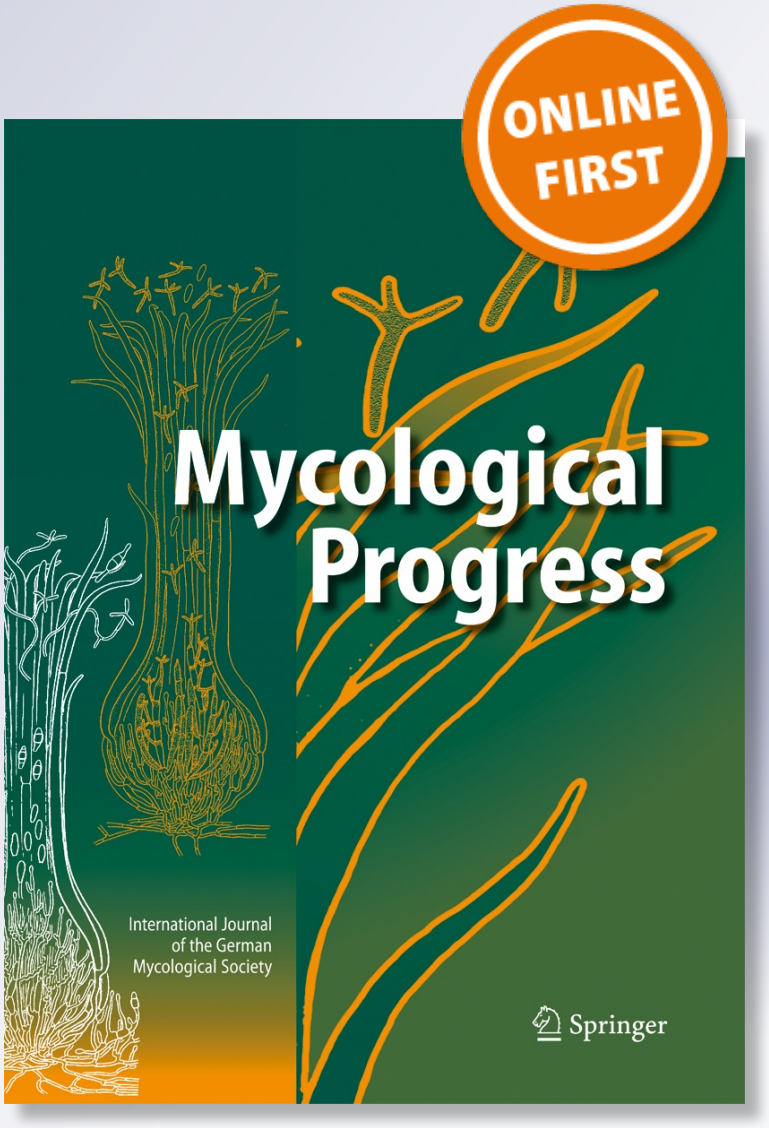
Taxonomic re-evaluation of the Ceratobasidium-Rhizoctonia *complex and* Rhizoctonia butinii, *a new species attacking spruce*

Franz Oberwinkler, Kai Riess, Robert Bauer, Roland Kirschner & Sigisfredo Garnica

Mycological Progress

ISSN 1617-416X

Mycol Progress
DOI 10.1007/s11557-013-0936-0



Springer

Mycol Progress
DOI 10.1007/s11557-013-0936-0

ORIGINAL ARTICLE

Taxonomic re-evaluation of the *Ceratobasidium-Rhizoctonia* complex and *Rhizoctonia butinii*, a new species attacking spruce

Franz Oberwinkler · Kai Riess · Robert Bauer · Roland Kirschner · Sigisfredo Garnica

Received: 11 September 2013 / Accepted: 22 September 2013

Abstract A taxonomic re-evaluation of the *Ceratobasidium-Rhizoctonia* group suggests that *Ceratobasidium* contains only the type species *C. calosporum*, which deviates in micromorphological and ultrastructural characters from all other species so far included in that genus. *Rhizoctonia* species are compared with the type species of *Ceratobasidium, Cejpomyces, Oncobasidium, Tofispora, Waitea,* and *Ypsilonidium*. The micromorphology, ultrastructure, cellular interaction with the host, and molecular phylogeny of a *Rhizoctonia* species parasitic on needles and young shoots of *Picea abies* have been studied. The parasite has been known for a long time, but misinterpreted, and not named so far. *Rhizoctonia butinii* is described and compared with related species of the genus.

Keywords Basidiomycota · Nomenclature · Phytopathology · Spruce pathogen · Taxonomy

Introduction

The genus *Ceratobasidium* was introduced by Rogers (1935) with *C. calosporum* as type species (Fig. 1a–c), and with the additional species *C. cornigerum* (Figs. 2c and 3a) and *C. obscurum*. Eriksson and Ryvarden (1973) proposed *C. stridii*, an apparently saprotrophic species with significantly smaller basidiospores than *C. cornigerum*. Jackson (1949) included *Tulasnella anceps* (Fig. 3b) in *Ceratobasidium*, a decision accepted in following treatments. The plant parasitic *Hypochnus setariae* was transferred into *Ceratobasidium* by Oniki et al. (1986). A leaf parasite on tropical woody plants was described as *Koleroga noxia* (Donk 1958) and was transferred into *Ceratobasidium* by Roberts (1999). The saprotrophic *C. pseudocornigerum* (Fig. 3c) proposed by Christiansen (1959), and *C. angustisporum*, isolated by Warcup and Talbot (1980) from the Australian orchid *Pterostylis mutica*, were considered to be synonymous (Roberts 1999). Species with globose to subglobose spores, isolated from Australian terrestrial orchids and induced to produce basidial stages on artificial media, were described by Warcup and Talbot (1971) as *C. sphaerosporum*, and (1980) as *C. globisporum*. Bisterigmate species described by Eriksson and Ryvarden (1973) as *C. bicorne*, by Warcup and Talbot (1980) as *Ypsilonidium anomalum*, and by Cízek and Pouzar (1992) as *Thanatephorus ovalisporus*, were all treated as synonyms by Roberts (1999).

Species of the genus *Rhizoctonia* (Fig. 2a) are considered to develop thickening hymenia, thus forming more than one layer of basidia with comparatively long sterigmata, sometimes called indeterminate, and the genera *Aquathanatephorus, Cejpomyces* (Fig. 4a), *Oncobasidium* (Fig. 2a), *Tofispora* (Fig. 4b), *Uthatobasidium* (Figs. 1d, e, 2c, and 3a), and *Ypsilonidium* (Fig. 3d) were put into synonymy (Roberts 1999).

The capability to form anastomoses has been considered to document a certain degree of relatedness. Group V in a study of *Rhizoctonia solani* by Schultz (1937), and group E of Richter and Schneider (1953) belong in the genus *Ceratobasidium*. Parmeter et al. (1969) distinguished four anastomosis groups (AGs) that were confirmed and complemented with an additional one by Ogoshi (1972a, b). Adams and Butler (1979) claimed AGs 1–4 as constituting biological species. These authors introduced serologic techniques, intending to elucidate certain chemical homologies, especially in proteins and

Dedicated to Prof. Dr. Heinz Butin on the occasion of his 85th birthday.

F. Oberwinkler · K. Riess · R. Bauer · S. Garnica
Institut für Evolution und Ökologie, Evolutionäre Ökologie der Pflanzen, Universität Tübingen, Auf der Morgenstelle 1, 72076 Tübingen, Germany

R. Kirschner (✉)
Department of Life Sciences, National Central University, Jhongli City 320, Taoyuan County, Taiwan (Republic of China)
e-mail: kirschner@ncu.edu.tw

Published online: 05 October 2013

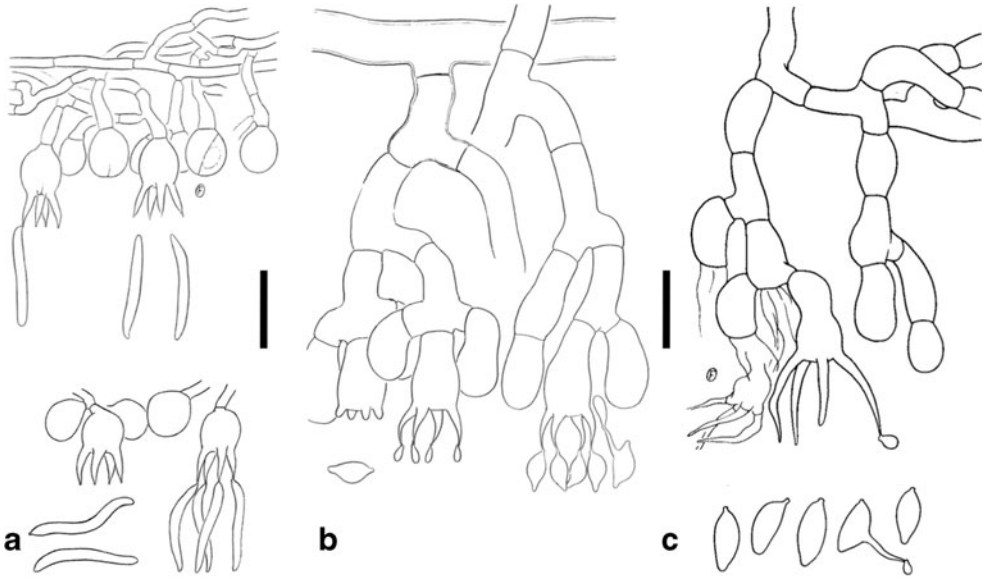


Fig. 1 **a** *Ceratobasidium calosporum*, from holotypus collection; section of basidiocarp with subhymenium, hymenium with a single layer of basidia, some of them partly or completely longitudinally septate; basidia of different developmental stages; basidiospores. **b** *Uthatobasidium fusisporum*; section of basidiocarp with basal hyphae, subhymenium, and basidia in different developmental stages, J. Poelt 31.5.1962; **c** parts of thickening hymenium, basidiospores, one spore germinating with a secondary spore, FO 28180.—Bars for all illustrations 20 μm

glycoproteins. They found that serologic groups correspond to all AGs, except for AG-2 type 1 and 2. Binucleate *Rhizoctonia* species (BNR), comprising *Ceratobasidium cornigerum* and related taxa were divided into seven *Ceratobasidium* AGs (CAGs) by Burpee et al. (1980) and into 17 (AG-A to AG-Q) by Ogoshi et al. (1983), a classification that has been widely used. They were extended to 21 BNR AGs by Sneh et al. (1991); however, 16 AGs are actually recognised, and this classification is supported by rDNA-ITS sequence data (Sharon et al. 2008). All publicly available ITS sequences of Ceratobasidiaceae were used by Veldre (2011) and Veldre et al. (2013) to test a non-random phylogenetic distribution of nutritional modes. These seem to be phylogenetically conserved, separated in parasites and orchid mycorrhizae (ORMs), including isolates from soil. Ceratobasidiaceous ectomycorrhizae (ECMs) appear to have evolved twice with considerable impact on mycoheterotrophy. Plant parasites occur worldwide on herbaceous and woody hosts and attack mainly living roots, leaves and young tissues. Hartig (1884) described *Trichosphaeria parasitica*, a needle-parasite on conifers,

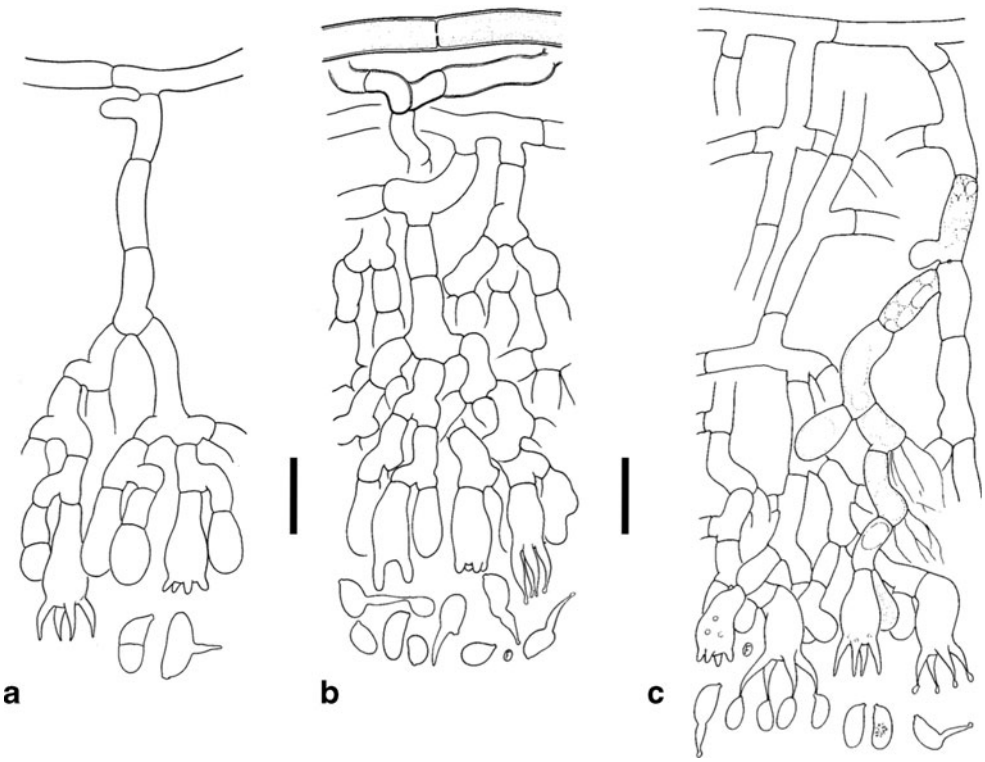


Fig. 2 **a** *Oncobasidium theobromae* from holotypus culture. Occasionally, basidiospores can be transversely septate, and they are capable of producing secondary spores. **b** *Rhizoctonia solani* on *Solanum tuberosum*, FO 19663, section through the whole basidiocarp showing basal hyphae, subhymenium, thickening hymenium, basidia in different developmental stages, and basidiospores, four germinating with secondary spores. **c** *Ceratobasidium cornigerum* s.l., FO 12904, from Oberwinkler (1972) as *Uthatobasidium* sp., section through the whole basidiocarp showing basal hyphae, subhymenium, thickening hymenium, basidia in different developmental stages, and basidiospores, two germinating with secondary spores.—Bars for all illustrations 20 μm

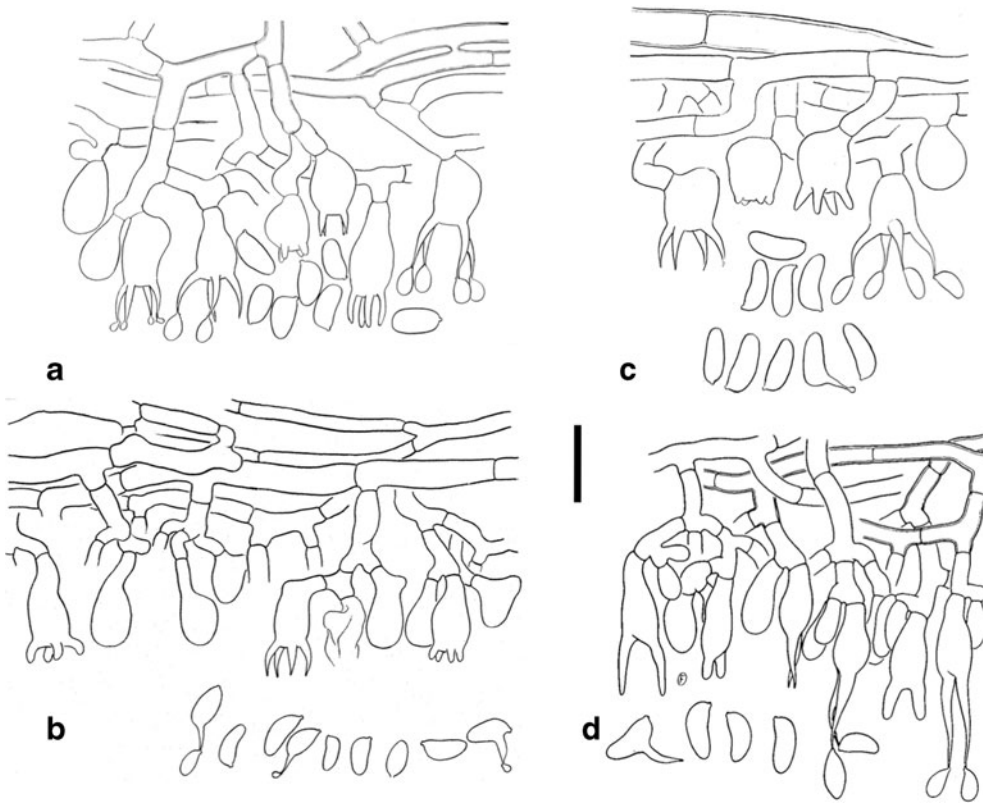


Fig. 3 **a** *Ceratobasidium cornigerum*, FO 44; section through the whole basidiocarp showing basal hyphae, subhymenium, hymenium with a single layer of basidia in different developmental stages, and basidiospores. **b** *Ceratobasidium anceps*, from holotypus collection; section through the whole basidiocarp showing basal hyphae, subhymenium, hymenium with a single layer of basidia in different developmental stages, and basidiospores, three germinating by repetition. **c** *Ceratobasidium pseudocornigerum*, from holotypus collection; section through the whole basidiocarp showing broad hyphae, basally slightly thickened, subhymenium, and hymenium with four-sterigmate basidia in different developmental stages, and basidiospores, one spore germinating by repetition. **d** *Thanatephorus sterigmaticus*, FO 7502; section through the whole basidiocarp showing basal hyphae, subhymenium, hymenium with a single layer of two-sterigmate basidia in different developmental stages, and basidiospores, one in a young stage to form a secondary spore.—Bar for all illustrations 20 μm

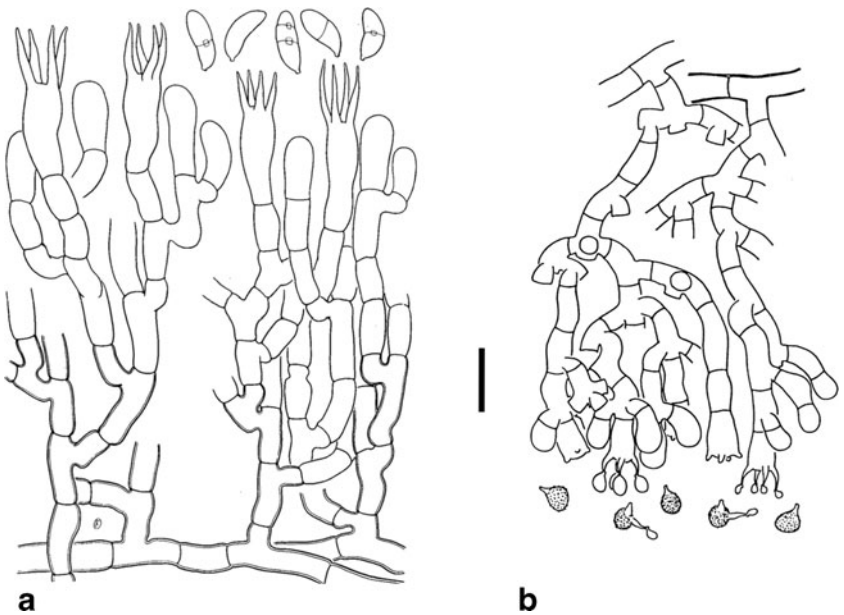


Fig. 4 **a** *Thanatephorus terrigenus*, Wakefield 9.10.1954; section through the whole basidiocarp showing broad hyphae, basally with slightly thickened walls, subhymenium, and hymenium with four-sterigmate basidia in different developmental stages, and basidiospores, four transversally septate. **b** *Tofispora repetospora* from Langer (1994).—Bar for all illustrations 20 μm

now named *Nematostoma parasiticum* (*Herpotrichia parasitica*). Butin and Kehr (2009) found that the needle blight is not caused by this ascomycete, but by *Ceratobasidium* sp. Needle blight of *Picea abies*, caused by a binucleate *Rhizoctonia* (i.e. *Ceratobasidium* sp.) has been reported from Southern Norway (Roll-Hansen and Roll-Hansen 1968), and from Florida on *Pinus palustris*, by English et al. (1986). Reeser et al. (2001) have molecularly characterised a *Rhizoctonia*-like fungus causing web-blight of *Pseudotsuga menziesii* and *Abies* spp. of Christmas trees from Oregon.

Material and methods

Collections and cultures studied with their respective GenBank accession numbers

Collections with FO-numbers in herbarium F. Oberwinkler and M, all others as indicated by acronyms of the Index Herbariorum.

Ceratobasidium calosporum, Iowa City, D.P. Rogers 224, 5.7.1932, type (IA). – *Ceratobasidium anceps,* Germany, Mecklenburg, near Graal, on *Pteridium aquilinum*, H. Sydow, Myc. Germ. 858, 8.1908, holotypus (S). – *Ceratobasidium cornigerum,* Germany, Bavaria, Bad Reichenhall Kirchholz, on wood, 520 m, FO 44, 30.3.1962 (M). – *Ceratobasidium cornigerum*, Venezuela, Mérida, 1,800 m, FO 12904, 1.10.1968, from Oberwinkler (1972) as *Uthatobasidium* sp., Tübingen, Schönbuch, 460 m, FO 29225, 2.8.1979 (M). – *Ceratobasidium pseudocornigerum* M.P. Christ., Denmark, Ermelunden, on *Fraxinus* sp., M.P. Christiansen 251, 22.5.1949, holotypus (C). – *Ceratobasidium* sp., Germany, Bavaria, Wertach, Grüntensee, on *Carex rostrata*, FO 38200, 7.9.1987 (M). – *Oncobasidium theobromae*, Papua New Guinea, New Britain, Keravat, on *Theobroma cacao*, P.J. Keane ASDW 1622, 1970, holotypus (ADW). – *Rhizoctonia butinii*, all on needles of *Picea abies*, collected and isolated by H. Butin, vouchers in M, cultures in DSMZ: Germany, Bavaria, Bavarian Forest, Spiegelau, 760 m, 10.9.2009, holotypus, isolate 11026, GenBank acc. no. KF386035; 29.6.2010. Bavaria, Ebersberger Forst near Ebersberg, 560 m, 30.6.2011, isolate 11024, GenBank acc. no. KF386033. Germany, Lower Saxony, Harz, Oderteich, ca. 700 m, 23.8.2009; 3.9.2009; 4.9.2009; 16.11.2009; 8.8.2012, isolate 11025, GenBank acc. no. KF386034; 20.1.2013; 24.4.2013 isolate BU-2a, GenBank acc. no. KF386030; Germany, Lower Saxony, Harz, Oderbrücke, 24.4.2013, isolate BU-2b, GenBank acc. no. KF386031; Germany, Lower Saxony, Harz, isolate BU-2c, GenBank acc. no. KF386032. – *Rhizoctonia solani* on *Solanum tuberosum*, Bavaria, Germering, FO 19663, 8.1972 (M). – *Rhizoctonia* sp., Germany, Baden-Württemberg, Schönbuch near Tübingen, on *Dryopteris filix-mas*, FO 23471, 17.2.1976 (M). – *Thanatephorus sterigmaticus*, Germany, Bavaria, Bad Reichenhall Kirchholz, 520 m, FO 7502, 6.6.1964 (M). – *Thanatephorus terrigenus*, Surrey, Virginia Water, Wakefield 9.10.1954 (K). – *Tofispora repetospora,* Ethiopia, Shoa, Chilomo silva, Ginchu, 2,400 m, L. Ryvarden 24060, 20.9.1992, holotypus (O), in G. Langer (1994). – *Uthatobasidium fusisporum*, Bavaria, Oberjoch, Iseler, 1,400 m, 26.9.1978, FO 28180 (M). – *Waitea circinata*, Australia, Adelaide, isolated from soil, O. Vartaja 5124 undated, holotypus culture (ADW) (Fig. 5).

List of scientific names of fungi and plants in alphabetical order

Abies alba Mill. – *Carex rostrata* Stokes – *Ceratobasidium anceps* (Bres. & Syd.) H.S. Jacks., *C. angustisporum* Warcup & P.H.B. Talbot, *C. bicorne* J. Eriksss. & Ryv., *C. calosporum* D.P. Rogers, C. *cornigerum* (Bourd.) D.P. Rogers, *C. globisporum* Warcup & P.H.B. Talbot, *C. noxium* (Donk) D.P. Rogers, *C. obscurum* D.P. Rogers, *C. pseudocornigerum* M.P. Christ., *C. ramicola* C.C. Tu, Roberts & Kimbr., *C. sphaerosporum* Warcup & P.H.B. Talbot, *C. stridii* J. Eriksss. & Ryv. – *Ceratorhiza* R.T. Moore – *Corticium roseum* Pers. – *Dryopteris filix-mas* (L.) Schott – *Herpotrichia parasitica* (R. Hartig) E. Rostrup – *Hypochnus setariae* Sawada – *Lepidium sativum* L. – *Nematostoma parasiticum* (R. Hartig) M.G. Barr – *Oncobasidium theobromae* P.H.B. Talbot & Keane – *Pellicularia filamentosa* (Pat.) D.P. Rogers – *Picea abies* (L.) Karst. – *Pinus palustris* Mill. – *Pinus sylvestris* L. – *Polytrichastrum formosum* (Hedw.) G.L. Sm. – *Pseudotsuga menziesii* (Mirbel) Franco – *Pteridium aquilinum* L. – *Pterostylis mutica* R. Br. – *Raphanus sativus* L. – *Rhizoctonia butinii* Oberw., R. Bauer, Garnica & R. Kirschner – *Rhizoctonia ramicola* W.A. Weber & D.A. Roberts – *Rhizoctonia solani* J.G. Kühn – *Sclerotium* Tode – *Sebacina calospora* (Bourd. &

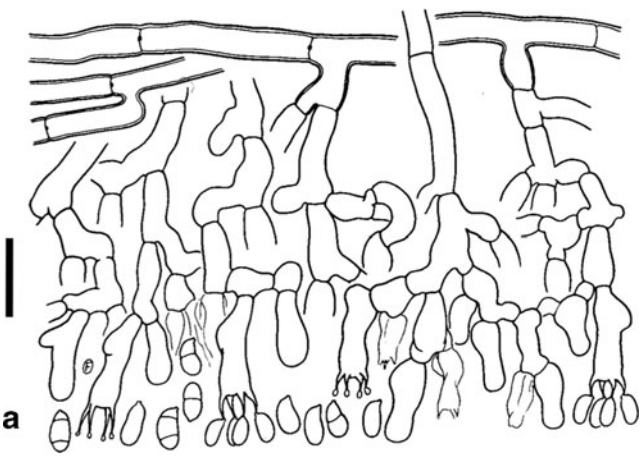


Fig. 5 *Waitea circinata*, from holotypus culture; section through the whole basidiocarp showing broad and basal hyphae with slightly thickened walls, subhymenium, and hymenium with suburniform, four-sterigmate basidia in different developmental stages, and basidiospores, four transversally septate.—Bar 20 μm

Galz.) Bourd. & Galz. – *Solanum tuberosum* L. – *Thanatephorus cucumeris* (A.B.. Frank) Donk, *Th. fusisporus* (J. Schröt.) Hauerslev & P. Roberts, *Th. ochraceus* (Massee) P. Roberts, *Th. ovalisporus* Cízek & Pouzar, *Th. sterigmaticus* (Bourdot) P.H.B. Talbot, *Th. terrigenus* (Bres.) G. Langer – *Theobroma cacao* L. – *Tofispora repetospora* G. Langer & Ryv. – *Trichosphaeria parasitica* R. Hartig – *Uthatobasidium fusisporum* (J. Schröt.) Donk – *Waitea circinata* Warcup & P.H.B. Talbot – *Ypsilonidium anomalum* Warcup & P.H.B. Talbot.

Light microscopy

Samples were mounted in tap water and studied as such with a Zeiss Standard and a Zeiss Axiostar Plus microscope. The preparations were then treated with 3 % KOH, phloxine and 0.1 % cotton blue and lactic acid alternatively. Drawings were made at a scale of 10 μm=3 cm or 6 cm, respectively. Measurements of cellular structures were done 20 times each. All drawings are originals of F. Oberwinkler, except when differently cited.

Electron microscopy

The ultrastructure was studied with a Zeiss EM 109 transmission electron microscope at 80 kV. Samples were fixed overnight with 2 % glutaraldehyde in 0.1 M sodium cacodylate buffer (pH 7.2) at room temperature. After six transfers in 0.1 M sodium cacodylate buffer, samples were postfixed in 1 % osmium tetroxide in the same buffer for 1 h in the dark, washed in distilled water, and stained in 1 % aqueous uranyl acetate for 1 h in the dark. After five washes in distilled water, samples were dehydrated in acetone, using 10 min changes at 25 %, 50 %, 70 %, 95 %, and three times in 100 % acetone, embedded in Spurr's plastic and sectioned with a diamond knife. Serial sections were mounted on formvar-coated, single-slot copper grids, stained with lead citrate at room temperature for 5 min, and washed with distilled water.

Material illustrated in Fig. 6b was prepared using freeze substitution. To remove air from intercellular spaces, samples were infiltrated with distilled water containing 6 % (v/v) (2.5 M) methanol for approximately 5 min at room temperature. Single samples were placed in an aluminum holder (one half with a hollow of 0.3 mm depth for the sample and the other with a flat top), and frozen immediately in the high-pressure freezer HPM 010 (Balzers Union, Lichtenstein). Substitution medium (1.5 ml per specimen) consisted of 2 % osmium tetroxide in acetone, which was dried over calcium chloride. Freeze substitution was performed at −90, −60 and −30 °C (8 h for each step) using a Balzers freeze substitution apparatus (FSU 010). The temperature was then raised to approximately 0 °C over a 30 min period, and samples were washed in dry acetone for another 30 min. Infiltration with Spurr's plastic was performed stepwise: 30 % resin in acetone at 4 °C for 7 h, 70 and 100 % resin at 8 °C for 20 h each and 100 % resin at 18 °C for approximately 12 h. Samples were then transferred to fresh medium and polymerised at 60 °C for 10 h. Finally, samples were processed as described above for chemically fixed samples, except that the sections were additionally stained with 1 % aqueous uranyl acetate for 1 h. TEM photos of Fig. 6a, c, d, e F. Oberwinkler; b, f R. Bauer.

DNA extraction, PCR, sequencing and sequence editing

Fungal material was removed with a sterile razor blade from spruce needles infested with *Rhizoctonia butinii* and placed into Eppendorf tubes. Total genomic DNA was extracted using the InnuPREP Plant DNA Kit (Analytik Jena, Jena, Germany) following the manufacturers' instructions. Dried fungal samples contained in the Eppendorf tubes were deep-frozen in liquid nitrogen and then ground several times with a sterile plastic pestle.

For the type specimen, we amplified the internal transcribed spacers (ITS1 and ITS2, including 5.8S) and D1/D2 regions of the rDNA with the primer combination ITS1F (Gardes and Bruns 1993) and NL4 (White et al. 1990), whereas additional collections included in our study were only amplified with the internal transcribed spacers (ITS1 and ITS2, including 5.8S) using the primers ITS1F (Gardes and Bruns 1993) and ITS4 (White et al. 1990). PCR reactions were carried out in a volume of 25 μl, containing 5.00 μl buffer 10×, 0.75 mM $MgCl_2$ (50 mM), 14.50 μl water, 1.00 μl dNTP mix (5 mM), 0.50 μl of each primer (25 pmol/μl), 0.25 μl Mango*Taq*™ DNA Polymerase (Bioline, Luckenwalde, Germany) (2 U/μl), and undiluted 2.50 μl DNA under the following thermal cycling profile: 10 cycles of 30 s at 94 °C, 45 s at 60 °C (−1 °C per cycle), and 75 s at 72 °C, followed by 26 cycles of 30 s at 94 °C, 45 s at 50 °C and 75 s at 72 °C, followed by an extension step of 10 min at 72 °C. PCR products were detected using standard agarose gel electrophoresis and ethidium bromide staining. The amplified DNA fragments were cleaned using a 1 : 20 diluted ExoSAP-IT® reagent (USB Corporation, Cleveland, OH, USA). Sequencing reactions were performed in both directions with a 1:6 diluted BigDye® Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems, Foster City, CA, USA) on an ABI Prism 3130*xl* Genetic Analyzer (Applied Biosystems). Sequence chromatograms were automatically assembled and manually edited using Sequencher version 4.10.1 (Gene Codes Corporation, Ann Arbor, MI, USA). Six complete ITS sequences of the new described species *Rhizoctonia butinii* have been submitted to GenBank database (www.ncbi.nlm.nih.gov).

Sequence alignments and phylogenetic placement of *Rhizoctonia butinii*

In order to infer the phylogenetic position of *Rhizoctonia butinii*, we assembled a data set including our six ITS

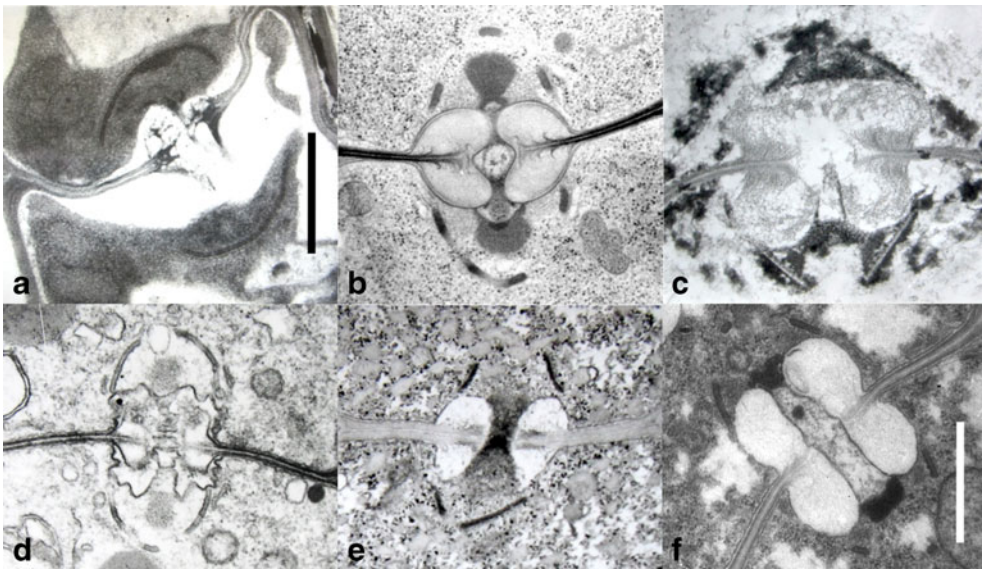


Fig. 6 Dolipores of representative species included in this study. **a** *Ceratobasidium calosporum*, from holotypus material. **b** *Ceratobasidium* sp., FO 38200. **c** *Oncobasidium theobromae* from holotypus culture. **d** *Rhizoctonia solani*, FO 19663. **e** *Rhizoctonia* sp. on *Dryopteris filix-mas*, FO 23471, **f** *Rhizoctonia butinii*, Butin, 3.10.2009, from holotypus culture, isolate 11026; Bars 0.5 μm

sequences (see above) and all those ITS sequences of species assigned to the family Ceratobasidiaceae in its present circumscription, including *Ceratobasidium*, *Thanatephorus*, *Uthatobasidium*, *Rhizoctonia*, and *Ceratorhiza* available from GenBank and UNITE (http://unite.ut.ee) databases. We aligned and analysed all sequences together (independently of the sequence length) with MAFFT version 6.884b under the E-INS-i algorithm (Katoh et al. 2005). Identical, incomplete ITS1 and/or ITS2 sequences were removed from the final alignment. This sequence matrix was automatically aligned using MAFFT (as described above) and POA version 2 (Lee et al. 2002). The most consistent alignment was selected using trimAl version 1.2 (Capella-Gutiérrez et al. 2009).

The POA sequence alignment was analysed with maximum likelihood method using 1,000 rapid bootstrap inferences and maximum likelihood (ML) search under the GTRCAT model as implemented in RAxML version 7.0.4 (Stamatakis 2006; Stamatakis et al. 2008). The best ML tree was midpoint rooted and displayed using FigTree version 1.3.1 (A. Rambaut: http://tree.bio.ed.ac.uk/software/figtree). Genetic distances within and between closely related species to *Rh. butinii* were calculated from an uncorrected pairwise distance (*p*-distance) ITS sequence matrix using Mesquite version 2.75 (Maddison and Maddison 2011). In addition, we assembled a data set comprising the sequence of the holotypus of *Rh. butinii* and sequences of the nuclear rDNA large subunit (LSU) of the Ceratobasidiaceae and analysed it in the same way as the ITS data set.

Results and discussion

Micromorphology and ultrastructure

Only few taxonomic treatments provided detailed and correct micromorphological analyses, documented by adequate illustrations (Oberwinkler 1972, 1982; Eriksson and Ryvarden 1973; Langer 1994; Kotiranta and Saarenoska 2005), an essential prerequisite for meaningful interpretations based on cellular constructions. In many publications, illustrations are lacking or do not show structural details as they really exist. This dilemma is one of the reasons why the taxonomy of the *Ceratobasidium-Uthatobasidium-Rhizoctonia* complex remains confusing until now. To optimise structural comparisons, all figures, most of them original ones, are shown here at the same magnification, i.e. bars of drawings are 20 μm, except two in Fig. 6 with 5 μm bars. Also the magnification of dolipores (Fig. 6) is at the same scale (0.5 μm).

Ceratobasidium

The genus *Ceratobasidium* was introduced by Rogers (1935) with the type species *C. calosporum* (Fig. 1a–c). The globose to subglobose basidia are mostly holobasidiate; however, partially or even completely longitudinally septate ones do occur. This has been overlooked by later workers studying the holotypus. Oberwinkler (1982) drew attention to these basidial features in a study on the significance of the morphology of the basidium in the phylogeny of Basidiomycetes. Unfortunately, Fig. 1.9–4 in Oberwinkler (1982) was not explained in the text. At that time, the author also tried to study the ultrastructure of the dolipore. Surprisingly, in the old holotypus material, continuous parenthesomes could be found (Fig. 6a).

The characters mentioned were circulating in Tübingen's lab-discussions and teaching programs, and were first published without illustrations by Langer (1994). This important information was again published by Weiß and Oberwinkler (2001) and repeated without citation by Moncalvo et al. (2006). In fact, dolipores with continuous parenthesomes are unique in the *Ceratobasidium-Rhizoctonia* complex because all other species studied so far have dolipores with discontinuous parenthesomes.

Roberts (1999) has used the latter ultrastructural feature for family and ordinal circumscriptions. In comparison with other *Ceratobasidium* and *Rhizoctonia* species, *C. calosporum* has comparatively small hyphae, and exceptionally long, vermiform basidiospores. Considering these facts, all other species so far assigned to *Ceratobasidium* appear misplaced. Since DNA sequences of *C. calosporum* are not available, excluding the other species from this genus is based on those cellular and ultrastructural characteristics. For the same reason, the anamorph genus *Ceratorhiza* proposed by Moore (1987) is considered a synonym of *Rhizoctonia*. In contrast, to our knowledge, *Sebacina calospora* shares the same main characters, provided that the species has continuous parenthesomes. Roberts (1993) transferred *S. calospora* into his newly erected genus *Ceratosebacina*.

The cosmopolitan and common *C. cornigerum* (Figs. 2c and 3a) is rather broadly conceived, especially with respect to its nutritional modes. It is assumed that the "species" can grow saprobically, parasitically on various plants, and endophytically as ORM. Simply, considered from morphological aspects, it does not coincide with generic features as explained above under type species criteria. Nevertheless, this species is not a *Ceratobasidium* because it does not share the micromorphological and ultrastructural characteristics of the type species, *C. calosporum*. It is a much better solution to include it in *Rhizoctonia*, even when traditional generic definitions do not fit adequately. If the synonymy with *C. ramifera* proposed by Roberts (1999) is correct, the best applicable name for this fungus would be *Rhizoctonia ramicola*.

The micromorphologically similar *C. pseudocornigerum* (Fig. 3c) deviates from C. *cornigerum* through cylindrical basidiospores. It grows saprobically on wood and occurs as ORM when the conspecificity with *C. angustisporum* (Warcup and Talbot 1980) is correct, as assumed by Roberts (1999), who recorded the unnamed anamorph as having monilioid hyphae.

Ceratobasidium anceps (Fig. 3b), described from Germany on *Pteridium aquilinum* and occurring on other ferns in Europe, is reported as parasite on various other plants in North America. The micromorphology of *C. anceps* and *C. cornigerum* is nearly identical. The shape of basidiospores is commonly used to discriminate both species, leaving much uncertainty about its meaningfulness. Only sclerotia are known for the anamorph of *C. anceps*, which was transferred from *Sclerotium* to *Ceratorhiza* by Roberts (1999). Unfortunately, nutritional modes and host specificities are only badly or not known at all, thus correlations with micromorphological features cannot be drawn.

Rhizoctonia, syn. *Thanatephorus*

Rhizoctonia was introduced as a nomen conservandum by De Candolle in 1815 for the anamorphic species *Rh. solani*. According to Article 59.1 of the Melbourne Code of Nomenclature for algae, fungi, and plants (McNeill et al. 2012a), "all legitimate fungal names are treated equally for the purposes of establishing priority". Therefore, *Rhizoctonia* has priority over *Thanatephorus*, a genus proposed by Donk (1956) for the teleomorphic stage of *Rh. solani* and named *Th. cucumeris*. Being a "widely used name" (Art. 57.2) in the sense of McNeill et al. (2012b), *Rhizoctonia* is suggested for inclusion in the planned lists of accepted names and to be preferred against *Thanatephorus* for new species and combinations.

Rhizoctonia solani (Figs. 2b and 6d) is a species of cosmopolitan distribution, and well documented as an important plant pathogen, but saprobic and endophytic growth as ORMs are also reported. All hyphae are multinucleate, clampless and broad, (8–)10–14(−16) μm wide, the basal ones mostly thick-walled and ochraceous to light brownish. Also, subhymenial and hymenial hyphae are broad, typically with rectangular branching, then upright and candelaber-like. Hyphal septa have dolipores with discontinuous parenthesomes (Fig. 6d). In the type and some other species, well-developed basidiocarps have thickening hymenia, i.e. a first basidial layer is overgrown by a next one, occasionally followed up by additional ones. The stout cylindrical basidia are only slightly broader than the supporting hyphae. Mostly four, basally broad sterigmata can become rather long, apparently depending on weather conditions. Secondary ballistospores are common. The anamorphic stage has monilioid hyphae, and often sclerotia are present.

The generic definition based on the type species allows the affiliation of various taxa, either already assigned to *Rhizoctonia* or *Thanatephorus* or kept in other genera so far. These are briefly discussed in the following part.

Cejpomyces

Thanatephorus terrigenus (Fig. 4a) prefers to grow on soil and litter, therefore, often, the hymenium is geotropically negatively oriented. Basidiospores are typically transversally septate, and apparently lack repetitive basidiospore germination. The latter character was used by Svrcek and Pouzar (1970) to propose a separate genus, *Cejpomyces*. Considering all morphological features, Langer (1994) transfered the species into *Thanatephorus*, a decision later accepted by Roberts (1999), and adopted here in the sense that *Thanatephorus* is a later synonym of *Rhizoctonia*. The anamorph is not known (Roberts 1999).

Oncobasidium

The parasite on leaves of *Theobroma cacao* from Papua New Guinea, *Oncobasidium theobromae* (Fig. 2a), has been described by Talbot and Keane (1971). In contrast to the opinion of the

authors, a deviating basidial morphology from *Rhizoctonia solani* cannot be verified, as was already stated by Roberts (1999). Transversely septate basidiospores are also found in *Th. terrigenus* (Fig. 4a). The anamorph is not known (Roberts 1999).

Tofispora

Langer (1994) erected *Tofispora* with the type *To. repetospora* (Fig. 4b) for three thanatephoroid species from tropical regions with uniquely asperulate spore walls. Roberts (1999) claimed about the inconsistency of uniting species with smooth and ornamented spores in *Botryobasidium* on the one hand and separating similarly structured species in the case of *Thanatephorus* on the other.

Uthatobasidium

Uthatobasidium, introduced by Donk (1956), is typified by *U. fusisporum* (Fig. 1d, e), a saprobic species lacking sclerotia, but of essentially the same cellular architecture and dolipore ultrastructure (Oberwinkler 1985) as *Rhizoctonia solani*, the latter predominently plant pathogenic and capable of producing sclerotia. Monilioid hyphae with swollen, ellipsoid compartments are produced in culture (Roberts 1999). Hauerslev and Roberts (in Knudsen and Hansen 1996) transferred *U. fusisporum* into *Thanatephorus*, a taxonomic rearrangement that was accepted by later workers. Consequently, *U. ochraceum* was also rearranged in *Thanatephorus,* as *Th. ochraceus* (Roberts 1998).

Waitea

A saprotrophic and plant parasitic species, isolated from soil in Adelaide, Australia, was described by Warcup and Talbot (1962) as *Waitea circinata* (Fig. 5). Hyphae are clampless, basally thick-walled and mainly branching rectangularly. Dolipores have discontinuous parenthesomes (Andersen 1996). Subhymenial and hymenial hyphae have thin walls, the hymenium is slightly thickening, and composed mostly of basidia with probasidial lateral sacks, constrictions above, and short sterigmata. Mature basidiospores are typically transversally septate, obviously without secondary spores. Monilioid hyphae and sclerotia of the anamorph stage, as well as basidial morphology were considered to indicate thanatephoroid affinities by Roberts (1999). However, the suburniform basidial ontogeny and sterigma morphology is distinctly different from the *Rhizoctonia* type.

When *Waitea circinalis* is included in phylogenetic analyses, it does not group with the *Ceratobasidium-Rhizoctonia* complex (Johanson et al. 1998; Gonzalez et al. 2001; Sharon et al. 2008), thus indicating that it is not a member of the Ceratobasidiaceae. In comprehensive samplings of Larsson (2007), it falls in the Corticiaceae, or it clusters directly with *Corticium roseum* (Veldre et al. 2013).

Ypsilonidium

The prominent bisterigmate basidia of *Thanatephorus sterigmaticus* led Donk (1972) to propose an additional satellite genus, *Ypsilonidium* (Fig. 3d), for a non-pathogenic species. However, Langer (1994) and Roberts (1999) did not accept this generic rearrangement. The unnamed anamorph produces monilioid hyphae (Roberts 1999).

A *Rhizoctonia* species that attacks young shoots and needles of *Picea abies*

As shown by Butin and Kehr (2009) and Butin (2011a, b), a needle blight of *Picea abies* in various stands of spruce in Germany and Austria is caused by a *Ceratobasidium*–like fungus. The parasite attacks young shoots and needles of various ages on twigs close to the ground. The material collected by Heinz Butin and provided to the authors has been studied in detail micromorphologically, ultrastructurally, and molecularly. Our results suggest that the parasite belongs to *Rhizoctonia cornigera* s. l., according to its overall teleomorph micromorphology. The widespread occurrence together with a presumably rather narrow host specificity, and a distinctive ITS sequence encourage us to propose a new species. We feel justified to introduce a taxonomic novelty in a complex group of fungi for the purpose of disentangling unsatisfactory assemblages and to draw attention to a biologically and taxonomically meaningful taxon. Additional investigations are going on to clarify the relationship of *Rhizoctonia* species on different coniferous hosts.

Rhizoctonia butinii Oberw., R. Bauer, Garnica & R. Kirschner, sp. nov., Figs. 7, 8, 9, and 10.

MycoBank: MB805505

Parasitic hyphae developing in young shoots and needles, emerging from the living substrate and forming thin, up to 50 μm hyphal mats, composed of binucleate, clampless hyphae. Basal hyphae 8–12 μm wide, slightly thick-walled, often branching with right angles, forming a thin subhymenium of thin-walled hyphae, 5–7 μm wide and terminating in a simple, non-thickening hymenium. Basidia obovate, apically slightly swollen, 5–10×10–20 μm, four-sterigmate. Sterigmata long, curved, 2–3×8–12 μm. Basidiospores ellipsoid to slightly bent, hyaline, thin-walled, inamyloid, 3.5–4.5×7–10 μm, germinating with secondary spores and hyphae. Hyphae in culture thin-walled, hyaline and mostly branching rectangularly. Young hyphae (Fig. 7j) 3–6 μm wide, with tapering hyphal tips, binucleate, and dolipores visible by light microscopy. Old hyphae (Fig. 7i) 5–12 μm wide, with anastomoses, often with irregularly constricted cell walls, reminding a moniliform type, with huge vacuoles and many collapsed cells. Sclerotia not observed in culture.

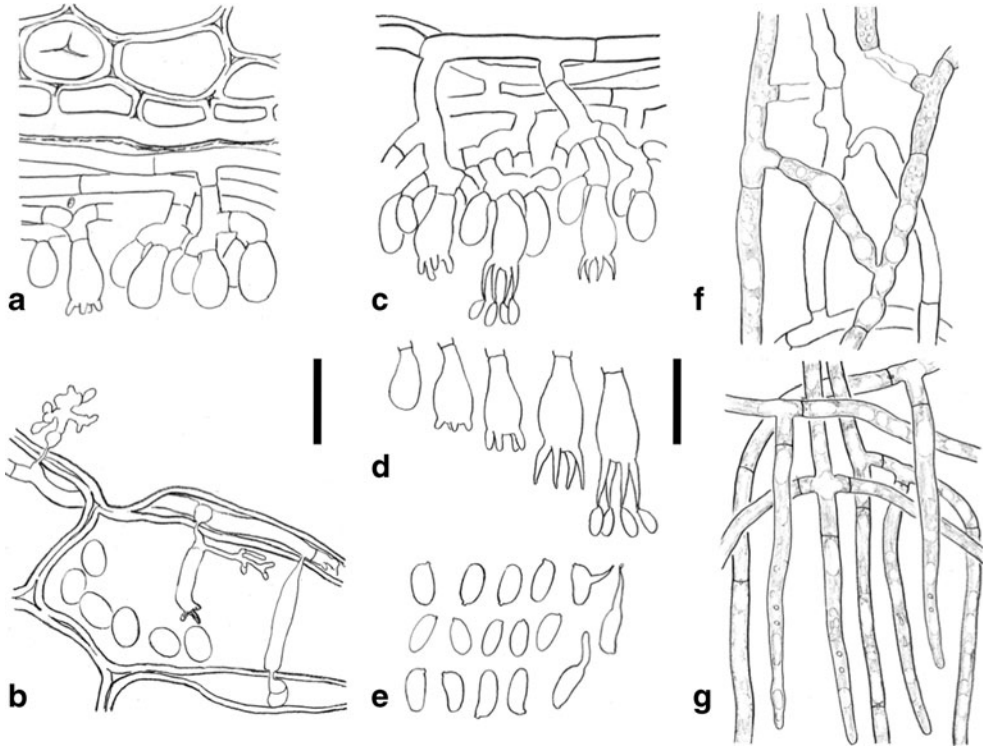


Fig. 7 **a**–**g** *Rhizoctonia butinii* from holotypus; **a**, **c** sections through whole basidiocarps; **a** young developmental stage with one basidium initiating sterigmata, above part of spruce needle; **c** mature basidiocarp with slightly thick-walled basal hyphae, subhymenia, hymenia with single layers of basidia in different developmental stages, one basidium with young basidiospores. **b** part of spruce needle tissue with hyphae penetrating cell walls and forming haustoria inside the host cells; few chloroplasts are illustrated as ellipsoid organelles. **d** developmental stages of basidia. **e** basidiospores, two with young stages to form secondary spores, one presumably germinating with a hypha. **f**, **g** hyphae in culture, isolated from holotypus. **f** approximately 5-month-old hyphae with partly irregular constrictions. **g** young hyphae with growing hyphal tips, two nuclei in one cell and dolipores visible with light microscopy.—Bars 20 μm

Parasitic on *Picea abies* with a known distribution in Germany and Austria, but most likely within the natural and artificial range of the host species.

A sequence comprising the internal transcribed spacers (ITS1 and ITS2), 5.8S and D1/D2 regions of the nuclear rDNA from the holotypus of *Rh. butinii* is available at GenBank (accession number KF386035). Type: Bavaria, Aufichtenwald/Spiegelau, Bavarian Forest, 760 m, N 48.91418, E 13.357186, 10.9.2009, H. Butin (M, holotype).

Etymology: In honour of Prof. Dr. Heinz Butin, famous forest pathologist.

Fig. 8 **a**–**c** *Rhizoctonia butinii* on needles of *Picea abies*. **a** upper needle covered by a basidiocarp of *R. butinii* on its underside, needle below without visible infection; from Butin 30.6.2011. **b** dead needle covered by a basidiocarp of the parasite; from Butin 20.1.2013, bar for a, b 5 mm. **c** parasite emerging through stoma of spruce to form a hyphal cushion; **d** outgrowth of generative hyphae from the hyphal cushion; Butin 10.9.2009, (holotypus). Bar for c, d 50 μm

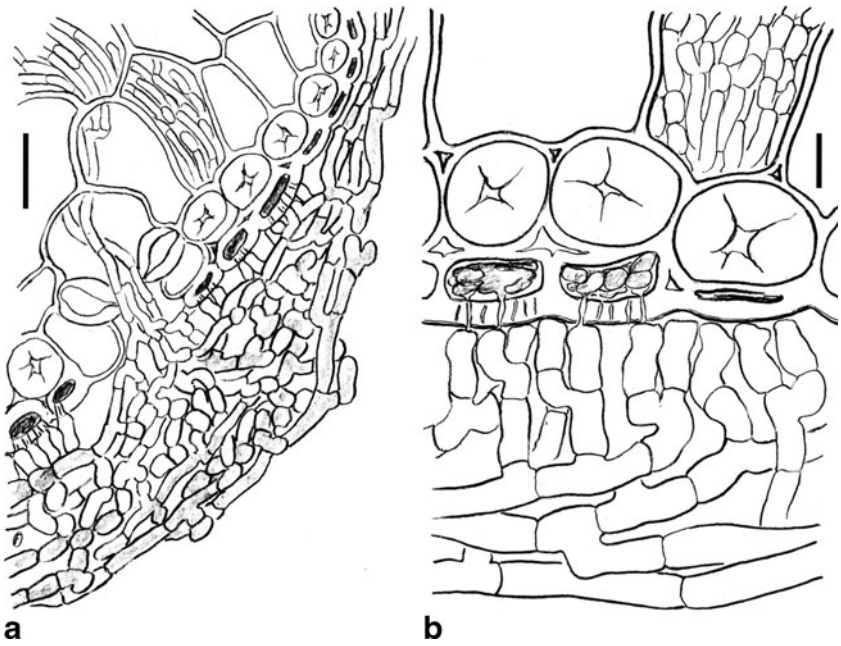


Fig. 9 **a**, **b** *Rhizoctonia butinii* on lower surface of needles of *Picea abies*, Butin 10.9.2009 (holotypus). **a** stoma with emerging hyphae forming a hyphal cushion of mostly ochraceous to brownish hyphae; hyphae close to the epidermis with interacting protuberances, bar 50 μm. **b** interaction of cushion hyphae with epidermal cells of spruce through cuticula and epidermis cell walls with microchannels, bar 10 μm

Rhizoctonia-host plant interactions

Cushion-like hyphal mats of ochraceous to brownish coloured hyphae in a mature stage (Figs. 8c, d, and 9a, b) develop on the underside of needles. Terminal hyphae can interact with host epidermal cells through tiny tubes of approximately 0.5 μm in diam. (Fig. 9). Such penetration hyphae of a needle parasite were illustrated and described already by Hartig (1900), and by Freyer (1976a) with scanning electron microscope (SEM) and transmission electron microscope (TEM) pictures on *Abies alba*. However, the parasite was misinterpreted as *Herpotrichia parasitica* by these authors. Thin-walled, uncoloured and relatively small hyphae can be found in various needle cells, however not in sclerenchyma cells (Fig. 9). Most likely, internal colonization of host cells can start from infected epidermal cells and stomatal cavities. First von Tubeuf (1890) and later Freyer (1976a, b) observed the occurrence of web blight on spruce, and putatively assumed *H. parasitica* as the parasitic agent.

Flentje (1957) was the first to carefully analyse the host penetration of *Pellicularia filamentosa* (= *Rhizoctonia solani*) attached to radish and tomato stems on a cellular level. He found fine infection pegs, originating from appressoria, and later rapidly growing and ramifying hyphae causing the collapse of the plant tissue. The infection and penetration of orchid protocorms and hypocotyls of *Lepidium sativum* and *Raphanus sativus* seedlings by *Thanatephorus cucumeris* and other *Rhizoctonia* isolates were studied comparatively by Williamson and Hadley (1970). Dome-shaped hyphal cushions were only found in the crucifer seedlings, and hyphae arising beneath these structures penetrated the epidermis of cotyledons. These infection hyphae were not described in detail and were also not illustrated. Weinhold and Motta (1972) studied the initial host responses in cotton after infection by *Rh. solani*. Their light microscopic pictures do not show fungal interactive structures, but illustrate a gross morphology of hyphal cushions at interaction sites similar to those found in our study. Unfortunately, the details of penetration itself were not examined adequately, and therefore they are only rather superficially explained. Clear micrographs show the penetration necks of *Rh. solani* causing barley stunt disorder in a study by Murray (1981). He found simple infection pegs and infection cushions, both quite different from the cellular structures in *Rh. butinii*. Similar results were published by Murray (1982) on penetration of barley root and coleoptile surfaces by *Rh. solani*.

We also studied the hyphal development in the needle tissue (Fig. 7b). Hyphae grow intercellularly and intracellularly and penetrate host cell walls with strongly narrowed hyphal tips, forming tiny channels as in most parasitic cell interactions of fungi in plants. Inside the host cells, the normal hyphal width can be regained, and coralloid haustoria are formed in living cells. Most likely, *Rh. butinii* spreads out on surface parts of the host and reinfects young shoots and needles repeatedly.

Ecology of *Rhizoctonia butinii* and other fungal parasites of *Picea abies*

Rhizoctonia butinii is known to parasitize young shoots and needles of *Picea abies* (Butin and Kehr 2009; Butin 2011a, b). The fungus develops in and on twigs, close to the ground and appears to be restricted to such habitat niches. Apparently, a high air humidity is essential for the parasite to grow on the

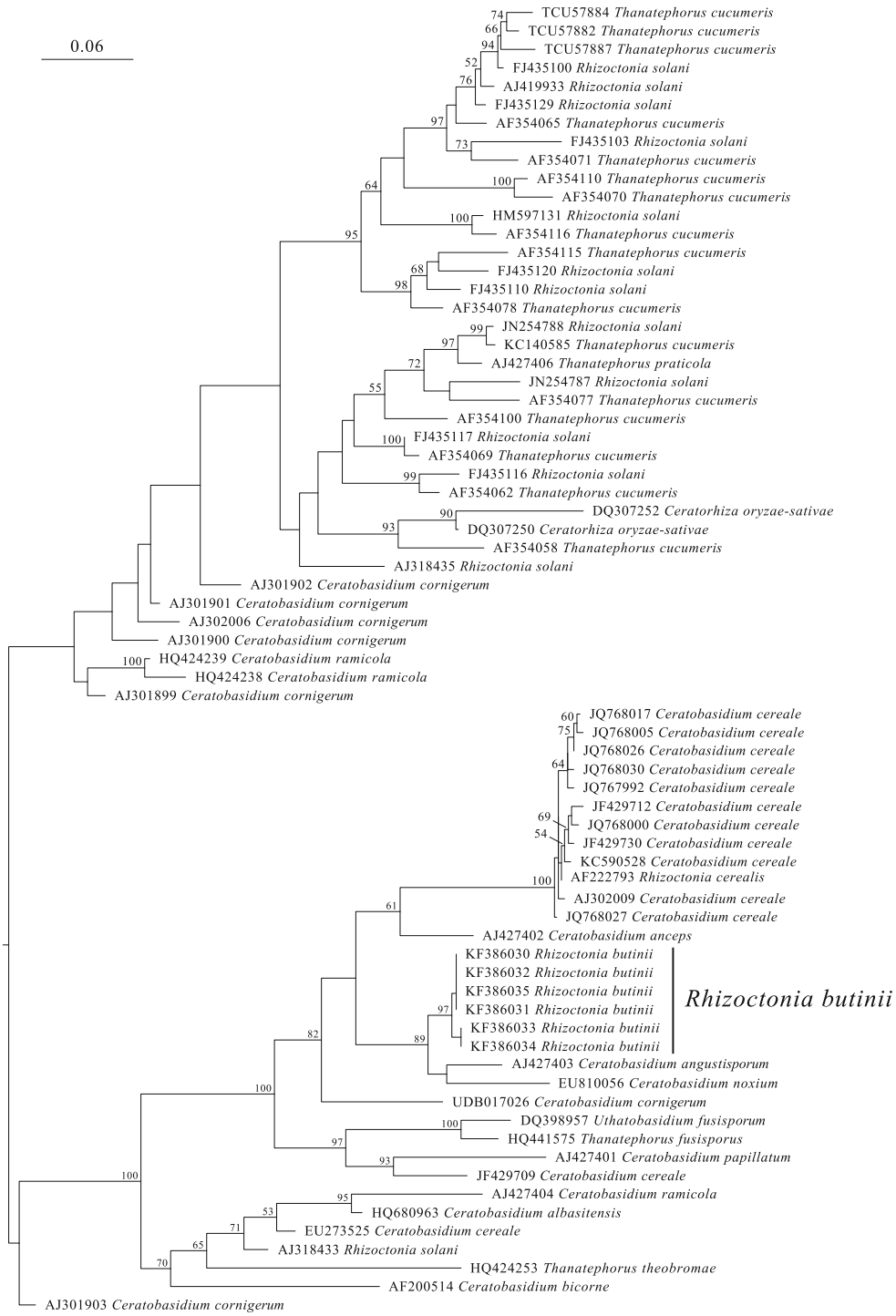


Fig. 10 Maximum likelihood phylogram showing the phylogenetic placement of *Rhizoctonia butinii* within the Ceratobasidiaceae, as inferred from complete ITS1 + 5.8S + ITS2 sequences. Tree topology was computed from 1,000 runs and was midpoint rooted. Bootstrap supports (> 50 %) are shown for each node

surface parts of the host. Under such conditions, a web blight develops, and the fungus commonly occurs in its basidial stage, producing basidiospores that may effectively propagate it in the lower twig area of spruce.

A binucleate *Rhizoctonia*, i.e. *Ceratobasidium* sp. in the traditional sense, has been reported from Southern Norway to cause a needle blight of *Picea abies* (Roll-Hansen and Roll-Hansen 1968).

Root dieback of *Picea abies* and *Pinus sylvestris* in Finland and Norway has been documented by Venn et al. (1986) and Lilja et al. (1994). The uninucleate *Ceratobasidium bicorne* was found to be the parasitic agent (Hietala et al. 1994, 2001; Hietala and Sen 1996) that was originally described as a parasite on *Polytrichastrum formosum* from Denmark (Eriksson and Ryvarden 1973).

Prediction of the AG status, host specificities and phylogeny

A serious problem in ceratobasidiaceous fungi is that morphospecies may not provide a correct picture of the functional biodiversity involved. Evidence for this arose through many experiments testing the compatibility of axenic cultures. The capability to form anastomoses has been considered to document a certain degree of relatedness. Over the time, a series of anastomosis groups (AGs) were detected (Schultz 1937; Richter and Schneider 1953; Parmeter et al. 1969; Ogoshi 1972a, b; Adams and Butler 1979; Burpee et al. 1980; Ogoshi et al. 1983; Sneh et al. 1991; Sharon et al. 2008).

To identify the AG status of binucleate *Rhizoctonia* species causing disease on strawberries, Martin (2000) used the analyses of ITS-rDNA sequence data. Rinehart et al. (2007) predicted AGs of hundreds of *Azalea* web blight isolates on the basis of ITS sequences, and confirmed them with traditional hyphal fusion experiments. They found 97 % of the isolates to belong to AG-U, and they did not observe these disease symptoms on any plant genera other than *Rhododendron* spp.

Surprisingly, until recently, molecular studies could not solve basic questions, like species and generic delimitations and positions, as well as a conclusive affiliation of the *Ceratobasidium-Rhizoctonia* group to any well-defined order.

Both *Ceratobasidium* and *Rhizoctonia* in their present circumscription appear polyphyletic (Gonzalez et al. 2001; Samuels et al. 2011; Veldre et al. 2013), and their ITS-based phylogenies did not recover clear distinctions between them. Nevertheless, Samuels et al. (2011) transferred *Oncobasidium theobromae* to *Ceratobasidium*, a genus based on misinterpreted characters of the type species, as explained above. According to Veldre et al. (2013), the *Thanatephorus fusisporus* clade is basal in the phylogenetic ITS-tree, and no AGs are assigned to it. The morphologically defined, widespread and nutritionally highly diverse *Ceratobasidium cornigerum* falls in the binucleate AG-A, AG-Bo, AG-D, AG-P, AG-Q, thus clearly showing a paraphyletic assemblage.

Roberts considered hyphal nucleation variable and not useful in defining genera (1999). The multinucleate cell organization appears to have evolved multiple times and is considered to be derived. This evolutionary trend includes many reversions to binucleate states (Veldre et al. 2013).

Phylogenetic placement of *Rhizoctonia butinii*

Our ITS sequence analysis shows *Rh. butinii* as a well-delimited species within the family Ceratobasidiaceae in the traditional sense (Fig. 10) and the non-monophyletic/BD group (Veldre et al. 2013). Little ITS sequence divergence (up to 0.7 %) exists between population samples of *Rh. butinii*. The closest species is the orchid associated *Ceratobasidium angustisporum* AJ427403, differing by 4.5 %. The phylogeny based on LSU sequences confirmed the isolated position of *Rh. butinii* within the Ceratobasidiaceae (data not shown).

Conclusions

The *Ceratobasidium-Rhizoctonia* group is composed of a highly complex assemblage of inconspicuous basidiomycetous fungi with rather diverse nutritional modes. We applied an integrative approach of field observations, comparative light microscopy, transmission electronmicroscopy, and molecular analysis to disentangle a parasitic taxon on *Picea abies* belonging to the *Ceratobasidium cornigerum* complex. We found sufficient evidence that this taxon can be well characterised and that it deserves to be named appropriately.

It was shown in our taxonomic part that the genus *Ceratobasidium* can only be applied for the type species *C. calosporum*. Based on our own comparative morphological studies and on a comprehensive evaluation of molecular data as cited above, we conclude that the genera *Koleroga, Oncobasidium, Uthatobasidium,* and *Ypsilonidium* cannot be accepted. In addition, the widely used old genus *Rhizoctonia* has priority over *Thanatephorus*, and is to be preferred for proposing new species and combinations. As for *Tofispora*, molecular data are needed before a conclusive taxonomic rearrangement can be recommended.

Accordingly, we propose the following new combinations:

Rhizoctonia amygdalispora (Hauersl., P. Roberts, & Å. Strid) Oberw., R. Bauer, Garnica, R. Kirschner, comb. nov., MycoBank: MB 805616, basionym *Thanatephorus amygdalisporus* (Hauersl., P. Roberts, & Å. Strid) Nordic Journ Bot 16:217 (1996).

Rhizoctonia anceps (Bres. & Syd.) Oberw., R. Bauer, Garnica, R. Kirschner, comb. nov., MycoBank: MB 805617, basionym *Tulasnella anceps* Bres. & Syd. in Syd., Ann Myc 8:490 (1910).

Rhizoctonia bicornis (J. Erikss. & Ryv.) Oberw., R. Bauer, Garnica, R. Kirschner, comb. nov., MycoBank: MB 805618, basionym *Ceratobasidium bicorne* J. Erikss. & Ryv., Cort N Eur 2:221 (1973).

Rhizoctonia fusispora (J. Schröt.) Oberw., R. Bauer, Garnica, R. Kirschner, comb. nov., MycoBank: MB 805619, basionym *Hypochnus fusisporus* J. Schröt., in Cohn, Krypt.-Fl. Schlesien 3:416 (1888).

Rhizoctonia globispora (Warcup & P.H.B. Talbot) Oberw., R. Bauer, Garnica, R. Kirschner, comb. nov., MycoBank: MB 805620, basionym *Ceratobasidium globisporum* Warcup & P.H.B. Talbot, New Phytol 86:267 (1980).

Rhizoctonia noxia (Donk) Oberw., R. Bauer, Garnica, R. Kirschner, comb. nov., MycoBank: MB 805621, basionym *Koleroga noxia* Donk, Fungus 28:35 (1958).

Rhizoctonia obscura (D.P. Rogers) Oberw., R. Bauer, Garnica, R. Kirschner, comb. nov., MycoBank: MB 805622, basionym *Ceratobasidium obscurum* D.P. Rogers, Univ Iowa Stud Nat Hist 17:6 (1935).

Rhizoctonia ochracea (Massee) Oberw., R. Bauer, Garnica, R. Kirschner, comb. nov., MycoBank: MB 805623, basionym *Coniophora ochracea* Massee, Jour Linn Soc Bot 25:137 (1889).

Rhizoctonia pseudocornigera (M.P. Christ.) Oberw., R. Bauer, Garnica, R. Kirschner, comb. nov., MycoBank: MB 805624, basionym *Ceratobasidium pseudocornigerum* M.P. Christ, Dansk Bo Ark 19:46 (1959).

Rhizoctonia sphaerospora (Warcup & P.H.B. Talbot) Oberw., R. Bauer, Garnica, R. Kirschner, comb. nov., MycoBank: MB 805625, basionym *Ceratobasidium sphaerosporum* Warcup & P.H.B. Talbot, New Phytol 70:38 (1971).

Rhizoctonia sterigmatica (Bourdot) Oberw., R. Bauer, Garnica, R. Kirschner, comb. nov., MycoBank: MB 805628, basionym, *Corticium sterigmaticum* Bourdot, Rev Sci Bourbon. 35:4 (1922).

Rhizoctonia stridii (J. Erikss. & Ryv.) Oberw., R. Bauer, Garnica, R. Kirschner, comb. nov., MycoBank: MB 805629, basionym, *Ceratobasidium stridii* J. Erikss. & Ryv., Cort N Eur 2:227 (1973).

Rhizoctonia terrigena (Bres.) Oberw., R. Bauer, Garnica, R. Kirschner, comb. nov., MycoBank: MB 805626, basionym, *Corticium terrigenum* Bres., Ann Mycol 1:99 (1903).

Rhizoctonia theobromae (P.H.B. Talbot & Keane) Oberw., R. Bauer, Garnica, R. Kirschner, comb. nov., MycoBank: MB 805627, basionym, *Oncobasidium theobromae* P.H.B. Talbot & Keane, Austr Jor Bot 19:203 (1971).

Acknowledgments We gratefully acknowledge the chance to study collections of a basidiomycetous spruce parasite, made available by Heinz Butin as herbarium collections and cultures. Wolfgang Maier, Julius Kühn-Institut, Braunschweig, kindly provided two additional sequences of *Rhizoctonia butinii*. The support of our technical staff, C. Karasch-Wittmann and S. Süßbrich, to carry out this work, is highly appreciated.

References

Adams GJ Jr, Butler EE (1979) Serological relationships among anastomosis groups of *Rhizoctonia solani*. Phytopathology 69:629–633

Andersen TF (1996) A comparative taxonomic study of *Rhizoctonia* senso lato employing morphological, ultrastructural and molecular methods. Mycol Res 100:1117–1128

Burpee LL, Sunders PL, Cole H Jr, Sherwood RT (1980) Anastomosis groups among isolates of *Ceratobasidium cornigerum* and related fungi. Mycologia 72:689–701

Butin H (2011a) *Ceratobasidium*-Krankheit nun auch in Österreich. Forstschutz Aktuell 54:29–32

Butin H (2011b) Krankheiten der Wald- und Parkbäume. Diagnose, Biologie, Bekämpfung. 4. Neubearbeitete Aufl. Ulmer Verlag Stuttgart

Butin H, Kehr R (2009) *Ceratobasidium*-Nadelsterben – eine neue Fichtenkrankheit. AFZ - Der Wald 23:1250–1251

Capella-Gutiérrez S, Silla-Martínez JM, Gabaldón T (2009) trimAl: a tool for automated alignment trimming in large-scale phylogenetic analyses. Bioinformatics 25:1972–1973

Christiansen MP (1959) Danish resupinate fungi. Part 1. Ascomycetes and heterobasidiomycetes. Dansk Bot Ark 19:1–55

Cízek K, Pouzar Z (1992) A new European species of the genus *Thanatephorus* subgen. *Ypsilonidium* (Corticiaceae). Ceská Myk 46:62–66

Donk MA (1956) Notes on resupinate fungi II. The tulasnelloid fungi. Reinwardtia 3:363–379

Donk MA (1958) Notes on resupinate hymenomycetes V. Fungus 28:16–36

Donk MA (1972) The Heterobasidiomycetes: a reconnaissance—I. A restricted emendation. Proc Konink Ned Akad Wetens C 5:365–390

English TR, Ploetz RC, Barnard BL (1986) Seedling blight of long leaf pine by a binucleate *Rhizoctonia solani*-like fungus. Plant Dis 70: 148–150

Eriksson J, Ryvarden L (1973) The Corticiaceae of North Europe. Vol. 2 Fungiflora, Oslo

Flentje NT (1957) Studies on *Pellicularia filamentosa* (Pat.) Rogers. III. Host penetration and resistance, and strain specialization. Trans Brit Mycol Soc 40:322–336

Freyer K (1976a) Untersuchungen zur Biologie, Morphologie und Verbreitung von *Herpotrichia parasitica* (Hartig) E. Rostrup (vormals *Trichosphaeria parasitica* Hartig). I. Verbreitung und Morphologie. Eur J For Pathol 6:152–166

Freyer K (1976b) Untersuchungen zur Biologie, Morphologie und Verbreitung von *Herpotrichia parasitica* (Hartig) E. Rostrup (vormals *Trichosphaeria parasitica* Hartig). II. Infektionsweg, Wirtsspektrum und Kulturverhalten. Eur J For Pathol 6:222–238

Gardes M, Bruns TD (1993) ITS primers with enhanced specificity for basidiomycetes: application to the identification of mycorrhizae and rusts. Mol Ecol 2:113–118

Gonzalez D, Carling DE, Kuninaga S, Vilgalys R, Cubeta MA (2001) Ribosomal DNA systematics of *Ceratobasidium* and *Thanatephorus* with *Rhizoctonia* anamorphs. Mycologia 93:1138–1150

Hartig R (1884) Ein neuer Parasit an Weißtanne. *Trichosphaeria parasitica* n. sp. Allg Forst- Jagd-Ztg 60:11–14

Hartig R (1900) Lehrbuch der Pflanzenkrankheiten. Für Botaniker, Forstleute, Landwirthe und Gärtner. Verlag Julius Springer, Berlin

Hietala AM, Sen R (1996) *Rhizoctonia* associated with forest trees. In: Sneh B, Jabaji-Hare S, Neate S, Dijst G (eds) *Rhizoctonia* species: taxonomy, molecular biology, ecology, pathology and disease control. Kluwer Academic Publishers, Dordrecht, pp 351–358

Hietala AM, Sen R, Lilja A (1994) Anamorphic and teleomorphic characteristics of a uninucleate *Rhizoctonia* sp. isolated form the roots of nursery grown conifer seedlings. Mycol Res 98:1044–1050

Hietala AM, Vahala J, Hantula J (2001) Molecular evidence suggests that *Ceratobasidium bicorne* has an anamorph known as a conifer pathogen. Mycol Res 105:555–562

Jackson HS (1949) Studies of Canadian thelephoraceae IV. *Corticium anceps* in North America. Can J Bot C27:241–252

Johanson A, Turner HC, McKay GJ, Brown AE (1998) A PCR-based method to distinguish fungi of the rice sheath-blight complex. *Rhizoctonia solani, R. oryzae* and *R. oryzae-sativae*. FEMS Microbiol Lett 162:289–294

Katoh K, Kuma K, Toh H, Miyata T (2005) MAFFT version 5: improvement in accuracy of multiple sequence alignment. Nucleic Acids Res 33:511–518

Knudsen H, Hansen L (eds) (1996) Nomenclatural notes to Nordic Macromycetes vol 1 & 3. Nord J Bot 16:211–221

Kotiranta H, Saarenoska R (2005) *Ceratobasidium* and *Oliveonia* (Basidiomycota, Aphyllophorales) in Finland. Ann Bot Fenn 42:237–245

Langer G (1994) Die Gattunge *Botryobasidium* Donk (Corticiaceae, Basidiomycetes). Bibl Myc 158

Larsson K-H (2007) Re-thinking the classification of corticioid fungi. Mycol Res 111:1040–1063

Lee C, Grasso C, Sharlow MF (2002) Multiple sequence alignment using partial order graphs. Bioinformatics 18:452–464

Lilja A, Hietala AM, Karjalainen R (1994) Identification of a uninucleate *Rhizoctonia* sp. by pathogenicity, hyphal anastomosis and RAPD analysis. Plant Pathol 45:997–1006

Maddison WP, Maddison DR (2011) Mesquite: a modular system for evolutionary analysis. Version 2.75. http://mesquiteproject.org

Martin FN (2000) *Rhizoctonia* spp. recovered from strawberry roots in central coastal California. Phytopathology 90:345–353

McNeill J, Turland NJ, Barria FR, Buck WR, Demoulin V, Greuter W, Hawksworth DL, Herendeen PS, Knapp S, Marhold K, Prado J, Prud'homme van Reine WF, Smith GF, Wiersema JH (2012a) International Code of Nomenclature for algae, fungi, and plants (Melbourne Code). Regnum Vegetabile 154. Koeltz Scientific Books. ISBN 978-3-87429-425-6

McNeill J, Redhead A, Wiersema JH (2012b) Guidelines for proposals to conserve or reject names. Taxon 61:248–251

Moncalvo JM, Nilsson RH, Koster B, Dunham SM, Bernauer T, Matheny PB, McLenon T, Margaritescu S, Weiß M, Garnica S, Danell E, Langer G, Langer E, Larsson E, Larsson K-H, Vilgalys R (2006) The cantharelloid clade; dealing with incongruent gene trees and phyogenetic reconstruction methods. Mycologia 98:937–948

Moore RT (1987) The genera of *Rhizoctonia*-like fungi: *Ascorhizoctionia*, *Ceratorhiza* gen. nov., *Epulorhiza* gen. nov., *Moniliopsis*, and *Rhizoctonia*. Mycotaxon 29:91–99

Murray DIL (1981) *Rhizoctonia solani* causing barley stunt disorder. Trans Brit Mycol Soc 76:383–395

Murray DIL (1982) Penetration of barley root and coleoptile surfaces by *Rhizoctonia solani*. Trans Brit Mycol Soc 79:354–360

Oberwinkler F (1972) The relationships between the Tremellales and the Aphyllophorales. Persoonia 7:1–16

Oberwinkler F (1982) The significance of the morphology of the basidium in the phylogeny of Basidiomycetes. In: Wells K, Wells EK (eds) Basidium and basidiocarp. Evolution, cytology, function, and development. Springer Verl. New York, Heidelberg, pp 9–35

Oberwinkler F (1985) Anmerkungen zur Evolution und Systematik der Basidiomyceten. Bot Jahrb Syst 107:541–580

Ogoshi A (1972a) Grouping of *Rhizoctonia solani* Kühn with hyphal anastomosis. Ann Phytopathol Soc Jpn 38:117–122

Ogoshi A (1972b) Some characteristics of hyphal anastomosis groups in *Rhizoctonia solani* Kühn with. Ann Phytopathol Soc Jpn 38:123–129

Ogoshi A, Oniki M, Araki T, Ui T (1983) Anastomosis groups of binucleate *Rhizoctonia* in Japan and North America and their perfect states. Trans Mycol Soc Jpn 24:79–87

Oniki M, Ogoshi A, Araki T (1986) *Ceratobasidium setariae, C. cornigerum,* and *C. gramineum*, the teleomorphs of the pathogenic binucleate rhizoctonia fungi from gramineous plants. Trans Mycol Soc Jpn 27:147–158

Parmeter JR Jr, Sherwood RT, Platt WD (1969) Anastomosis grouping among isolates of *Thanatephorus cucumeris*. Phytopathology 59: 1270–1278

Reeser PW, Putnam ML, Winton LM, Nesson M (2001) Characterization of a *Rhizoctonia*-like fungus causing web-blight of Douglas-fir and true fir Christmas trees. Phytopathology 91:S189

Richter H, Schneider R (1953) Untersuchungen zur morphologischen und biologischen Differenzierung von *Rhizoctonia solani*. Phytopathol Z 20:167–226

Rinehart TA, Copes WE, Toda T, Cubeta MA (2007) Genetic characterization of binucleate *Rhizoctonia* species causing web blight on *Azalea* in Mississippi and Alabama. Plant Dis 91:616–623

Roberts P (1993) *Exidiopsis* species from Devon, including the new segregate genera *Ceratosebacina, Endoperplexa, Microsebacina,* and *Serendipita*. Mycol Res 97:467–478

Roberts P (1998) *Thanatephorus ochraceus* a saprotrophic and orchid endomycorrhizal species. Sydowia 50:252–256

Roberts P (1999) *Rhizoctonia*-forming fungi—a taxonomic guide. The Herbarium, Royal Botanic Gardens, Kew, p 239

Rogers DP (1935) Notes on the lower Basidiomycetes. Univ Iowa Stud Nat Hist 17:3–43

Roll-Hansen F, Roll-Hansen H (1968) A species of *Rhizoctonia* DC. ex Fr. damaging spruce plants in nurseries in Southern Norway. Meddelelser fra det Norske Skogforsøksvesen 82:421–440

Samuels GJ, Ismaiel A, Rosmana A, Junaid M, Guest D, McMahon P, Keane P, Purwantara A, Lambert S, Rodriguez-Carres M, Cubeta MA (2011) Vascular streak dieback of cacao in Southeast Asia and Melanesia: in planta detection of the pathogen and a new taxonomy. Fungal Biol 116:11–23

Schultz H (1937) Vergleichende Untersuchungen zur Ökologie, Morphologie und Systematik des "Vermehrungspilzes". Arb Biol Reichsanst Land- Forstw, Berlin 22:1–41

Sharon M, Kuninaga S, Hyakumachi M, Naito S, Sneh B (2008) Classification of *Rhizoctonia* spp. using rDNA-ITS squence analysis supports the genetic basis of the classical anastomosis grouping. Mycoscience 49:93–114

Sneh B, Burpee L, Ogoshi A (1991) Identification of *Rhizoctonia* species. Am Phyt Soc Press, St. Paul

Stamatakis A (2006) RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. Bioinformatics 22:2688–2690

Stamatakis A, Hoover P, Rougemont J (2008) A rapid bootstrap algorithm for the RAxML web servers. Syst Biol 57:758–771

Svrcek M, Pouzar Z (1970) *Cejpomyces* gen. nov., a new genus of resupinate hymenomycetes (Corticiaceae). Ceská Myk 24:5–11

Talbot PHB, Keane PJ (1971) *Oncobasidium*: a new genus of tulasnelloid fungi. Aust J Bot 19:203–206

Veldre V (2011) Insights into the ecology of the *Ceratobasidium-Thanatephorus* complex based on phylogeny reconstruction using all publicly available ITS sequences. Master thesis, University of Tartu

Veldre V, Abarenkov K, Bahram M, Martos F, Selosse M-A, Tamm H, Kõljalg U, Tedersoo L (2013) Evolution of nutritional modes of Ceratobasidiaceae (Cantharellales, Basidiomycota) as revealed form publicly available ITS sequences. Fungal Ecol 30:1–13

Venn K, Sandvik M, Langerud BRP (1986) Nursery routines, growth media and pathogens affect growth and root dieback in Norway spruce seedlings. Med Nordk Inst Skogf 39:313–328

von Tubeuf K (1890) *Trichosphaeria parasitica* an der Fichte. Botan Centralbl 41:376–377

Warcup JH, Talbot PHB (1962) Ecology and identity of mycelia isolated from soil. Trans Brit Mycol Soc 45:495–518

Warcup JH, Talbot PHB (1971) Perfect states of *Rhizoctonias* associated with orchids II. New Phytol 70:35–40

Warcup JH, Talbot PHB (1980) Perfect states of *Rhizoctonias* associated with orchids III. New Phytol 86:267–272

Weinhold AR, Motta J (1972) Initial host responses in cotton to infection by *Rhizoctonia solani*. Phytopathology 63:157–162

Weiß M, Oberwinkler F (2001) Phylogenetic relationships in Auriculariales and related groups—hypotheses derived from nuclear ribosomal DNA sequences. Mycol Res 105:403–415

White TJ, Bruns T, Lee S, Taylor JW (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis MA, Gelfand DH, Sninsky JJ, White TJ (eds) PCR protocols: a guide to methods and applications. New York, Academic Press, pp 315–322

Williamson B, Hadley G (1970) Penetration and infection of orchid protocorms by *Thanatephorus cucumeris* and other *Rhizoctonia* isolates. Phytopathology 60:1092–1096