

Rhizoctonia Species: Taxonomy, Molecular Biology, Ecology, Pathology and Disease Control

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A SYNOPSIS OF THE TAXONOMY OF TELEOMORPHS CONNECTED WITH *RHIZOCTONIA* S.L.

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I. INTRODUCTION

The genus *Rhizoctonia* s.l., was originally characterized by the presence of sclerotia different from those of *Sclerotium* and the ability to infect living plant tissue (DeCandolle, 1815). This has already served to exclude the saprophytic ascomycetous genera *Ascorhizoctonia* (teleomorph: *Tricharina*, Yang and Korf, 1985; Moore, 1987) and *Oedocephalum* p.p. (teleomorph: *Iodophanus*, Gamundi and Ranalli, 1964; Stalpers, 1974) and to restrict it to the basidiomycetes. Duggar (1915) and Parmeter and Whitney (1970) listed additional characteristics to delimit *Rhizoctonia* s.l., among them hyphal constrictions at septa, hyphal branching at right angles just before septa, and production of monilioid cells. Unfortunately, these criteria are not sufficiently diagnostic to delimit a homogeneous taxon, and the teleomorphs of *Rhizoctonia* s.l. (as far as known) are now classified in various basidiomycete orders. A natural concept, in which anamorph taxonomy reflects teleomorph taxonomy, is now also being adopted in *Rhizoctonia* (Moore, 1987).

The type species of *Rhizoctonia* is *Rhizoctonia crocorum*, but as this typification would necessitate the introduction of the name *Moniliopsis napaeae* for the well known *Rhizoctonia solani* (Andersen and Stalpers, 1994), a proposal has been made to change the typification of *Rhizoctonia* by conservation and to adopt *R. solani* as the type. This proposal was unanimously supported at ISR '95, the International Symposium on *Rhizoctonia* in Noordwijkerhout, The Netherlands; its acceptance by the 1999 Botanical Congress is anticipated. As a consequence, *Thanatophyllum* Nees, a former obligate synonym of *Rhizoctonia* would become the correct name for the anamorph of *Helicobasidium*.

The scope of this book does not allow a comprehensive study of teleomorph taxonomy, but a short analysis of the characteristics considered important in both teleomorph and anamorph classification is provided, the position of the teleomorph genera in the system is discussed, and keys to genera and species are given. The teleomorphs of *Rhizoctonia* s.l. mainly occur in the Ceratobasidiaceae and Tulasnellaceae; the key to the teleomorphs contains all genera for which a *Rhizoctonia* state is known, and some that incorrectly have been connected with *Rhizoctonia*. For many species of the genera concerned no cultural characteristics are known, and more representatives are expected to display *Rhizoctonia* characteristics. Hence for *Tulasnella* and the generic complex *Ceratobasidium* - *Thanatephorus*, condensed keys to all species have been compiled.

II. INDUCTION OF BASIDIOME PRODUCTION

Most of the work on *Rhizoctonia* spp. is performed with cultures (Warcup and Talbot 1966; 1967; 1971), which are often isolated from sources not displaying the teleomorph. Techniques to induce sporulation are particularly useful and outlined below.

A. Transferring strains from high nutrient agar to low nutrient agar

Flentje (1956) obtained basidiomes by growing the cultures on PDMA (potato dextrose 'marmite' agar, 15 g potato, 40 g Marmite, 7.5 g dextrose per liter) for 7-8 days, and then transferred them to weak nutrient agar (soil extract agar). Murray (1982b) found that the initial medium was important and recommended PDMA and DMA (dextrose 'marmite' agar, 25 g marmite, 12.5 g dextrose per liter). Murray (1984) used the following method successfully for many species of *Rhizoctonia* s.l. Strains were pregrown on DMA prepared with distilled deionized water. Inocula were taken from margins of 3-day-old colonies and transferred to dishes with WA (water agar) or CMA (cornmeal agar) in Petri dishes with or without studs, thus with varying aeration. The time needed for the production of basidia was up to 34 days for many *Ceratobasidium* strains.

B. Soil-over-culture

(Tu *et al.*, 1969; Tu and Kimbrough 1975a). The strain was grown on PDA + 5% yeast extract (PYDA = potato yeast dextrose agar). Mycelial disks were cut from the periphery of 3 day old colonies and incubated at 28°C in the dark on PYDA, which contained 0.75% yeast extract. After 3-5 days the lid was removed and the culture covered with 1 cm sterilized soil (about 90g). The soil was watered 1-3 times a day to keep the relative humidity within acceptable limits. Sporulation generally occurred after 3-14 days. Important parameters were the age of the colony before covering it with soil (sporulation occurred only when mycelium of 3-7 days old was used for inoculation), the amount of yeast extract (sporulation occurred only in the range of 0.25-0.9%), the presence of dextrose and the choice of the soil (silty clay, Urrbray loam, sandy loam and even coarse river sand), the pH of the soil (between 6-10) and possibly light. The relative humidity seems to be less critical, but 40-60% is considered optimal. Stretton *et al.* (1964) and Warcup and Talbot (1965) also obtained good results after grinding cultures grown for 7-10 days on PDMA with sterile sand in a mortar, after which they were incorporated into soil.

C. Infection of plants

(Flentje, 1956). Unsterilized soil was inoculated with 25% (v/v) of a culture grown on maizenchal-sand. Seeds of wheat or tomato or sprouted potato cutlings were planted in 7cm diam, 9cm high glass jars in the soil, and placed in a glass house. Origin of inoculum as well as soil type was important for induction of sporulation.

III. CHARACTERISTICS ANALYSIS

Vegetative characteristics such as mycelial coloration, hyphal diameter, number of nuclei, length of cells, shape and size of monilioid cells, and sclerotial size, have generally been used in the characterization of *Rhizoctonia* s.l. (e.g. Duggar, 1915; Parmeter and Whitney, 1970). Andersen (1990) challenged this, arguing that, as these characteristics are mostly studied under *in vitro* conditions, care is needed in the evaluation, as most characteristics vary considerably with temperature, light and composition of the medium. In view of an integrated anamorph-teleomorph system (Moore, 1987), some of these characteristics may be useful in the description of the holomorphs along with studies of the septal pore ultrastructure, which is now considered a basic character of ordinal rank.

The diameter of hyphae is quite variable under culture conditions (Andersen, 1990), and have been reported to swell to eight times their original diameter in a concentrated substrate (Burgeff, 1936). The diameter may vary considerably within each genus, e.g., 0.5-1.5 μm in *Tulasnella permacra* (Roberts, 1993) to 3-7 μm in *T. brinkmannii* (Roberts, 1994). Only a few guidelines can therefore be suggested. *Tulasnella* and *Sebacina* spp. tend to have the narrowest hyphae, and if the hyphal diameter is less than 4 μm , the strain probably belongs to one of these genera. *Thanatephorus* and *Waitea* spp. possess the widest hyphae, and the occurrence of hyphae wider than 9-10 μm indicates that the strain probably belongs there. The cell length in the runner hyphae was once thought to be of diagnostic value, but Andersen (1990) demonstrated that such measurements are of no value in characterizing taxa in *Rhizoctonia* s.l.

Clamp connections have been reported for some *Rhizoctonia* strains, e.g. *Tulasnella calospora*' (Warcup and Talbot, 1967), *T. allantospora* (Warcup and Talbot, 1971), and '*Ceratobasidium fibulatum*' (Tu and Kimbrough, 1978); among teleomorphic genera with a *Rhizoctonia*-like anamorph, only *Tulasnella* has a considerable number of clamped species (Roberts, 1992, 1993, 1994, and see the present key). The occurrence of clamped septa in the basidiome need not be constant; in some species clamps are restricted to the subhymenium (Warcup and Talbot, 1967), in others they only occur at some septa of the subicular hyphae and then not necessarily in all strains of the species concerned (Warcup and Talbot, 1971). Clamp connections are here considered valuable at the species level, but not as a main character in the delimitation of genera.

Vegetative cells can be uni-, bi- and/or multinucleate. This condition is rarely absolute: for example, a small percentage of cells of a binucleate strain may show one or three nuclei, and multinucleate species may display a large variation in number (e.g., 4-15), often correlated with hyphal width. In *Tulasnella* the number of nuclei per cell is only known for a few species which are generally binucleate, in one case multinucleate (Boidin and Lanquetin, 1984; Andersen, 1996). Also *Sebacina* shows varying numbers of nuclei, from uninucleate strains of *S. umbrina* and *S. grisea* (Andersen, 1996) to the multinucleate *S. vermifera* (Williams and Thilo, 1989). In anamorphic *Rhizoctonia*-like fungi the number of nuclei per cell has been used in the description and delimitation of genera (e.g., the binucleate *Ceratorhiza* and the multinucleate *Rhizoctonia* (*Moniliopsis*)). *Thanatephorus* is considered to be multinucleate (Duggar, 1915; Parmeter and Whitney, 1970), but in fact the nuclear condition is only known for about 50% of the species; *Ceratobasidium* is generally binucleate (Parmeter *et al.*, 1967, Burpee *et al.*, 1980), but *C. koleroga* has been reported to be multinucleate (Boidin and Lanquetin, 1984). Although the number of nuclei is occasionally different from the expected, it is valuable as a diagnostic character in combination with other features in some genera, but not in others. However, recent investigations suggest that bi-multinucleate relations should be used with great care in taxonomy, as for example *Ceratobasidium* and *Thanatephorus* are closer related to each other than to *Waitea* (Andersen, 1996), although the two latter are multinucleate, with anamorphs until now classified in *Moniliopsis*, and the former is binucleate and consequently placed in *Ceratorhiza* (Moore, 1987); the taxonomy of aphyllporaceous species presents several examples of similar situations (e.g., *Gloeocystidiellum*, *Aleurodiscus*, Boidin and Lanquetin, 1984).

Monilioid cells are inflated cells which occur as more or less branched chains that remain intact (Duggar, 1915; Saksena and Vaartaja, 1961). Ontogenetical studies have shown that in *Rhizoctonia* these cells can be considered as precursors of sclerotia (Tu and Kimbrough, 1975b), and as such their presence has been taken as indicative of a

relationship to this genus (Bernard, 1909; Burgeff, 1936; Saksena and Vaartaja, 1960, 1961). However, the shape and size of the monilioid cells is extremely variable, and also medium dependent, and their morphology is considered to be of limited taxonomical value (Butler and Bracker, 1970; Andersen, 1990). Certain taxa may possess characteristic monilioid cells, e.g., *Epulorhiza anaticula* (Currah *et al.*, 1987) and *Ceratorhiza pernacatena* (Zelmer and Currah, 1996), and the morphology of monilioid cells may turn out to be characteristic for more anamorph taxa in *Rhizoctonia* s.l. at the species level.

Sclerotial production has been considered as a very important character not only for distinguishing the form genus (DeCandolle, 1815; Duggar, 1915; Parmeter and Whitney, 1970), but also for the distinction of both anamorph and teleomorph taxa at the species level (e.g., Bernard, 1909; Matz, 1921; Tu and Kimbrough, 1975b). Later investigations have shown that taxa belonging to *Ceratobasidium* and *Thanatephorus* can produce sclerotia that are indistinguishable from each other (Andersen, 1996). At least in these genera the distinction of species based on sclerotial structure seems unwarranted. However, it suggests a close relation between these two genera, and certainly helps in delimiting them from other genera like *Waitea*. In teleomorphic *Tulasnella* no records of sclerotia could be traced in the literature, but they have been described in cultural studies of sclerotial anamorphs referable to this genus on account of their dolipore structure (Bernard, 1909, Currah *et al.*, 1987; Zelmer and Currah, 1996; Andersen, 1996). Nevertheless, research on cultures derived from teleomorphs is highly needed, and may show some difference in sclerotial morphology within *Tulasnella*. Sclerotia have not been reported for *Sebacina*, but in culture monilioid cells are formed.

The basidia of the Ceratobasidiaceae and Tulasnellaceae, where most of the *Rhizoctonia* species belong, display much variation. As these families are in several respects intermediates between the homo- and heterobasidiomycetes, this is very informative about possible lines of development, as described e.g., by Talbot (1965) and Donk (1958b). Fig. 1 illustrates the developmental stages in four species that are or have been associated with *Rhizoctonia*: the holo- and homobasidiomycetous *Athelia* (1), the holo- and heterobasidiomycetous *Thanatephorus* (2), the heterobasidiomycetous *Tulasnella*, which is holobasidiomycetous, but has been considered to be phragmobasidiomycetous because of false septa produced under the sterigmata (3), and the phragmobasidiomycetous and heterobasidiomycetous *Sebacina* (4). The terminology is after Donk (1954a, 1956) and Talbot (1973). The development starts with a terminal cell, that can be anything between globose and cylindrical and is called a protobasidium in the Heterobasidiomycetes and basidiole or young basidium in the Homobasidiomycetes. Then meiosis and subsequent mitosis occurs and the nuclei migrate towards the apex. Now various things may happen: protosterigmata (Donk 1954a) may be formed as small or larger semiglobose to globose protuberances. In *Athelia* and *Thanatephorus* the protosterigmata are small and form only a brief stage in a continuous development, but in *Tulasnella* they are large and there is often a pause before further development; thus this stage is more obvious and the protuberance has been called epibasidium (Martin, 1938) and the remaining main body hypobasidium. In *Sebacina* there are no external protosterigmata; here the development is internal, and the development of two longitudinal walls or septa is considered as homologous to the protosterigmata. It should be recalled that these walls or septa have a variable length: they may be short and only apical, leaving most of the basidium undivided as in *Oliveonia* (Talbot, 1965) or (almost) to the very base of the basidium (nearly) dividing it into four cells. The third developmental stage includes the development of a secondary protosterigma (Donk 1954b, 1956), which is a hyphoid elongation of the protosterigma. The stage may be

completely absent (in *Athelia*), very short and sometimes difficult to distinguish (in species of *Ceratobasidium*) or quite distinct (*Tulasnella*, especially the species formerly classified in *Gloeotulasnella*) to very long (in *Sebacina*). The main function of this structure is probably to reach the air by growing through the gelatinous layer. In the absence of a gelatinous layer (or a high humidity) secondary protosterigmata are short or absent. Moreover the ability to produce a secondary protosterigma seems to be correlated with the ability to produce secondary basidiospores. The fourth and final stage is the formation of the spiculum, the apical apparatus that produces the ballistospore.

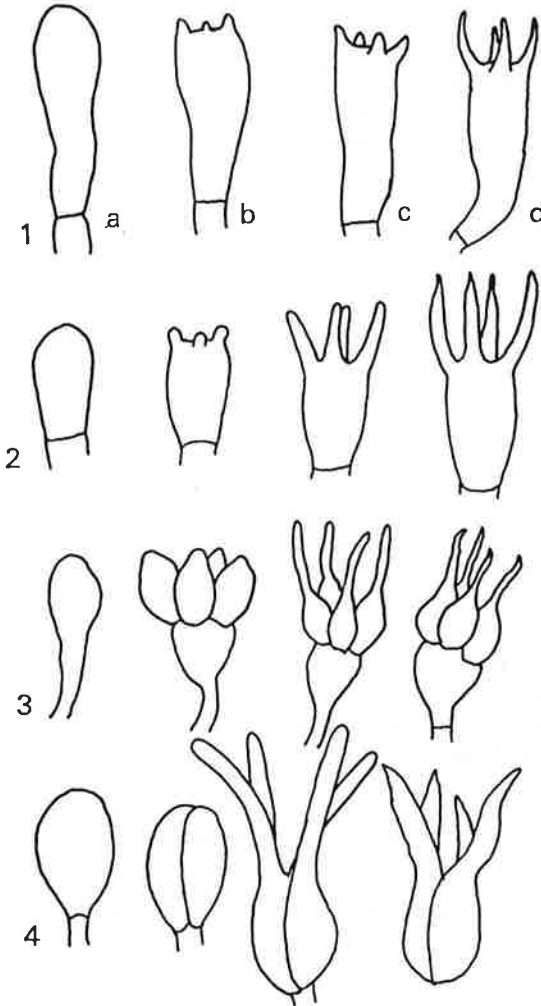


FIGURE 1. Various types of basidia found in teleomorph genera associated with *Rhizoctonia*-like anamorphs. 1: *Athelia*; 2: *Thanatephorus*; 3: *Tulasnella*; 4: *Exidia*. a: protobasidium, b: basidium with protosterigmata; c: basidium with secondary protosterigmata; d: mature basidium, sterigmata with spiculum.

The shape and septation of the basidia determines the generic classification of most *Rhizoctonia* teleomorphs. However, many teleomorphs have only been described from cultures, where some characteristics vary more widely than in nature. Humidity, medium composition, light and changes in orientation may cause aberrations, as for example many lateral basidia, larger variation in sterigmatal and basidial size (cf Murray, 1982a) etc.

Oberwinkler (1985) and Bauer and Oberwinkler (1986) launched an interesting theory on the ontogeny of basidia and basidiospores, based on observations in heterobasidiomycetous species. They interpreted the basidial cell as the final ontogenetic state in the meiotic process, thereby suggesting that all basidiospores were actually secondary spores, i.e. asexual spores or conidia.

Basidiospores in *Rhizoctonia* teleomorphs are hyaline, smooth, thin-walled, not amyloid and typically uninucleate. The shape varies from globose to ovoid, ellipsoid, cylindrical, allantoid or sigmoid and from citriform to fusiform. All species are known to be able to produce secondary spores, except *Waitea* and some species of *Thanatephorus*. The intraspecific variation increases with increasing length-width ratio, while the overall variation is larger than in homobasidiomycetous species because of the potential to produce secondary spores, which are generally slightly smaller, but otherwise indistinguishable.

IV. TAXONOMY

The genera with *Rhizoctonia* s.l. anamorphs are classified in three orders, the Platygloales (Platygloeaceae), and the related Exidiales (Sebacinaceae) and Tulasnellales (Ceratobasidiaceae and Tulasnellaceae); the Ceratobasidiaceae are often placed in a separate order Ceratobasidiales. Sclerotium-producing homobasidiomycetous species in the genus *Athelia* have sometimes been mentioned in connection with *Rhizoctonia* s.l., while *Sistotrema* has not, although e.g., *S. brinkmannii* may produce both sclerotia and monilioid cells. However, in culture all these species may produce clamps (although sometimes rarely). Homobasidiomycetous species have not been considered here further.

KEY TO THE TELEOMORPH FAMILIES CONTAINING RHIZOCTONIA-LIKE ANAMORPHS

- | | |
|--|-------------------|
| 1a. Basidia (ustidia) transversely septate (<i>Helicobasidium</i>) | Platygloeaceae |
| 1b. Basidia not transversely septate | 2 |
| 2a. Basidia longitudinally septate (<i>Sebacina</i>) | Exidiaceae |
| 2b. Basidia not septate | 3 |
| 3a. Basidia producing rather large, globose protosterigmata, which grow out to form pyriform sterigmata (<i>Tulasnella</i>) | Tulasnellaceae |
| 3b. Basidia without pyriform sterigmata | 4 |
| 4a. Spores capable of producing secondary spores and/or basidia with long sterigmata, often blunt or hyphoid (<i>Cejpomyces</i> , <i>Ceratobasidium</i> , <i>Tofispora</i> , <i>Metabourdotia</i> , <i>Oliveonia</i> , <i>Scotomyces</i> , <i>Thanatephorus</i> , <i>Uthatabasidium</i>) | Ceratobasidiaceae |
| 4b. Spores never producing secondary spores, basidia with (slightly) curved, rather short sterigmata (<i>Waitea</i> and similar fungi, for example <i>Athelia</i> , <i>Botryobasidium</i>) | |

Ceratobasidiaceae

Basidiome annual, effused, arachnoid, hypochnoid, pellicular, (sub)membranaceous or ceraceous. Hymenial surface smooth, sometimes discontinuous. Hyphal system monomitic. Subicular hyphae hyaline or brownish, thin- to thick-walled, often branching at right angles, often constricted near branching point, generally wider than subhymenial hyphae. Parenthesomes of dolipores with 3-4 large perforations. Subhymenial hyphae typically hyaline, relatively short-celled, thin-walled. Basidia hyaline, thin-walled, ovoid, sphaeropedunculate or barrel-shaped to subcylindrical to broadly clavate, (1-)2-4(-7) sterigmata. Sterigmata typically stout, with relatively broad base. Spores hyaline to pale yellowish, thin-walled, smooth, subglobose to ellipsoid or cylindrical, not amyloid, typically producing secondary spores, sometimes becoming secondarily 1-2-septate. Sclerotia may be present. Substrate: soil-inhabiting, mycorrhizal, parasitic or saprophytic on plants and wood.

The differences used to distinguish *Thanatephorus* from *Ceratobasidium* are gradual. The basidial shape, which is typically ovoid or sphaeropedunculate, may become short-cylindrical to broadly clavate in e.g., *C. anceps*. The basidiome of *Ceratobasidium* is typically thin, ceraceous, but it is pellicular to arachnoid in e.g., *C. anceps*, *C. koleroga* and *C. gramineum*. The rather narrow (up to 6 μm) and scant subicular hyphae in typical *Ceratobasidium* spp. may become rather wide (up to 10 μm in *C. koleroga*), brown sclerotia are also known in *Ceratobasidium*. Also the two-spored species (of which the non-ceraceous species have been classified in *Ypsilonidium*) also contain intermediate taxa. The ceraceous ones with an ovoid to sphaeropedunculate basidium have always been referred to *Ceratobasidium*, but *T. ovalisporus* is pellicular, forms hyphal strands and has sphaeropedunculate basidia. *Y. anomalum* shows besides septate basidiospores intermediate basidia and relatively narrow subicular hyphae; the number of nuclei is unknown. To conclude, there is a continuum of species displaying various combinations of characteristics, making the separation of the typical ceraceous, saprophytic *Ceratobasidium* with ovoid to sphaeropedunculate basidia and the typical hypochnoid, parasitic *Thanatephorus* with barrel-shaped basidia vague. *Waitea* is generally considered to belong to the Ceratobasidiaceae, despite the lack of secondary spore production and the homobasidiomycete-like basidia; the spores become secondarily septate.

Ceratobasidium D.P. Rogers (syn.: *Koleroga* Donk; type species: *Ceratobasidium calosporum* D.P. Rogers; anamorph: *Ceratorhiza* R.T. Moore)

Basidiome pellicular to ceraceous. Subicular hyphae without clamps, typically binucleate. Cystidia and other hymenial elements lacking. Basidia hyaline, thin-walled, subglobose to pyriform or sphaeropedunculate, about twice as wide as the supporting hypha. Sterigmata rather stout to stout (especially the two-spored species).

Thanatephorus Donk (syn.: *Ypsilonidium* Donk, *Aquathanatephorus* Tu and Kimbrough; incl.: *Cejpomyces* Svrcek and Pouzar, *Uthatobasidium* Donk; type species: *Hypochnus solani* Prillieux and Delacroix 1891; anamorph: *Rhizoctonia* DC.:Fr.

Basidiome arachnoid, hypochnoid, pellicular or (sub)membranaceous. Subicular hyphae often constricted near branching point, relatively wide (up to 17 μm), without clamps, multinucleate. Cystidia and other sterile hymenial elements lacking. Basidia hyaline, thin-walled, barrel-shaped to subcylindrical or broadly clavate, about the same width or slightly wider than the supporting hyphae, with (1-)2-4(-6) sterigmata. Sterigmata stout, with relatively broad base.

Talbot (1970) treated *T. cucumeris* extensively. Tu and Kimbrough (1978) distinguished *Aquathanatephorus* from *Thanatephorus* because of the globose metabasidium and swollen protosterigmata and the number of nuclei, despite the fact that they identified the anamorph as *Rhizoctonia solani*. The fungus normally grows at nearly 100% humidity, which is known to cause irregularities in size and shape of various hyphal structures including the basidia; the number of nuclei does not differ significantly from that of some strains of *R. solani* (Andersen, 1996). *Ypsilonidium* has been separated from *Thanatephorus* on the base of its basidia with two large sterigmata. However, a similar phenomenon is known for e.g., *Ceratobasidium bicorne* and *C. oryzae-sativae* and we see no reason to value this character higher in *Thanatephorus*. *Cejpomyces* was synonymized with *Thanatephorus* by Langer (1994), but the number of nuclei was not mentioned. In a number of other cases no data of the number of nuclei per cell was found; when at least the subicular hyphae turn out to be binucleate in one or more species, the position of these species may have to be reconsidered. For this very reason *Uthatabasidium* is not considered synonymous, although its species are keyed out here for convenience. The key below treats the members of the Ceratobasidiaceae as characterized in the key to the families, thus exclusive *Metabourdotia* (not treated) and *Waitea* (see below). When only a generic name is given, the genus is not known to contain *Rhizoctonia*-like species.

KEY TO THE SPECIES (C = *Ceratobasidium*, T = *Thanatephorus*,
U = *Uthatabasidium*, Y = *Ypsilonidium*)

- | | | | |
|------|---|---|----|
| 1a. | Cystidia or gloecystidia present | <i>Oliveonia</i> Donk | |
| 1b. | Cystidia and gloecystidia absent | | 2 |
| 2a. | Clamps present | <i>Scotomyces</i> Jülich | |
| 2b. | Clamps absent | | 3 |
| 3a. | Spores ornamented, citriform. Basidia with 4-6 sterigmata | <i>Tofispora</i> G. Langer | |
| 3b. | Spores smooth. Basidia only incidentally with more than 4 sterigmata | | 4 |
| 4a. | Spores filiform-flexuous to subsigmoid, 23-36 x 3-3.6 µm | <i>C. calosporum</i> D.P. Rogers | |
| 4b. | Spores globose, ovoid, ellipsoid or cylindrical. | | 5 |
| 5a. | Basidia with (1-)2(-3) stout sterigmata. | | 6 |
| 5b. | Basidia with (2-)4(-5) sterigmata | | 12 |
| 6a. | Spores globose to subglobose or broadly ellipsoid, at least 10 µm wide | | 7 |
| 6b. | Spores ovoid, ellipsoid or cylindrical, less than 10 µm wide | | 8 |
| 7a. | Spores (8-)9-17(-21) x (8-)9-16(-19) µm (anam.: <i>Rhizoctonia oryzae-sativae</i> (Sawada) Mordue) | <i>C. oryzae-sativae</i> P.S. Gunnell & R.K. Webster | |
| 7b. | Spores 11-15 x 10-12 µm (anam.: <i>Rhizoctonia fumigata</i> (Nakata ex Hara) P.S. Gunnell and R.K. Webster) | <i>C. setariae</i> (Sawada) P.S. Gunnell & R.K. Webster | |
| 8a. | Spores ovoid to ellipsoid, 8-15(-17) x (5-)6-9(-10.5) µm | | 9 |
| 8b. | Spores ellipsoid to cylindrical, 10-17 (-20) x 5-8(-9) µm | | 10 |
| 9a. | Hyphal strands present. Subicular hyphae hyaline | <i>T. ovalisporus</i> Cizek & Pouzar | |
| 9b. | Hyphal strands absent. Subicular hyphae brownish | <i>T. langlei-regis</i> D.Reid | |
| 10a. | Subicular hyphae up to 6 µm wide | <i>C. bicorne</i> J. Erikss. & Ryv. | |
| 10b. | Subicular hyphae wider. <i>T. sterigmaticus</i> complex | | 11 |
| 11a. | Basidiospores becoming 1-2-septate when old | <i>Y. anomalum</i> Warcup & Talbot | |
| 11b. | Basidiospores remaining aseptate | <i>T. sterigmaticus</i> (Bourdot) Talbot | |

- 12a. Spores cylindrical to slightly fusiform, (7-)9-16 x (2.5-)3-4.5(-5) μm 13
- 12b. Spores globose to subcylindrical, Q (length:width) < 2.5 14
- 13a. Saprophytic. Basidiome ceraceous, adnate. Sclerotia absent. Incl. *C. angustisporum*
C. pseudocornigerum M.P. Christ.
- 13b. Parasitic on leaves. Basidiome pellicular, separable. Sclerotia present (*Pellicularia*
koleroga complex pp, see also note under 27b) *C. stevensii* (Burt)
- 14a. Subicular hyphae brownish, often some wider than 10 μm .
Brown sclerotia present; hyphae multinucleate (*Thanatephorus* s. str.) 15
- 14b. Subicular hyphae hyaline or pale yellowish, up to 10 μm wide (in *U. fusisporum* wider) 20
- 15a. Spores globose to broadly ovoid 16
- 15b. Spores ovoid to ellipsoid 17
- 16a. Spores globose, hyaline, 6-7 μm diam. *T. pennatus* Currah
- 16b. Spores broadly ovoid, pale brown, 9-12 x 7-9.5 μm *T. orchidicola* Warcup & Talbot
- 17a. Spores ovoid to ellipsoid, 4-6.5 x 3-4 μm . Protosterigmata swollen. Aquatic.
(Basionym: *Aquathanatephorus pendulus* Tu and Kimbrough 1978, Bot. Gaz.
139: 459) *T. pendulus* (Tu & Kimbrough) comb. nov.
- 17b. Spores larger. Protosterigmata not swollen. Terrestrial. *T. cucumeris* complex 18
- 18a. Spores ovoid, 5-12.5 x 3-6.3 μm *T. corchori* Tu et al.
- 18b. Spores ellipsoid to ovoid 19
- 19a. Basidia barrel-shaped to subcylindrical, (10-)12-20(-23) x 8-12(-13) μm . Spores (7-
)8-13.5 x (4-)5-7 μm (incl.: *Hypochnus sasakii* Shirai and *Corticium microsclerotium*
Weber; anam.: *Rhizoctonia solani* Kühn) *T. cucumeris* (Frank) Donk
- 19b. Basidia cylindrical to suburniform or subclavate, 20-37 long, 10-13 μm wide at the apex
and 8-10 μm near the base. Spores 9.5-13.5 x 5.5-6.5 μm *T. gardneri* Warcup
- 20a. Spores globose to broadly ovoid 21
- 20b. Spores ovoid to ellipsoid, cylindrical or slightly fusiform 23
- 21a. Basidiospores broadly ovoid or broadly ellipsoid, 7.5-10 x 6-8 μm
C. obscurum D.P. Rogers
- 21b. Spores globose to subglobose 22
- 22a. Spores 6.5-9 μm diam. *C. sphaerosporum* Warcup & Talbot
- 22b. Spores 10-12(-14) μm diam. *C. globosisporum* Warcup & Talbot
- 23a. Spores ovoid or citriform, Q (length:width) < 2 24
- 23b. Spores narrowly ellipsoid or subcylindrical to slightly fusiform, Q \geq 2 27
- 24a. Spores citriform, biapiculate, 9-16(-18) x 6-10 μm . Subicular hyphae 8-14(-20) μm wide
U. fusisporum (J. Schroeter) Donk
- 24b. Spores not biapiculate. Subicular hyphae up to 10 μm wide 25
- 25a. Basidiome ochraceous. Spores 8-10 x 5-6.5 μm *U. ochraceum* (Masee) Donk
- 25b. Basidiome whitish or pale greyish. Spores narrowly ovoid, 5.2-10.5 x 3.5-7 μm 26
- 26a. Cells with (2-)3-5(-10) nuclei. Brown sclerotia present *T. corchori* Tu et al.
- 26b. Cells binucleate. Sclerotia absent (incl. *T. papillatum*, which may be an aberrant form)
C. ramicola Tu et al.
- 27a. Spores 6-7.5 x 3-3.5 μm *C. stridii* J. Erikss. & Ryv.
- 27b. Spores larger, at least on average 28

- 28a. Basidia short cylindrical, 20-30 x 8-10 μm . Spores not repetitive
Cejpomyces terrigenus (Bres.) Svrcek & Pouzar
- 28b. Basidia obovoid, up to 15(-20) μm long. Spores producing secondary spores 29
- 29a. Saprophytic on wood. Basidiome ceraceous, adnate. Spores narrowly ellipsoid, 6.5-10.5(-11.5) x 3.5-6(-7) μm
C. cornigerum (Bourdot) D.P. Rogers
- 29b. Parasitic on leaves, causing web blights. Basidiome often pellicular, separable 30
- 30a. On Gramineae. Hyphal strands absent. Spores ellipsoid, 6.5-12.7 x 3.2-6.3 μm . (syn.: *C. cereale* Murray and Burpee; anam.: *Cerathorhiza cerealis* (v.d. Hoeven) R.T. Moore)
C. gramineum (Ikata & T. Matsuura) Oniki *et al.*
- 30b. On leaves of dicotyledonous trees. Hyphal strands present. Spores ellipsoid to slightly fusiform, 9-15(-18) x 4.5-7(-8) μm .
C. anceps (Bres. & Syd.) H.S. Jacks.

Note: there is still considerable confusion concerning the *C. anceps* - *Pellicularia koleroga* complex. Höhnelt (1910) described the spores of the type *P. koleroga* as länglich-keulig, etwa gebogen¹, 10-12 x 4-4.2 (Q = 2.5-2.9), which is narrower than the description of Stevens and Hall (1909; 10.5-11.6 x 4.7-5.8, Q = 2-2.3), on its turn narrower than the spores of *Hypochnus ochroleucus* Noack in Saccardo and Sydow (1902), described as ovoid, 8.5-10 x 5.5-6 (Q = 1.5-1.7). Burt (1918), in his description of *Corticium stevensii* (proposed as nom. nov. for *H. ochroleucus*!) gave 8-11 x 3-4 (Q=2.6-2.8), which agrees with *P. koleroga*. There is no overlap between these taxa, which definitely need further study; we hesitate to declare any of them synonymous.

Waitea Warcup and Talbot (type species: *Waitea circinata* Warcup and Talbot)

Anamorph: *Chrysorhiza* T.F. Andersen and Stalpers gen. nov.

Hyphae multinucleatae, septa dolipori praedita. Parenthesoma 3-4-perforatum. Sclerotia globosa vel aggregata et irregularia, glabra, aurantiaca vel salmonea, brunnescentia, saepe tecta strato gelatinoso. Typus: *C. zae* (Voorhees) T.F. Andersen and Stalpers comb. nov. Basionym: *Rhizoctonia zae* (Voorhees 1934).

Basidiome hypochnoid to ceraceous, separable. Subicular hyphae multinucleate. Cystidia absent. Basidia subcylindrical to urniform, not much wider than supporting hyphae, with 4 curved sterigmata, up to 6 μm long. Spores hyaline, thin-walled, smooth, ellipsoid, pear-shaped or cylindrical, sometimes slightly curved, not amyloid, becoming 1-2-septate. Sclerotia globose to irregular, ochraceous to salmon, becoming brownish, often covered with a gelatinous layer.

The anamorph of *Waitea* has so far been accommodated in *Moniliopsis* (now *Rhizoctonia* s.str.) together with the anamorphs of *Thanatephorus*. However, the latter genus is more closely related to *Ceratobasidium*, because of basidia with typical elongating sterigmata and sclerotial morphology. The sclerotia of *Chrysorhiza* are smooth, globose or aggregating into irregular structures, often covered with a gelatinous layer, contrary to those of *Thanatephorus*, which are irregular, brown, without a smooth, delimited surface and never covered with a gelatinous substance.

A possible other member of the genus is the anamorph of *Waitea nuda* Cléménçon, which may be identical with *Rhizoctonia oryzae* (nom. inval.).

KEY TO THE SPECIES

- 1a. Basidiome hypochnoid. Some subhymenial cells irregular to contorted
W. circinata Warcup & Talbot
- 1b. Basidiome ceraceous. Irregular, contorted subhymenial cells absent
W. nuda Cléménçon

Platyglloeaceae

The only genus containing *Rhizoctonia* like species is *Helicobasidium*, which has until recently been considered to belong to the Auriculariaceae in the Auriculariales (Jülich, 1981), mainly because it was interpreted to have transversely septate basidia and is not an obligate parasite. However, the genus differs from *Auricularia* in a number of characteristics that are considered of some taxonomic importance. The so-called basidiospores (sporidia) germinate by budding and grow in a yeast-like manner. Bourett and McLaughlin (1986) described the pores of *Helicobasidium mompa* Tanaka as simple, i.e. lacking dolipores and a conspicuous parenthesome. The pores were sometimes occluded by globose bodies of electron-dense material, and the presence of microbodies close to the pore was observed. The spindle pole body (SPB) resembles that of the Uredinales, although differing in the number of layers (four in rusts, five in *Helicobasidium*) and the relationship of the discs to the nuclear envelope from the late interphase through telophase, while *Auricularia fuscosuccinea* has a spheroid, monoglobular SPB like in the other basidiomycetes (Bourett and McLaughlin, 1986). Additional support came from the study of 5S-rRNA, where Gottschalk and Blanz (1985) found a strong divergence between *Rhizoctonia crocorum* and *Hirneola auricula-judae* (as close relative of *Auricularia*). *Helicobasidium* is currently classified in the Ustomycota, Platyglloeales (Moore, 1990).

Helicobasidium Pat. (Type species: *Hypochnus purpureus* Tul.; anamorph: *Thanatophyllum* Nees)

Basidiome annual, resupinate, arachnoid or pellicular to membranaceous or felty. Hymenial surface even, whitish to pink or purplish. Hyphal system monomitic. Generative hyphae hyaline, thin- to thick-walled, without clamps, binucleate. Simple septa without parenthesome. Cystidia absent. Basidia hyaline, thin-walled, transversally septate, cylindrical, often curved or spirally. with 2-4 hyphoid sterigmata. Spores hyaline, thin-walled, smooth, ellipsoid to cylindrical or fusiform, not amyloid.

Substrate: soil-inhabiting, saprophytic or parasitic on plants.

Only the species of *Helicobasidium* producing thick, reddish-purplish basidiomes, which are known to produce *Rhizoctonia*-like anamorphs, are keyed out.

KEY TO THE SPECIES

- 1a. Spores ovoid to ellipsoid, 10-13.5 x 6-8(-9) μm *H. purpureum* Pat.
 1b. Spores fusiform, sometimes slightly curved, (10-)13-24(-29) x 4-7 μm . (= *H. mompa* auctt.)
H. compactum (Boedijn) Boedijn

Sebacinaceae with only a single genus containing *Rhizoctonia*-like species:

Sebacina Tulasne (syn.: *Cristella* Pat.; type species: *Thelephora incrustans* Fr.:Fr.; anamorph: *Opadorhiza* R.T. Moore)

Basidiome annual, resupinate or encrusting, ceraceous to gelatinous. Hymenial surface even to warted or irregular, whitish, cream, brownish, reddish or grey. Hyphal system monomitic or (seemingly) dimitic. Generative hyphae hyaline, thin- to thick-walled, with or without clamps, binucleate or multinucleate. Dolipore septa with imperforate parenthesome, or with a single, asymmetrically positioned perforation. Thin-walled (gloeo)cystidia rare. Basidia hyaline, thin-walled, longitudinally septate, globose to subpyriform, much wider than supporting hyphae, with 2-4 hyphoid sterigmata. Spores

hyaline, thin-walled, smooth, globose, ovoid, ellipsoid, cylindrical, allantoid or fusiform, not amyloid.

Because a *Rhizoctonia* anamorph has only been described for *S. vermifera* (Warcup and Talbot, 1967) and an unidentified species (Warcup and Talbot, 1966) and because our taxonomic knowledge does not permit the construction of a reliable key to the species, this is not attempted.

Tulasnellaceae with only a single genus containing *Rhizoctonia*-like species:

Tulasnella J. Schroeter (syn.: *Pachysterigma* J. Olsen 1888; *Prototremella* Patouillard 1888; *Muciporus* Juel 1897; *Gloeotulasnella* Höhnelt and Litschauer 1906; type species: *Hypochrus violens* Quélet; anamorph: *Epulorhiza* R.T. Moore)

Basidiome annual, effused, membranaceous to ceraceous or subgelatinous. Hymenial surface smooth to warted. Hyphal system monomitic. Subicular hyphae hyaline, thin- to thick-walled, not typically branching at right angles, with or without clamps, predominantly binucleate. Subhymenial hyphae hyaline, thin-walled, often somewhat irregular. Dolipores with imperforate parentheses, which are often recurved at the margin. Gloeocystidia sometimes present. Basidia hyaline, thin-walled, subglobose to broadly clavate, pyriform or sphaeropedunculate, often twice as wide as the supporting hypha. Sterigmata (or epibasidia) subglobose to broadly ellipsoid at first, then producing a tubular apex, broadly fusiform to pyriform. Spores hyaline, thin-walled, smooth, subglobose, cylindrical or fusiform to sigmoid, not amyloid, typically producing secondary spores. Sclerotia may be present.

KEY TO THE SPECIES

- | | | |
|------|--|---|
| 1a. | Spores fusiform, allantoid, sickle-shaped or helicoid, Q (length:width) > 2. | 2 |
| 1b. | Spores globose, ellipsoid, ovoid, reniform or short-fusiform, Q ≤ 2. | 19 |
| 2a. | Spores sickle-shaped to helicoid | 3 |
| 2b. | Spores cylindrical, fusiform, allantoid or reniform | 6 |
| 3a. | Clamps present | 4 |
| 3b. | Clamps absent | 5 |
| 4a. | Spores spirally coiled, 13.2-30 x 1.8-3.6 μm | <i>T. anguifera</i> P. Roberts |
| 4b. | Spores sickle-shaped, 12-30 x 1.2-1.8 μm | <i>T. interrogans</i> P. Roberts |
| 5a. | Gloeocystidia present, 24-54 x 6 μm. Spores sickle-shaped, 11.4 x 16.8 x 1.8-3 μm | <i>T. falcifera</i> P. Roberts |
| 5b. | Gloeocystidia absent. Spores sickle-shaped, 20-30 x 1.8-3.6 μm | <i>T. helicospora</i> Raunk. |
| 6a. | Spores on average larger than 20 μm | 7 |
| 6b. | Spores up to 18 μm long | 9 |
| 7a. | Spores narrowly curved-fusiform to sinuous, 25-50 x 2-3(-4) μm | <i>T. detiquescens</i> (Juel) Juel |
| 7b. | Spores fusiform to curved-fusiform, up to 30 μm long | 8 |
| 8a. | Hyphae up to 2 μm wide. Spores curved-fusiform with a swelling near the apiculus, 18-25 (-28) x 3-4 μm | <i>T. quasiflorens</i> P. Roberts |
| 8b. | Hyphae up to 7 μm wide. Spores fusiform to slightly curved-fusiform, 16-30 x (3-)3.5-5 μm | <i>T. calospora</i> (Boud.) D.P. Rogers |
| 9a. | Clamps present | 10 |
| 9b. | Clamps absent | 12 |
| 10a. | Spores allantoid, 7-14 x 2.5-4 μm, on average at least 8 μm long (incl. <i>T. caroliniana</i> (L.S. Olive) L.S. Olive and <i>T. curvispora</i> Donk) | <i>T. allantospora</i> Wakef. & Pearson |
| 10b. | Spores up to 8(-8.5) μm long, on average shorter | 11 |

- 11a. Spores allantoid, 5-8(-8.5) x 2-2.5(-3) μm *T. permacra* P. Roberts
 11b. Spores cylindrical to slightly allantoid or slightly fusiform, 5-6.5 x 2-2.5 μm *T. bifrons* Bourdot & Galzin
- 12a. Spores up to 9(-10) μm long 13
 12b. Spores 9-18 μm long, on average at least 10 μm 15
- 13a. Spores 4-7(-8) x 2.5-3.5(-4) μm , reniform 28
 13b. Spores 6-9(-10) μm long, allantoid 14
- 14a. Gloeocystidia present *T. aggregata* (L.S. Olive) L.S. Olive
 14b. Gloeocystidia absent (incl. *T. saveloides* P. Roberts) *T. rubropallens* Bourdot & Galzin
- 15a. Spores strongly allantoid, (7-)9-15(-17.5) x (2.5-)3-4 μm . *T. danica* Hauerl.
 15b. Spores cylindrical to fusiform, sometimes slightly allantoid. (*T. fuscoviolacea* complex) 16
- 16a. Spores cylindrical, (8-)9-14 μm long 17
 16b. Spores cylindrical to fusiform, (10-)12-18(-20) μm long 18
- 17a. Capitulate structures present, capitae becoming thick-walled chlamydospores, 13.5-17 μm diam. Spores 11-14 x 4.5-5 μm *T. irregularis* Warcup & Talbot
 17b. Capitulate structures and chlamydospores absent. Spores (8-)9-13 x 3-4.5 μm (incl. *T. pallidocrema* Jülich) *T. fuscoviolacea* Bres.
- 18a. Spores cylindrical, slightly curved, 12-18 x 3.5-4.5 μm . Sterigmata widely spaced, nearly lateral *T. cruciata* Warcup & Talbot
 18b. Spores fusiform, more rarely cylindrical, 10-20 x 3.5-6 μm . Sterigmata normally apical, not widely spaced (*T. violacea* auctt.) *T. brinkmannii* Bres.
- 19a. Gloeocystidia present. Spores 4.5-6(-6.5) x 3.5-5(-5.5) μm 20
 19b. Gloeocystidia absent 23
- 20a. Clamps present 21
 20b. Clamps absent 22
- 21a. Gloeocystidia 9-35 x 5.5-10 μm (incl. *T. guttulata* L.S. Olive) *Gloeocystidia metachroa* Bourdot & Galzin
 21b. Gloeocystidia 50-100(-200) x 5-16 μm (*T. traumatica* auctt.) *T. opalea* D.P. Rogers
- 22a. Gloeocystidia 22-162 x 6.8-10.5 μm . Chlamydospores may be present *T. pacifica* L.S. Olive
 22b. Gloeocystidia 10-75 x 6-12 μm . Chlamydospores absent 23
 23a. Gloeocystidia hyaline. Basidia 7-11 x 4-6 μm . On gymnosperms *T. hyalina* Höhn. & Litsch.
 23b. Gloeocystidia yellowish. Basidia 12-18 x 8-10 μm . On angiosperms *T. cystidiophora* Höhn. & Litsch.
- 24a. Clamps present 25
 24b. Clamps absent 27
- 25a. Spores subglobose to ellipsoid, 12.2-14.5 x 9-10 μm *T. conidiata* L.S. Olive
 25b. Spores 6-8.5 μm long 26
- 26a. Spores ellipsoid, 6-8.5 x 3.5-4.5 μm *T. crema* Jülich
 26b. Spores subglobose to ovoid or broadly ellipsoid, 6-7.5 x 4.8-5.8 μm . (incl. *T. bourdotii* Jülich) *T. inclusa* M.P. Christ.
- 27a. Spores reniform, 4-7(-8) x 2.5-3.5(-4) 28
 27b. Spores globose to ellipsoid, not reniform 29
- 28a. Sterigmata widely spaced. Hyphae 1-2(-3) μm wide *T. dissitispora* P. Roberts
 28b. Sterigmata closely adnate. Hyphae 2.5-3.5 μm wide *T. tomaculum* P. Roberts
- 29a. Spores up to 6 μm long. (incl.: *T. lactea* Bourdot & Galzin, *T. obscura* Bourdot & Galzin and *T. microspora* Wakef. & Pearson. These 'species' are mainly based on colour variants and slight differences in the size of spores and basidia) *T. eichleriana* Bres.
 29b. Spores 6-12 μm long 30

- 30a. Spores globose, (8-)10-12 μm diam. *T. sphaerospora* Martin
 30b. Spores ovoid to ellipsoid, up to 6 μm wide. (*T. pinicola* complex = *T. violea* auctt.) 31
- 31a. Spores narrowly ellipsoid, 6-8(-9) x (3.2-)3.5-4.5 μm . (incl. *T. araneosa* Bourdot & Galzin, *T. papillata* (L.S. Olive) L.S. Olive and *T. asymmetrica* Warcup & Talbot)
T. pruinosa Bourdot & Galzin 32
- 31b. Spores ovoid to ellipsoid, 6.5-9(-10) x (4-)4.5-5.5(-6) μm
- 32a. Hymenial surface whitish to pale violaceous. Basidiome up to 80 μm thick. Associated with angiosperms? (incl. *T. albida* Bourdot and Galzin) *T. albolilacea* Bourdot & Galzin
- 32b. Hymenial surface pink to purplish, plumbeous to blackish when dry. Basidiome gelatinous-plicate. Associated with gymnosperms? (incl. *T. sordida* Bourdot & Galzin and *T. tremelloidea* Wakef. & Pearson) *T. pinicola* Bres.

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