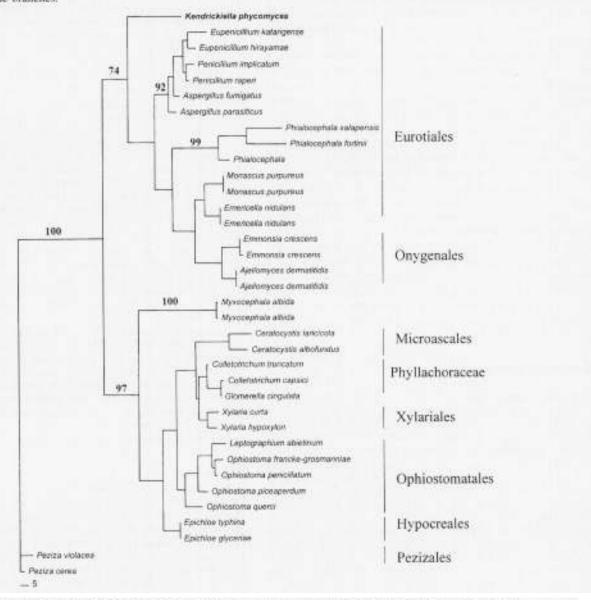


Table 1. Tolerance of Ophiostoma piliferum, Leptographium lundbergii, Phialocephala dimorphospora, and Kendrickiella phycomyces to various concentrations of cycloheximide after 6 days of growth at 25°C.

Cycloheximide concentration (g/L)	Colony size (mm)			
	L. lundbergii	O. piliferum	P. dimorphospora	K. phycomycoides
0	40±3	14±2	9±0.5	9±1
0.05	29±2	11±2.5	7±0.2	6±0.5
0.1	30±2	11±2	6±0.3	4±0.5
0.5	25±1.5	9±1	4±0.5	0
1	24±2	10±1	4±0.2	0

Note: Values are means ± SD.

nyl acetate and 10 min in lead citrate and examined with a Philips CM100 transmission electron microscope.

The optimal growth temperatures for *P. phycomyces* (MUCL 38565), *L. lundbergii* (CMW 30), *P. dimorphospora* (CMW 168) and *Ophiostoma piliferum* (Fries) H. & P. Sydow (CMW 2481) were determined by inoculating eight MEA plates with 6 mm di-

ameter agar disks taken from the actively growing margins of a 2-week-old isolate. The plates were incubated at temperatures ranging from 5 to 35°C at 5°C intervals. Cycloheximide tolerance was determined for *P. phycomyces* (MUCL 38565), *L. lundbergii* (CMW 30), *P. dimorphospora* (CMW 168), and *O. piliferum* (CMW 2481) by inoculating five MEA plates amended with

Jacobs et al. 113

increasing concentrations (0, 0.05, 0.1, 0.5, 1.0 g/L) of cycloheximide and incubating them at 25°C. Colony diameters were measured after 8 days, and growth was computed as an average of ten readings (two per plate).

Results

Molecular comparisons

Amplification using primers ITS3 and LR3, yielded products of more or less 1.3 kb (kilobasepairs). A region of 304 bp (basepairs) of the LSU was successfully sequenced for all species. From the analysis, three most parsimonious trees were obtained displaying similar topologies. The shortest tree length was 640 steps with a consistency index (CI) of 0.534 a homoplasy index (HI) of 0.466, and a retention index (RI) of 0.785. Two distinct clades were observed (Fig. 1). The first of these includes genera in the Eurotiales and Onygenales. Kendrickiella phycomycoides clustered together with this group. Species of Phialocephala was also found to group in the first clade, although distinct from K. phycomycoides. Isolates of M. albida grouped away from Phialocephala and Kendrickiella in the second clade. This clade also contained genera from the Microascales (Ceratocystis spp.) and Ophiostomatales (Ophiostoma and Leptographium spp.).

Morphological and growth characteristics

Comparison of the isolate of P. phycomyces (MUCL 38565) with the herbarium type specimens and the complete description provided by Kendrick (1964b), confirmed its identity. Both the isolate, as well as the herbarium material are characterized by reddish brown colonies as a result of the pigmentation of the conidiophore stipes. This was reported by Kendrick (1964b) and appears to be characteristic of the species. It is also unlike the colony colour typical of species in Leptographium or Phialocephala. Closer examination of the isolate of P. phycomyces using scanning as well as transmission electron microscopy indicated that the conidiogenous cells of P. phycomyces are distinctly phialidic with periclinal thickening (Figs. 5 and 6) although the collarettes are inconspicuous. These are unlike the pronounced collarettes of P. dimorphospora and most other Phialocephala spp. The isolate of P. phycomyces was found to have a tolerance to cycloheximide, although lower than other Phialocephala spp. that have been tested (Table 1).

These results lead us to conclude that *P. phycomyces* cannot be adequately accommodated in either *Leptographium* or *Phialocephala*. We, therefore, propose that this species be placed in a new genus, *Kendrickiella*, with *K. phycomycoides* comb. nov. as the type of this genus.

Kendrickiella K. Jacobs & M.J. Wingf. gen. nov.

Conidiophora recta, solitaria. Stipites pigmentosi, rubrobrunnei. Apparatus conidiogenus complexus cum seriebus pluribus ramorum, in cellulis conidiogenis terminantium. Celluli conidiogeni phialidosi, collariculis inconspicuis, manifeste periclinaliter incrassatis. Ameroconidia non catenata, conidia in massa mucosa in apice conidiophori. Resistunt densissimo soluto corpori vulgo dictu *cycloheximide*.

Conidiophores straight, solitary. Stipes pigmented, reddish brown. Complex conidiogenous apparatus with several series of branches on the apex of the stipe, terminating in conidiogenous cells. Conidiogenous cells phialidic with poorly developed collarettes, pronounced periclinal thickening, visible under the transmission electron microscope. Ameroconidia not in chains, conidia in mucilaginous mass on the apex of the conidiophore. Able to tolerate cycloheximide.

TYPE SPECIES: Kendrickiella phycomycoides comb. nov.

Kendrickiella phycomycoides (Auerswald) K. Jacobs & M.J. Wing. comb. nov.

- ≡ *Hantzschia phycomyces* Auerswald. Fungi Eur. 411. 1862. (Basionym)
- ≡ Graphium phycomyces (Auerswald) Saccardo. Sylloge Fungorum 4: 614. 1886.
- ≡ Leptographium phycomyces (Auerswald) Grosmann. Hedwigia, 71: 193. 1932.
- ≡ *Phialocephala phycomyces* (Aerswald) Kendrick. Can. J. Bot. **42**: 1292. 1964*b*.

TELEOMORPH: none known.

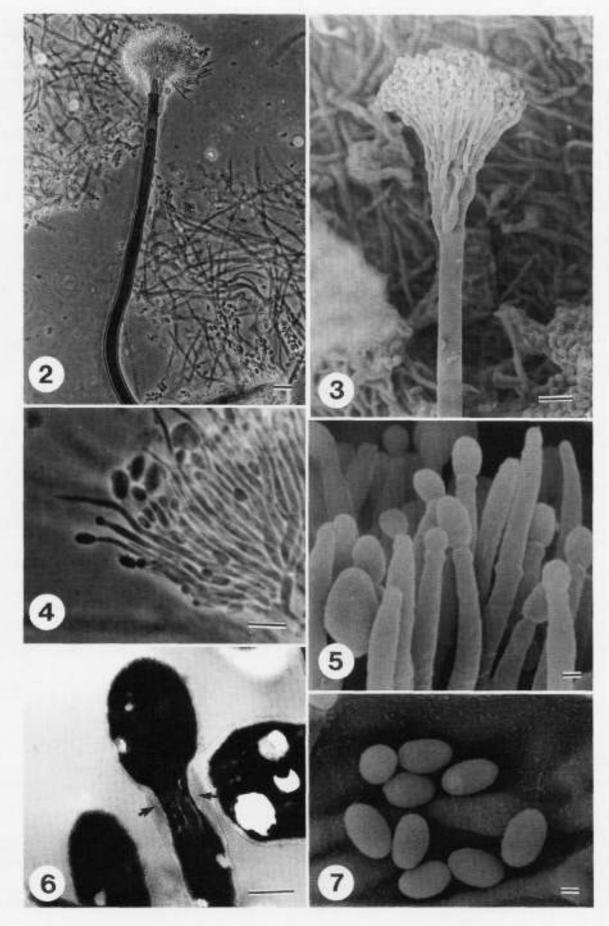
Colonies with optimal growth at 25°C on 2% MEA, reaching 12 mm in diameter in 12 days. No growth below 20°C or above 30°C. Able to withstand high concentrations of cycloheximide with a 53% reduction in growth on 0.1 g/L cycloheximide after 8 days at 25°C in the dark. Colony chestnut (9′m) in centre, becoming cream buff (19″f). Colony margin smooth. Hyphae submerged or on top of solid medium with no aerial mycelium, hyaline, smooth, not constricted at the septa, (2.0–)2.5(–4.0) µm diameter.

Conidiophores occurring singly, arising directly from the mycelium, erect, macronematous, mononematous, (150-) 316(-520) µm in length, rhizoidlike structures absent (Figs. 2 and 8A). Stipe reddish brown, smooth, cylindrical. simple, one to four septate, (100-)247(-450) µm long (from first basal septum to the base of the primary branches), (6.0-) 8.0(-9.0) µm wide below primary branches, apical cell not swollen, (8.0-)11(-15.5) µm wide at base, basal cell not swollen. Conidiogenous apparatus (50-)68(-90) long, excluding the conidial mass, with three or four series of cylindrical branches; two to four primary branches, reddish brown, smooth, cylindrical, aseptate, (12-)15.5(-20) µm long and (5.0-)6.0(-9.0) µm wide, secondary branches light reddish brown to hyaline, aseptate, $(8.0-)10(-12) \mu m \log$, (3.0-)4.5(-6.0) μm wide; tertiary branches hyaline, aseptate, (4.0-) $8.5(-12) \mu m long$, $(6.0-)8.0(-11) \mu m wide$, quaternary branches aseptate, hyaline, $(6.0-)8.5(-10) \mu m long$, (1.0-)2.0(-3.0) µm wide (Figs. 3 and 8B). Conidiogenous cells discrete, two or three per branch, cylindrical, tapering slightly at the apex, $(8.0-)13(-22) \mu m$ long and $(1.0-)1.5(-2.0) \mu m$ wide. Conidium development phialidic with poorly developed collarettes (Figs. 4-6). Conidia, aseptate, ellipsoidal, $(3.0-)4.0(-7.0) \times (1.0-)2.0(-3.0) \mu m$. Conidia accumulating in cream-coloured slimy droplets at the apex of conidiogenous apparatus (Figs. 7 and 8C).

LECTOTYPE: DAOM 34098 (slides), oak barrel in Germany, collected C.A. Hantzsch, described: Auerswald in Rabenhorst, Fungi europaei 441. 1862.

ADDITIONAL SPECIMENS: DAOM 64734 (herbarium material), Isolated as contaminant of culture of polypore, collected: R.

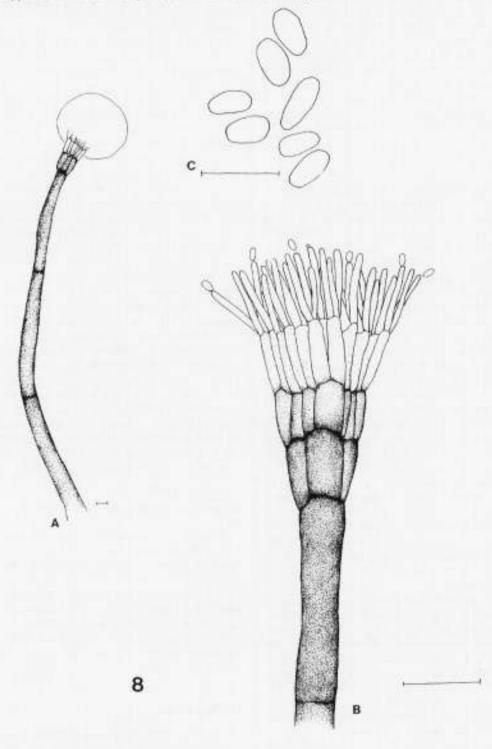
114 Can. J. Bot. Vol. 79, 2001



Jacobs et al. 115

Figs. 2–7. Light, scanning and transmission micrographs of conidiophore and conidia of Kendrickiella phycomycoides (MUCL 38565).
Fig. 2. Conidiophore. Scale bar = 10 μm. Fig. 3. Conidiogenous apparatus. Scale bar = 10 μm. Figs. 4 and 5. Conidiogenous cell.
Scale bars = 10 and 1 μm, respectively. Fig. 6. Section through a conidiogenous cell. The arrow indicates periclinal thickening. Scale bar = 1 μm. Fig. 7. Conidia. Scale bar = 1 μm.

Fig. 8. Conidiophores and conidia of Kendrickiella phycomycoides (MUCL 38565). (A) Conidiophore without rhizoids. (B) Conidiogenous apparatus. Scale bar = 10 μm. (C) Conidia. Scale bar = 10 μm.



Cailleux, St. Laurant du Maroni, French Guiana, August 1952; DAOM 63899 (herbarium material), isolated from soil, Belgian Congo, collected J. Meyer, December, 1954; MUCL 38565 (live isolate), isolated as a contaminant of a polypore (*Ganoderma* sp.), Reserva de Produccion Faunistica Cuyabeno, Prov. Sucumbios, Equador, collected C. Decock, July 1993.

ETYMOLOGY: Kendrickiella was chosen as generic name for this fungus, instead of the name Hantzschia originally given to this fungus. Hantzschia Auerswald was declared an illigitimate name (Art. 53), after Lagerberg et al. (1927) noted that the name Hantzschia Grunow was already in use for an algal genus. The specific name of this fungus has been changed from phycomyces to phycomycoides to be grammatically correct. Kendrickiella is the female form of the name Kendrick. For the specific name phycomyces, which is a neuter form, to be used with this generic name, it had to be changed to the female form, namely phycomycoides.

Discussion

Leptographium and Phialocephala spp. have traditionally been distinguished based on obvious differences in conidium development. In some cases, these differences are not so obvious. This was illustrated by Mouton et al. (1992) who studied the anamorph of Ophiostoma francke-grosmanniae. Based on morphology, this species was thought to best reside in Phialocephala (Upadhyay 1981) and, thus, would have been the only Ophiostoma sp. with an anamorph in Phialocephala. However, closer examination revealed that conidium development in this species is annellidic, and it is thus a typical Leptographium. The closely packed annellations at the apex of the conidiogenous cells lead to the appearance of poorly developed collarettes when the fungus is viewed using light microscopy. Likewise, initial examination of the conidiogenous cells of K. phycomycoides, prompted us to question the nature of its poorly developed collarettes.

Electron microscope studies revealed that conidia in *K. phycomycoides* emerge from phialides that have pronounced periclinal thickening. This is despite the fact that the conidiogenous cells are tapered, and the collarettes are inconspicuous. In the broad sense, the species could be accommodated in *Phialocephala*. However, when compared with the type of *Phialocephala*, namely *P. dimorphospora*, the morphology of the conidiogenous cells is entirely different. *Phialocephala dimorphospora* is characterized by deep-seated phialides with pronounced collarettes, whereas those of *K. phycomycoides* are poorly developed and hardly visible under the light microscope.

Harrington (1988) observed that species in *Phialocephala* are generally sensitive to the antibiotic cycloheximide, whereas *Leptographium* spp. are tolerant to high concentrations of the antibiotic. Marais (1996), however, found species in *Phialocephala* to be quite variable in their tolerance towards cycloheximide. *Kendrickiella phycomycoides* exhibits a lower level of tolerance to cycloheximide and, in this characteristic, resembles *Leptographium*.

Kendrickiella phycomycoides superficially resembles other species described in *Phialocephala*. However, *K. phycomycoides* can be distinguished from other *Phialocephala* and *Leptographium* spp. based on the characteristic reddish brown

colour of the colony and conidiophore stipes. Species in *Leptographium* and *Phialocephala* are generally characterized by olivaceous colonies and olivaceous brown stipes (Lagerberg et al. 1927; Jacobs et al. 1997, 1999; Van der Westhuizen et al. 1995).

Kendrickiella phycomycoides, like Phialocephala spp., has not been associated with a teleomorph genus. This is in contrast to many species of Leptographium that are known to be anamorphs of Ophiostoma (Grosmann 1932; Kendrick and Molnar 1965; Robinson-Jeffrey and Davidson 1968). Comparison of the habitat of these taxa, revealed that Leptographium spp. occupy mostly woody substrates, in contrast to Phialocephala spp. that are found to inhabit leaves, soil, and lignified tissues (Kendrick 1961, 1963; Siegfried et al. 1992). Kendrickiella phycomycoides has been reported from a variety of habitats including spruce and pine (Mathiesen 1950), oak barrels, polypores, and soil (Kendrick 1964b), although the reliability of these records on pine and spruce should be questioned. Two separate records of the fungus from polypores in the tropics (Kendrick 1964b) suggest that it might be a mycoparasite or fungicolous fungus.

Kendrickiella phycomycoides superficially resembles M. albida, the single species described in Myxocephala (Weber et al. 1989). In both cases isolates are characterized by complex conidiophores and phialides with poorly developed collarettes. However, K. phycomycoides can be distinguished from Myxocephala based on the reddish-brown colonies of the former compared with the brown colonies of the latter. Also conidiophores of M. albida are twice as long as those found in K. phycomycoides and occur in groups. This is in contrast to the solitary conidiophores of K. phycomycoides.

Molecular data generated in this study show that *K. phycomycoides* cannot be accommodated in either *Leptographium* or *Phialocephala* and that it represents a distinct taxon. The data also show that it is a distinct taxon from *Myxocephala*. *Kendrickiella phycomycoides* appears to be related to the Eurotiales, which include species of *Penicillium* and *Aspergillus*. *Kendrickiella phycomycoides* can, however, be confidently distinguished from the other genera in this group based on morphology and molecular differences to support the establishment of a new genus.

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