# *Oidiodendron*: A survey of the named species and related anamorphs of *Myxotrichum*

#### Adrianne V. Rice\* and Randolph S. Currah

Department of Biological Sciences, University of Alberta, Edmonton, Alberta, T6G 2E9 Canada\*\*

\*Correspondence: Arice@NRCan.gc.ca

Abstract: Synoptic and dichotomous keys to 23 species of *Oidiodendron* and similar arthroconidial anamorphs of *Myxotrichum* were developed using morphological and physiological characters. Illustrations and brief descriptions based on living isolates and published descriptions are provided for all species treated. Included are the unnamed *Oidiodendron* states of *Myxotrichum arcticum*, *M. cancellatum*, *M. emodense*, *M. setosum*, and *M. striatosporum*, as well as the anamorphic species *O. ambiguum*, *O. cerealis*, *O. chlamydosporicum* (inclusive of *O. scytaloides* as a synonym), *O. echinulatum*, *O. fimicola*, *O. flavum*, *O. fuscum*, *O. griseum*, *O. hughesii* (inclusive of *O. reticulatum* as a synonym), *O. maius* (inclusive of *O. maius* var. *citrinum* and *O. maius* var. *maius*), *O. muniellense*, *O. myxotrichoides*, *O. periconioides*, *O. pilicola*, *O. rhodogenum*, *O. setiferum* (inclusive of *O. ramosum* as a synonym), *O. tenuissimum*, and *O. truncatum*. *Oidiodendron fuscum*, the original type species, is recognized as distinct. *Oidiodendron robustum* is excluded because of its large conidia and conidiophores and because the original drawings do not convincingly portray arthroconidia. *Oidiodendron terrestre* is excluded because its large, two-celled conidia, rapid growth, and hyaline conidiophores are inconsistent with the generic diagnosis and because the mode of its conidiogenesis is unclear from the original descriptions and illustrations.

Taxonomic novelties: Oidiodendron maius var. citrinum (Barron) Rice & Currah stat. nov. Key words: dichotomous key, Myxotrichum, morphological characters, Oidiodendron, Oidiodendron fuscum, Oidiodendron maius var. citrinum, Oidiodendron maius var. maius, physiological characters, synoptic key.

#### **INTRODUCTION**

Species of Oidiodendron Robak and the anamorphs of Myxotrichum arcticum Udagawa, Uchiyama & Kamiya, M. cancellatum Phillips, M. emodense Udagawa & Uchiyama, M. setosum (Eidam) Orr & Plunkett, and M. striatosporum (Barron & Booth) Sigler produce distinctive chains of small (<  $6 \mu m \log$ ), unicellular arthroconidia through the basipetal fragmentation of hyaline fertile hyphae. The fertile hyphae arise from the apices of solitary, erect, smooth to asperulate, melanized conidiophores that are normally 5-500 µm long, though some species diverge significantly from this pattern. Oidiodendron myxotrichoides Calduch, Gené & Guarro produces fertile hyphae from the melanized branches of a reticulate conidioma. Oidiodendron hughesii Udagawa & Uchiyama, O. muniellense Calduch, Stchigel, Gené & Guarro, and O. setiferum Udagawa & Toyazaki have branched, melanized appendages surrounding the conidial mass at the conidiophore apices. Oidiodendron cerealis (Thüm.) Barron and *M. setosum* have short, hyaline to lightly melanized conidiophores and O. chlamvdosporicum Morrall has thick-walled, melanized chlamydospores.

The anamorph of *M. arcticum* also produces whorls of conidia that occur singly and in truncated chains along the conidiophore apex.

Conidia are hyaline to dark and are lens-shaped, globose, subglobose, ellipsoidal, cylindrical, barrelshaped, pyriform, or irregular. Surface texture is asperulate, verruculose, dimpled, rugose, spinulose, or reticulate. Scanning electron microscopy (SEM) shows that the characteristic surface ornamentation is due to the presence of a persistent perispore membrane derived from the wall of the conidiogenous hypha. Wall material from the conidiogenous hypha also persists between adjacent conidia where it eventually collapses to form "connectives".

Species of *Oidiodendron* have been isolated worldwide, mostly from soil and decaying plant materials (Peyronel 1914, Smith 1946, Malan 1949, Barron 1962, Morrall 1968, Kobayasi 1969, Ellis 1971, Udagawa & Toyazaki 1987, Hambleton *et al.* 1998, Sigler & Flis 1998, Hambleton *et al.* 1998, Calduch *et al.* 2004, Roose-Amsaleg *et al.* 2004).

Despite the widespread occurrence of this genus, there is no comprehensive key to the species. The keys in Barron (1962), Ellis (1971, 1976), Domsch *et al.* (1980), and Calduch *et al.* (2004) are out of date and rely exclusively on morphological characters. Calduch *et al.* (2004) include 23 species but four are not well accommodated in *Oidiodendron*, and three are

<sup>\*\*</sup>Current address for Adrianne V. Rice; Northern Forestry Centre, Natural Resources Canada, 5320-122 St., Edmonton, AB T6H 3S5 Canada

synonyms of other species. The unnamed anamorphs of *Myxotrichum* species are not included in previous keys.

Because morphological characters alone may be inadequate in hyphomycete species identification, as is often revealed by molecular studies, we sought additional phenotypic characters by investigating a suite of simple physiological tests. These have been incorporated into updated dichotomous and synoptic keys to 24 species or varieties. Preceding the keys is a review of the taxonomic history, distribution and ecology of the genus. Following a description of the procedures used to describe morphological and physiological characters is an assessment of their taxonomic value. Species descriptions follow the keys and are in alphabetical order.

#### **Taxonomic History**

The hyphomycete genus *Oidiodendron* was established by Robak (1932) for three species isolated from wood pulp, *O. fuscum* Robak, *O. nigrum* Robak, and *O. rhodogenum* Robak. The genus has since grown to encompass 18 species named in *Oidiodendron* and the unnamed anamorphs of five species of *Myxotrichum* Kunze.

Four species were added to the genus over the next 30 years. Newly described species included *O. griseum* Robak from wood pulp (Melin & Nannfeldt 1934) and *O. flavum* von Szilvinyi from soil (von Szilvinyi 1941). Species transferred into the genus included *Dicyma ambigua* Peyronel, the putative anamorph of *Myxotrichum aeruginosum* Mont. (Peyronel 1914, Malan 1949), as *O. ambiguum* (Peyronel) Malan (Malan 1949) and *Periconia tenuissima* (Peck) as *O. tenuissimum* (Peck) Hughes (Hughes 1958).

In 1962, Barron reviewed the genus, adding four new species, transferring a fifth, and designating two pairs of synonyms. The new species Oidiodendron citrinum Barron, O. echinulatum Barron, O. maius Barron, and O. truncatum Barron were all isolated from peat soils in Ontario. Trichosporium cerealis Thüm. was transferred into Oidiodendron as an earlier synonym of O. nigrum Robak. Barron also considered O. fuscum synonymous with O. tenuissimum and designated it as the type of the genus. The first key to the genus appeared in this publication and included nine species, O. cerealis, O. citrinum, O. echinulatum, O. flavum, O. griseum, O. maius, O. rhodogenum, O. tenuissimum, and O. truncatum (Barron 1962). Hambleton et al. (1998), using ribosomal DNA sequences, determined that O. tenuissimum sensu Barron comprised two species. Our morphological and physiological evidence indicate that these correspond with O. fuscum Robak and O. tenuissimum (Peck) Hughes. We therefore recommend reinstatement of the original type.

Between 1962 and 1968, three additional species were described. The first of these was *O. gracile* Zhdanova from the rhizosphere of maize (Zhdanova 1963). Morrall (1968) declared *O. gracile* a nomen dubium because no type was designated and because the original description and figures failed to clarify whether the conidia were arthroconidial or were produced by acrogenous budding. Morrall (1968) also described *O. chlamydosporicum* and *O. periconioides* Morrall from boreal forest soils.

In 1968, Tewari and MacPherson (1968) discovered a fungus appearing to cause neuropathology in mice in vitro. They later described this species as Oidiodendron kalrae Tewari & MacPherson (Tewari & MacPherson 1971) [as "kalrai"]. This species was ultimately transferred to Arthrographis as Arthrographis kalrae (Tewari & MacPherson) Sigler & Carmichael [as "kalrai"] on the basis of its hyaline conidiophores and smooth conidia, which lack connectives (Sigler & Carmichael 1976). Two new species were described in 1969, Oidiodendron pilicola Kobayasi, based on an isolate colonizing human hair in contact with soil (Kobayasi 1969), and O. terrestre Roy & Singh from Indian soil (Roy & Singh 1969). We exclude O. terrestre from Oidiodendron because of its rapid growth, large, two-celled conidia, and hyaline conidiophores, and because the mode of its conidiogenesis is unclear in the original descriptions and illustrations.

(1974) Stalpers transferred Oedocephalum sulphureum Cooke & Massee into Oidiodendron as O. sulphureum (Cooke & Massee) Stalpers but was concerned that the species might be a synonym of O. *flavum*. We have not examined the type, no cultures are available, and Stalpers' brief descriptions and illustrations leave room for doubt. Further details are found under "notes" following the description of O. flavum. Tokumasu (1973) and Söderström and Bååth (1978) isolated a species similar to O. chlamydosporicum from soil in Japan and Europe; it appeared as O. scytaloides in the key by Domsch et al. (1980) although it was not validly published as O. scytaloides Gams & Söderström until three years later (Gams & Söderström 1983). Molecular evidence (Hambleton et al. 1998, Calduch et al. 2004) and our examination of ex-type cultures of O. scytaloides and O. chlamydosporicum suggest that they are synonyms. Cultures of "O. sindenia Beyer" were deposited in the American Type Culture Collection (1976) but the name was never validly published (Beyer, pers. comm., 2002).

Two more species were described during the 1980s. The first, *O. robustum* Mercado Sierra & Castañeda Ruiz, from bark of *Bauhinia cumanensis* Kunth in Cuba (Mercado Sierra & Castañeda Ruiz 1985), is excluded based on its inordinately large conidia and conidiophores and because the mode of its conidiogenesis is unclear in the description and illustrations. *Oidiodendron setiferum* was described with branched, melanized appendages at the conidiophore apex, and the generic description was emended to accommodate this character (Udagawa & Toyazaki 1987).

From this point on, a succession of new species bearing such spiny or myxotrichoid appendages was described. A second species with melanized appendages that were more elaborate than those of O. setiferum and that formed a "reticuloperidium-like" structure surrounding the arthroconidia was named O. hughesii in 1998 (Udagawa & Uchiyama 1998). Calduch et al. (2002) described O. myxotrichoides, which produces arthroconidia on the melanized hyphae of a reticulate conidioma that superficially resembles the "reticuloperidium" of Myxotrichum ascomata. Calduch et al. (2004) described three more species with melanized appendages: O. muniellense Calduch, Stchigel, Gené & Guarro with setiform appendages and subglobose, roughened conidia, O. ramosum Calduch, Stchigel, Gené & Guarro with recurved appendages and smooth to slightly roughened conidia, and O. reticulatum Calduch, Stchigel, Gené & Guarro with ellipsoidal, roughened conidia and appendages resembling those of O. hughesii. Comparisons of the original descriptions and illustrations of O. hughesii, O. muniellense, O. ramosum, O. reticulatum, and ex-type material of O. setiferum suggest that O. reticulatum is a synonym of O. hughesii and O. ramosum is a synonym of O. setiferum.

Finally, Rice and Currah (2005–this volume) describe *O. fimicola* Rice & Currah from mushroom compost. The description is based on two cultures obtained from the Pennsylvania State University Mushroom Spawn Laboratory.

In addition to the binomials in Oidiodendron, listed above, one named species and five unnamed species constitute the anamorphic components of holomorphs named in Myxotrichum. Oidiodendron ambiguum (Peyronel 1914, Malan 1949) is listed as the anamorph of Myxotrichum aeruginosum and unnamed Oidiodendron anamorphs are connected with M. cancellatum (Orr & Kuehn 1964), M. setosum (Orr et al. 1963), M. striatosporum  $[\equiv Byssoascus]$ striatisporus (Barron & Booth) von Arx] (Barron & Booth 1966, Sigler & Carmichael 1976), M. arcticum (Udagawa et al. 1994), and M. emodense (Udagawa & Uchiyama 1999). A relationship between the species of Oidiodendron and teleomorphic taxa within the Myxotrichaceae is strongly supported by molecular evidence (Hambleton et al. 1998) in addition to these anamorph-teleomorph connections. Placement of the Myxotrichaceae among the inoperculate discomycetes (Leotiomycetes) is supported by molecular data

(Sugiyama *et al.* 1999, Mori *et al.* 2000, Gibas *et al.* 2002) and by a study indicating that the type of ascocarp development occurring in *Myxotrichum* is discomycetous in nature (Tsuneda & Currah 2004).

#### Distribution, occurrence, and ecology

Species of Oidiodendron are known as saprobes and come from a variety of living and decomposing plant, animal, and fungal substrates, including peat, soil, humus, wood, lichens, marine sediments and holothurians, human skin (incidental contamination only) and decomposing human hair (e.g. Robak 1932, Smith 1946, Barron 1962, Morrall 1968, Kobayasi 1969, Domsch et al. 1980, Hambleton et al. 1998, Sigler & Flis 1998, Pivkin 2000, Lumley et al. 2001, Calduch et al. 2004). They have also been identified from human food supplies (Delamarre & Batt 1999, Krysińska-Traczyk et al. 2001) and indoor air and dust samples (Udagawa & Toyazaki 1987, Horak et al. 1996, Reiman & Uitti 2000). They occur throughout the temperate regions (e.g. Domsch et al. 1980, Hambleton et al. 1998, Sigler & Flis 1998) and there are scattered reports from tropical and subtropical locales (Ellis 1971, Hambleton et al. 1998, Sigler & Flis 1998, Calduch et al. 2004, Roose-Amsaleg et al. 2004).

*Oidiodendron maius* var. *maius* appears to form ericoid mycorrhizas in nature with members of the *Ericaceae* (Couture *et al.* 1983, Douglas *et al.* 1989, Hambleton & Currah 1997, Johansson 2001, Lacourt *et al.* 2001) and other species can produce morphologically similar structures *in vitro* (Dalpé 1986, 1989, 1991, Currah *et al.* 1993). This relationship is facultative for the fungi because they also persist as free-living saprobes in the same habitat (Tsuneda *et al.* 2001, Piercey *et al.* 2002, Rice & Currah 2002, in press).

Despite the reports of Oidiodendron species from a diverse array of substrates and environments, little is known about their ecological roles in nature. Most reports are incidental and indirect (e.g. Delamarre & Batt 1999, Pivkin 2000, Lumley et al. 2001, Roose-Amsalag et al. 2004). Few researchers try to isolate Oidiodendron species specifically, and few speculate on their ecological roles (Rice & Currah 2002). The exception is O. maius var. maius, which is conceived as having a mutualistic relationship with ericaceous roots and can predictably be isolated from them (Rice & Currah, in press). Most recent research on Oidiodendron has focused on the mycorrhizal status of various species and on the ecological significance of this association (e.g. Couture et al. 1983, Dalpé 1986, 1989, Douglas et al. 1989, Dalpé 1991, Currah et al. 1993, Perotto et al. 1995, Bending & Read 1997, Hambleton & Currah 1997, Currah et al. 1999, Xiao & Berch 1999, Piercey et al. 2002, Usuki et al. 2003).

While benefits to the host plants have been observed in resynthesis studies, potential benefits to the mycobiont (*O. maius* var. *maius*) have not been investigated. Ecological assessments have been hampered by the inability to identify species accurately (Hambleton & Currah 1997, Hambleton *et al.* 1998, Lacourt *et al.* 2001). Misidentification of ericoid mycorrhizal isolates has led to difficulty in interpreting the specificity of these associations (Hambleton & Currah 1997, Hambleton *et al.* 2001, Rice & Currah, in press).

Targeted isolation studies are required to determine which habitats and substrates are occupied by *Oidiodendron* species. These studies must be based on precise identifications so that estimations of the range, abundance, and distribution of *Oidiodendron* species in nature can be determined. Functional assessments, including enzyme assays and physiological profiles, mycorrhizal resynthesis and decomposition studies, and tests for pathogenicity are required to elucidate the niches occupied by these fungi. Data from functional assessments and from distributional studies should be compiled to provide a more accurate ecological picture.

In vitro studies on the physiology of Oidiodendron species can provide insight into the potential roles these species play, although such studies do not provide information about actual ecological niches. Enzymatic studies on Oidiodendron have so far concentrated on the ecological implications of the cellulolytic abilities that have been detected (Dalpé 1991). All but two of the Oidiodendron species tested degraded cellulose azure, and various species produced other enzymes, including pectinases, lipases, gelatinases, and polyphenol oxidases, that potentially allow them to degrade a variety of plant, fungal, and animal-based substrates, including those found in soils. Broader substrate utilization profiles, including those generated by BIOLOG analyses (Rice & Currah 2005-this volume) could provide more information about the nutrition and potential ecological roles of Oidiodendron spp.

Three *Oidiodendron* and two related *Myxotrichum* species (*M. cancellatum*, *M. setosum*, *O. hughesii*, *O. myxotrichoides*, and *O. truncatum*) are psychrophilic, with temperature optima below 20 °C. The remaining species are psychrotolerant, with temperature optima of 20–25 °C but with the ability to grow at temperatures as low as 5 °C. These species show decreased growth at temperatures over 25 °C. Such observations may explain the prevalence *Oidiodendron* species in temperate climates, where average summer temperatures are below 25 °C, and the scarcity of these species in warmer tropical and subtropical ecosystems. Most species of *Oidiodendron* are acidophilic with pH optima of 3–5. Their predilection for acidic growth

media may explain their abundance in peat (Barron 1962, Sigler & Flis 1998, Rice & Currah 2002, Rice, unpublished, Thormann et al. 2001, 2002, 2004) as well as in the acidic soils of coniferous forests (e.g. Morrall 1968, Gams & Söderström 1983). The reported growth of Oidiodendron species in marine Holothurians and associated sediments (Pivkin 2000) is unusual, but tolerance to relatively high salt concentrations does occur in some species (i.e. O. maius and O. truncatum see Rice & Currah 2001). The enzymatic abilities and acidophilic nature of ericoid mycorrhizal Oidiodendron species may partially explain the success of their host plants in acidic nutrient-poor soils (Rice & Currah 2001, in press). The failure of other Oidiodendron species to form either in vitro or in situ mycorrhizal associations may be explained by the relatively high pH optima and different enzymatic abilities of these species. For example, *M. setosum* has a high pH optimum and is unable to utilize either cellulose or tannic acid. These attributes may partly explain its apparent absence from in situ ericoid mycorrhizal associations even though it has been shown to form intracellular coils in these hosts in vitro (Dalpé 1989).

The predilection shown by many Oidiodendron species for cold, acidic environments rich in plant, animal, and fungal debris may occur across the Mvxotrichaceae. In addition to Mvxotrichum and Oidiodendron, the family includes Gymnostellatospora Udagawa, Uchiyama & Kamiya, Pseudogymnoascus Raillo, and the widespread anamorphic Geomyces Traaen (Currah 1985, Sigler et al. 2000). Species of Geomyces produce small, dry, unicellular, barrelshaped to pyriform arthroconidia in dendritic clusters at the apices of erect, hyaline conidiophores (Sigler & Carmichael 1976). Species of Gymnostellatospora, Mvxotrichum, and *Pseudogymnoascus* produce small, fusiform ascospores in deliquescent, globose asci within reticuloperidia (Currah 1985, Sigler et al. 2000). The physiological requirements of most Geomyces, Gymnostellatospora, and species of Pseudogymnoascus are poorly studied, but there are reports of cellulolytic activity (Dalpé 1991, Udagawa et al. 1993, Uchiyama et al. 1995, Sigler et al. 2000, Udagawa & Uchiyama 2000) and psychrophily (Uchiyama et al. 1995, Sigler et al. 2000, Udagawa & Uchiyama 2000). Reports of isolation of the teleomorphic taxa are rare, but most isolations have been from decaying plant material and soils in temperate and cool environments (Udagawa et al. 1993, Uchiyama et al. 1995, Sigler et al. 2000, Udagawa & Uchiyama 2000) where corresponding anamorphs may be common. Myxotrichum chartarum Kunze : Fr. lacks an anamorph but is also reported to be psychrophilic (Tribe & Weber 2002).

Myxotrichaceous fungi are common on types of decaying plant material that are attractive to insects.

It has been suggested that the reticuloperidium of myxotrichaceous fungi is adapted for dispersal by arthropods (Currah 1985, Currah 1994, Greif & Currah 2003). Dispersal may be effected when the mesh-like peridial wall is impaled by the body hairs of insects or other arthropod carriers and plucked away from its substratum (Greif & Currah 2003). Wind dispersal of the small, dry conidia of Oidiodendron and Geomyces is likely, but these conidia may also be adapted for arthropod dispersal, adhering to carrier exoskeletons electrostatically (Greif & Currah 2003). Greif and Currah (2003) hypothesized that small arthropods may be important in dispersing the conidia locally while larger insects might disperse the ascocarps over longer distances to fresh substrates. It is possible that the reticulate conidiomata of O. myxotrichoides and the appendages of O. muniellense, O. setiferum and O. hughesii may function in a similar manner by attaching masses of conidia to arthropod vectors.

### **MATERIALS AND METHODS**

Isolates were obtained from the University of Alberta Microfungus Collection and Herbarium (UAMH, Edmonton, Alberta, Canada), the Mushroom Spawn Laboratory, Pennsylvania State University (DC, University Park, PA, U.S.A.), and the Centraalbureau voor Schimmelcultures (CBS, Utrecht, the Netherlands).

Information for some species was obtained solely from the literature. No ex-type or authentic cultures of *O. ambiguum, O. hughesii, O. sulphureum, O. terrestre* or *M. emodense* are available from culture collections. *Oidiodendron muniellense, O. myxotrichoides, O. ramosum,* and *O. reticulatum* were published too close to the completion of this manuscript to be studied directly. Isolates of *O. pilicola* and *M. striatosporum* from UAMH had degenerated to a point that made morphological study unreliable. A permanent slide of the anamorph of *M. striatosporum* was obtained from UAMH and used for microscopic measurements and description.

#### Morphology

Three replicates each of 40 isolates (16 species, Table 1) were grown as single-point-inoculated cultures on plates of cornmeal agar [CMA; 17 g Difco-Bacto corn meal agar (Difco Laboratories, Detroit, MI), 1 L  $dH_2O$ ] amended with 0.01 % oxytetracycline (Sigma Chemical Co., St. Louis, MO). Incubation was at room temperature in the dark. Colonies were measured and described at 28 d. Colony colour was determined without reference to a colour standard.

Two separate slide cultures on 10 % (w/v) cereal agar (CER) (Sigler & Flis 1998) of each isolate were

mounted after 14 d incubation at room temperature in the dark. Conidiophore colour, texture, and branching pattern were recorded, as were conidial shape, colour, and surface ornamentation. Conidiophores were described as "branched" when conidium-bearing branches arose from the pigmented apical region of the conidiophore. Whether branches were dichotomous or trichotomous was also noted. Conidiophore length was measured from the point of origin to the end of the melanized portion. Mean conidiophore lengths and conidial dimensions were calculated using at least 10 randomly selected conidiophores and conidia from each slide culture. Measurements are given as minimum-(mean)-maximum. Appendages (n = 10)of O. setiferum were measured from their origin on the conidiophore to the tip of the longest branch. The number of appendages per conidiophore was noted. Observations and measurements were made under oil immersion using an Olympus BX 50 light microscope (Olympus Optical Co., Tokyo, Japan). Photographs were made using an Olympus DP 12 Digital camera (Olympus Optical Co., Tokyo, Japan).

SEM images of conidia were prepared using Mycelial plugs (5 mm  $\times$  5 mm) from five-wk-old cultures on CMA. These were freeze-dried in liquid nitrogen, and viewed on a cryo-stage in a JEOL #JSM6301FX7V SEM (JEOL U.S.A. Inc., Peabody, MA).

#### **Physiological Studies**

Thirty-eight isolates, representing 15 species, were used in the physiological tests (Table 1). Light, temperature and pH tolerance tests follow Rice and Currah (2001). Unless otherwise stated, enzymatic assays follow Hutchison (1990) and Rice and Currah (2001). The effects of three light, six temperature, and five pH treatments were studied using two replicates of each isolate grown on CMA. Growth rates (mm/d) were calculated using two independent measurements of colony radius of each replicate at 7, 14, 21, and 28 d, and were compared with designated 'control' growth conditions for each factor studied.

Light treatments were diffuse natural daylight, 24 h darkness, and so-called "black light" regime combining ultraviolet light (Philips F20T12-BL, 20 W; Philips Lighting, New Jersey) and a fluorescent "growlight" (Sylvania F20T12, 20W; Osram Sylvania, Mississauga, ON, Canada) (Hambleton & Currah 1997, Rice & Currah 2001). Temperature treatments were 5, 10, 15, 20, 25, and 30 °C ( $\pm$  1.5 °C). To determine the effect of pH, isolates were grown on CMA adjusted to pH 3, 5, 7, 9, and 11 using 1 N hydrochloric acid (HCl) and 10 % potassium hydroxide (KOH).

For enzyme assays, cultures were grown at room temperature in the dark on media containing the target macromolecule with or without an indicator.

Species	Strain	Source (original identification where taxonomically significant)	CEL <sup>1</sup>	GEL <sup>2</sup>	LIP <sup>3</sup>	PEC <sup>4</sup>	STA <sup>5</sup>	TAM <sup>6</sup>	WDG <sup>7</sup>
Myxotrichum arcticum	UAMH 7565 <sup>T</sup>		+	+	1	+	+	+	ı
M. arcticum	UAMH 9243	Decayed spruce, Canada	+	+	ı	+	+	ı	ı
M. cancellatum	UAMH 1996	Soil, Japan	ŗ	+	ı	+	+		ı
M. setosum	UAMH 3835	Soil, Canada	ŗ	+	+	+	+		ı
	UAMH 4535	Washed mineral soil, Canada	ı	+	+	+	+	ı	·
Oidiodendron cerealis	UAMH 504	Human hair, Canada	+	+	I	+	+	ı	ı
O. cerealis	UAMH 1522	Peat soil, Canada	+	+	ı	+	+		
	CBS 349.62	Soil, Italy	+	+	ı	+	+		
O. chlamydosporicum	$UAMH 6520^{T}$	Soil, Canada	+	+	+	+	+		+
	$UAMH 6521^{T}$	Soil, Sweden (O. scytaloides)	+	+	ı	+	+		+
	UAMH 6527	Soil, Sweden (O. scytaloides)	+	+	ı	+	+	,	ı
	UAMH 8510	Fir roots, Germany (O. scytaloides)	+	+	+	+	+		
	UAHM 9751	Sphagnum, Canada (O. scytaloides)	+	+	+	+	+	+	
O. echinulatum	UAMH 8467 <sup>A</sup>	Peat soil, Canada	+	+	+		+	+	+
O. fimicola	UAMH 10459 <sup>T</sup>	Mushroom compost, U.S.A.	NA						
	UAMH 10523	Mushroom compost, U.S.A.	NA						
O. flavum	UAMH 1524 <sup>A</sup>	Peat soil, Canada	+	+	+	+	+		
O. fuscum	UAMH 8511 <sup>T</sup>	Wood pulp, Norway	ı	+	+	+	+		·
O. griseum	UAMH 1403 <sup>A</sup>	Wood pulp, Norway	+	+	ı	+	+	+	,
	UAMH 4080	Wood chips, Canada	+	+	ı	+	+	+	·
	UAMH 8925	Vaccinium roots, Canada	+	+	ı	+	+	+	,
O. maius var. citrinum	UAMH 1525	Cedar bog soil, Canada	+	+	+	+	+	+	+
	UAMH 7089	Ex sclerotia, stream drift, Canada	+	+	+	+	+	+	+
	UAMH 9275	Ex mycorrhizal root tip, Canada	+	+	+	+	+	+	+
O. maius var. maius	UAMH $1540^{\mathrm{T}}$	Peat soil, Canada	+	+	+	+	+	+	ı
	UAMH 8920	Oxycoccus roots, Canada	+	+	+	+	+	+	,
	UAMH 9749	Decaying Sphagnum, Canada	+	+	+	+	+	+	ı
	UAMH 10460	Vaccinium roots, Canada	÷	+	+	+	+	+	ı
	UAMH 10461	Vaccinium roots, Finland	+	+	+	+	+	+	ı

Table 1. Sources and enzymatic profiles for *Oidiodendron* isolates studied.

Table 1. (Continued).

Species	Strain	Source (original identification where taxonomically significant)	CEL <sup>1</sup>	GEL <sup>2</sup>	LIP <sup>3</sup>	PEC <sup>4</sup>	STA <sup>5</sup>	TAM <sup>6</sup>	WDG <sup>7</sup>
O. periconioides	UAMH 6084	<i>Calypso</i> roots, Canada	+	+	ı	+	+	+	
	UAMH 7289	Humus, Japan (O. echinulatum)	+	+	I	ı	+	+	ı
	$UAMH 8527^{T}$	Soil, Canada	+	+	I	+	+	+	ı
O. rhodogenum	UAMH 1405 <sup>A</sup>	Pulp sludge, Norway	+	+	I	+	+	ı	ı
	CBS 401.69	Soil, Canada	+	+	ı	+	+		
O. setiferum	$UAMH 5715^{T}$	House dust, Japan	+	+	ı	+	+	+	ı
O. tenuissimum	UAMH 1523	Forest soil, Canada	+	+	+	+	+	ı	ı
	UAMH 8513	Leaf litter, Spain	+	+	+	+	+	ı	ı
O. truncatum	UAMH 1399 <sup>T</sup>	Forest soil, Canada	+	+	+	+	ı	ı	ı
	UAMH 8443	Soil, Italy (O. ambiguum)	+	+	+	+	·	·	ı
	UAMH 10464	Decaying spruce, Canada	+	+	+	+	ı	ı	ı

<sup>1</sup>CEL = cellulose azure.

<sup>2</sup>GEL = gelatin. <sup>3</sup>LIP = TWEEN 20 (lipid). <sup>4</sup>PEC = pectin. <sup>5</sup>STA = starch. <sup>6</sup>TAM = tannic acid medium. <sup>7</sup>WDG = wood guaiacol (lignin). <sup>7</sup>WDG = wood guaiacol (lignin). <sup>7</sup> = ex-type. <sup>A</sup> = authentic. <sup>A</sup> = authentic. <sup>+</sup> = positive reaction.

NA = not tested.

OIDIODENDRON: SURVEY OF THE NAMED SPECIES AND RELATED ANAMORPHS OF MYXOTRICHUM

Polyphenol oxidase (PPO) activity was assessed using tannic acid medium (TAM), consisting of 5 g tannic acid (BDH Inc., Toronto, ON, Canada) autoclaved in 200 mL dH<sub>2</sub>O then combined with a still-warm, previously autoclaved mixture of 15 g Difco malt extract, 20 g Difco agar, and 800 mL dH<sub>2</sub>O (Rice & Currah 2001) and wood guaiacol medium (WDG), consisting of 2 g powdered Picea glauca stem wood, collected locally, plus 18 g Difco agar and 1 L dH<sub>2</sub>O, all autoclaved together, with 100 µL guaiacol (Sigma Chemical Co., St. Louis, MO) then added to the autoclaved materials (Miyamoto et al. 2000). Mycelial plugs (5 mm  $\times$  5 mm) were placed on plates of TAM and incubated for 48 hr. Darkening of the medium under the plug was considered a positive reaction, indicating the ability to degrade soluble phenolic polymers (Bending & Read 1997). Isolates were point-inoculated on plates of WDG and incubated for 5 wk. Red discoloration of the medium around the mycelium indicated a positive reaction for the degradation of insoluble phenolic polymers, including lignin (Miyamoto et al. 2000).

Cellulases were detected using cellulose azure (Smith 1977, Hutchison 1990, Rice & Currah 2001). Modified Melin-Norkrans agar (MMN) was made up as 12 g Difco agar, 3 g Difco malt extract, 1 g d-glucose anhydrous (Sigma), 1 g CaCl<sub>2</sub>, 0.5 g NaCl, 10 g KH<sub>2</sub>PO<sub>4</sub>, 3 g MgSO<sub>4</sub>·7H<sub>2</sub>O, and 1 L dH<sub>2</sub>O. Twenty-ml volumes were added to 50 mL Pyrex tubes, autoclaved, and allowed to solidify. A 2 % (w/v) solution of washed cellulose azure (Sigma) in MMN was autoclaved and 2 mL was pipetted as a layer over the solidified plain MMN medium in each tube. Reactions were scored after 5 wk based on the release of azure dye from the upper layer into the basal MMN layer.

Amylase activity was scored after isolates had grown for 3 wk on plates of MMN containing 2 g/L potato starch (BDH Inc., Poole, U.K.). Plates were flooded with iodine solution (5 g KI, 1.5 g I, 100 mL dH<sub>2</sub>O) and decanted after several minutes to reveal a clear zone around the mycelium in strains positive for this enzyme.

Pectinase activity was determined after incubation for 5 wk on MMN containing 5 g/L citrus pectin (Sigma). After plates were flooded for 6 hr with a 1 % aqueous solution of hexadecylmethylammonium bromide (Sigma), a clear zone around the mycelium against an otherwise opaque background was interpreted as a positive indication of pectinase activity.

Gelatinase activity was determined using MMN containing 60 g/L gelatin (Sigma) instead of agar. The gelatin was dissolved in 900 mL dH<sub>2</sub>O and autoclaved, the remaining ingredients were autoclaved in 100 mL dH<sub>2</sub>O. The solutions were combined before pouring. Inoculated plates were incubated for a maximum of

5 wk or until decomposition of the gelatin caused liquefaction of the medium.

Lipase synthesis was determined using MMN containing 0.1 g/L  $CaCl_2$  and 10 mL/L TWEEN 20 [polyoxyethylene sorbitan monolaurate (Sigma)], added after autoclaving. Isolates were incubated for 16 wk and scored for the presence of macroscopically visible crystals of the calcium salt of the fatty acid beneath the mycelium.

#### **RESULTS AND DISCUSSION**

#### **Evaluation of Key Characters**

*Morphology*: To date, keys to *Oidiodendron* species (Ellis 1971, 1976, Barron 1962, Domsch *et al.* 1980, Calduch *et al.* 2004) have been based exclusively on morphological characters, especially conidiophore length, conidial morphology, and cultural characteristics (Hambleton *et al.* 1998).

Conidiophores typically are erect and melanized and they branch at the apices to produce chains of arthroconidia. Conidiophore length, used regularly to delimit species, ranges from less than 5 to 500 µm. However, this character varies significantly among and even within conspecific isolates. For example, it ranged from 45 to 455 µm among 21 isolates of O. maius var. maius and from 123 to 455 µm within a single isolate (Rice & Currah 2001). Length ranges overlap among all species except O. cerealis (5-30 µm long) and M. *setosum* [typically  $< 5 \mu m$  long, though conidiophores up to 140 µm long have been observed (Sigler & Carmichael 1976)]. Consequently, the value of this character in identification is limited. Nonetheless, because conidiophore length is a readily observable character and because ranges are given in all species descriptions, we have incorporated these measurements into the dichotomous key. Users should be aware that this character is most useful when tendencies toward very short or very long conidiophores are considered in conjunction with other features.

Conidiophore branching, surface texture and pigmentation are useful in some instances. Some species have conidiophores that do not branch within the melanized portion, while in others, dichotomous, and occasionally trichotomous, branching occurs. The conidiophores of most species are either consistently smooth or faintly and inconsistently asperulate but those of *O. fimicola* are scaly in SEM and asperulate in LM. *Oidiodendron cerealis* and *M. setosum* typically do not produce dark conidiophores; instead, conidiophores are short (typically < 5  $\mu$ m long in our observations of *M. setosum*, up to 30  $\mu$ m long in *O. cerealis*) and hyaline, resembling vegetative hyphae. In other species, inconspicuous conidiophores are always accompanied by larger, melanized conidiophores.

The structures commonly called "connectives" are the remains of the hyphal sleeve in which the conidia differentiate. This material persists as collapsed wall material between mature conidia. It is visible in many species, but its conspicuous presence is not consistent within or among isolates. This character is therefore not useful for distinguishing species. On the other hand, M. arcticum displays a unique form of conidiogenesis. Termed "geniculate conidiogenesis," it produces truncate chains of one or two conidia borne in whorls at the conidiophore apex, and oriented perpendicular to the conidiophore axis (Udagawa et al. 1994, Tsuneda & Currah 2004). The ontogeny of these conidia is difficult to discern using light microscopy, but the conidiophores involved terminate in a small, dense head of conidia, easily distinguished from the more diffuse conidial arrangements produced by conidiophores terminating in normal branched chains of arthroconidia.

Conidial size varies little among species. It ranges from  $1.5-3 \times 1-2 \mu m$  to  $3-7 \times 2-4 \mu m$ , but most species produce conidia that are  $1.5-5 \times 1-2.5 \mu m$ . Colour, shape, and ornamentation are variable but are consistent within species, and therefore are useful characters. In light microscopy, conidia may appear hyaline, lightly pigmented, or dark. This trichotomy is important in our keys. Conidial colour *en masse*, as determined using the dissecting microscope, varies from white to pale grey to green-grey to brown to yellow. It largely accounts for the characteristic colours of colonies.

Rice and Currah (2001) found that conidial ornamentation was consistent among 21 isolates of O. maius var. maius but distinct from that of a superficially similar isolate of O. truncatum. This character provided a clearer distinction between these species than did conidiophore length and conidial size. Other species also have distinctive conidial surfaces. For example, the conidia of O. cerealis are lens-shaped with a thickened ring and have a rugose (wrinkled) perispore. Conidia of O. pilicola, O. truncatum, M. cancellatum, and M. striatosporum are all barrel-shaped with truncate ends but differ in surface ornamentation. In O. truncatum and M. cancellatum, conidia have a wrinkled, netlike perispore (resulting in characteristic "reticulate ornamentation") while those of O. pilicola are smooth to minutely asperulate and those of M. striatosporum are asperulate. Oidiodendron ambiguum, O. echinulatum, and O. periconioides, all with subglobose to ellipsoidal conidia, differ in that the conidia of O. ambiguum have rounded and minutely verruculose (warty) surface projections, while those of O. echinulatum have larger, but still rounded, warty projections, and those of O. periconioides have pointed and spinulose projections. Oidiodendron muniellense and O. setiferum, which are morphologically similar to one another, can be distinguished by conidial ornamentation, which is asperulate to spinulose in *O. muniellense* and smooth to reticulate in *O. setiferum*. Conidia of other species may be only slightly asperulate, reticulate, warty, or dimpled in SEM and look smooth, or nearly so, by light microscopy. *Oidiodendron flavum* and *O. fimicola* produce a variety of conidial shapes with smooth to asperulate ornamentation, and can be seen to differ significantly in this feature only in SEM. Conidial shapes are illustrated in Table 2.

Unique features, when they occur, may be useful characters. Examples include the chlamydospores seen in *O. chlamydosporicum*, and the melanized appendages that arise at the conidiophore apices of *O. muniellense*, *O. setiferum* and *O. hughesii*, and that make up the peridium-like enclosure of the conidiomata of *O. myxotrichoides*. The appendages of *O. hughesii* are larger and more highly branched and complex than those of *O. muniellense* and *O. setiferum*, but are similar to those of *O. myxotrichoides* in forming a peridium-like structure surrounding the arthroconidia. In *O. hughesii*, peridium-like branches are borne on the conidiophore apex and do not form a sessile, ascocarplike conidioma.

Colonial morphology, especially colour and the production of diffusible pigments and exudates, has also been used as a source of characters. It has the disadvantages, however, that it can vary according to the growth medium used and that it is not constant within isolates of the same species. Cultural characteristics are used in the keys only when they were reasonably consistent. Sigler & Gibas (2005–this volume) report a culture-based method for distinguishing *O. maius* from other species.

*Physiology*: Physiological tests, including enzyme profiling and tests for tolerance of different growth conditions, have seldom been used to distinguish *Oidiodendron* species (Rice & Currah 2001). Some such characters do, however, appear to have discriminating value and are used in our dichotomous key where appropriate, as well as in the species descriptions and synoptic key. These characters are presented with the caveat that only a small number of isolates (1–5 per species) were tested to obtain profiles. The range of variation within species and across the genus may be underestimated.

Neither light nor temperature preferences discriminated among most species but some minor distinctions are noted. For example, the growth of *O. echinulatum* was suppressed by daylight. *Oidiodendron setiferum* grew optimally at 25 °C and *O. truncatum*, *M. cancellatum*, and *M. setosum* grew optimally below 20 °C, with suppressed growth at 25 °C. All others grew optimally at 20 °C. *Oidiodendron hughesii* and *O. myxotrichoides* were not tested here but were described as psychrophilic, with optimal growth at 15 °C (Udagawa & Uchiyama 1998, Calduch *et al.* 

2002) and *O. muniellense* grows optimally at 25 °C (Calduch *et al.* 2004).

Species fell into two groups with respect to pH optima. *Oidiodendron cerealis*, *O. chlamydosporicum*, *O. flavum*, *O. fuscum*, *O. griseum*, *O. maius*, *O. periconioides*, *O. rhodogenum*, *O. setiferum*, *O. tenuissimum*, *M. cancellatum*, and *M. arcticum* were acidophilic (pH optima < 5) while *O. echinulatum*, *O. truncatum*, and *M. setosum* grew optimally at higher pH (> 7).

Substrate degradation tests can distinguish among morphologically similar species (Table 1). *Oidiodendron fuscum*, *M. cancellatum*, and *M. setosum* were unable to degrade cellulose azure, but the other tested species could all do this. *Oidiodendron cerealis*, *O. periconioides, O. rhodogenum, O. setiferum, M. arcticum,* and *M. cancellatum* were unable to degrade TWEEN 20, while this ability varied within *O. chlamydosporicum.* Only *O. echinulatum* was unable to degrade pectin, while the character was variable within *O. periconioides. Oidiodendron cerealis, O. flavum, O. fuscum, O. rhodogenum, O. tenuissimum, O. truncatum, M. cancellatum,* and *M. setosum* were unable to degrade tannic acid, but *O. chlamydosporicum* and *M. arcticum* varied in this ability. Only *O. maius* var. *citrinum* and *O. echinulatum* consistently degraded lignin, while isolates of *O. chlamydosporicum* varied in their ability to degrade this substrate. All species liquefied gelatin, and all but *O. truncatum* degraded potato starch.

#### Keys to Oidiodendron

The numbers given in parentheses after the species name in the keys below refers to the place of the taxon in the list of descriptions.

#### Synoptic Key to Oidiodendron

Character	Character State	Species
Conidiomata	Present	O. myxotrichoides (18)
	Absent	All others
Melanized appendages	Simple, antler-like	O. muniellense (17) O. setiferum (22)
	Peridium-like	O. hughesii (14)
	Absent	All others
Chlamydospores	Present	O. chlamydosporicum (8)
	Absent	All others
"Geniculate conidiogenesis"	Present	M. arcticum (1)
	Absent	All others
Conidial colour	Darkly pigmented	M. striatosporum (5) O. cerealis (7) O. echinulatum (9) O. flavum (11) O. muniellense (17) O. myxotrichoides (18) O. periconioides (19) O. tenuissimum (23) O. truncatum (24)
	Hyaline	M. arcticum (1) M. cancellatum (2) M. emodense (3) M. setosum (4) O. ambiguum (6) O. chlamydosporicum (8) O. fuscum (12) O. griseum (13) O. maius (15, 16) O. pilicola (20)
	Lightly pigmented	O. fimicola (10) O. hughesii (15) O. rhodogenum (21) O. setiferum (22)

Character	Character State	Species
Conidial ornamentation	Thickened ring	O. cerealis (7)
	Reticulate	<i>M. cancellatum</i> (2) <i>O. truncatum</i> (24)
	Warty or spiny	<i>O. ambiguum</i> (6) <i>O. echinulatum</i> (9) <i>O. periconioides</i> (19)
	Asperulate	M. striatosporum (5) O. fimicola (10) O. flavum (11) O. hughesii (14) O. muniellense (17) O. tenuissimum (23)
	Indistinct	M. arcticum (1) M. emodense (3) M. setosum (4) O. chlamydosporicum (8) O. fuscum (12) O. griseum (13) O. maius (15, 16) O. myxotrichoides (18) O. pilicola (20) O. rhodogenum (21) O. setiferum (22)
Conidial shape	Lens-shaped	O. cerealis (7)
	Globose-ellipsoidal	O. ambiguum (6) O. echinulatum (9) O. fuscum (12) O. hughesii (14) O. muniellense (17) O. myxotrichoides (18) O. periconioides (19)
	Barrel-shaped (truncate)	M. cancellatum (2) M. striatosporum (5) O. pilicola (20) O. truncatum (24)
	Subglobose, ellipsoidal or elongate	M. arcticum (1) M. emodense (3) M. setosum (4) O. chlamydosporicum (8) O. griseum (13) O. maius (15, 16) O. rhodogenum (21) O. setiferum (22) O. tenuissimum (23)
	Variable	<i>O. fimicola</i> (10) <i>O. flavum</i> (11)
Conidiophore branching	Branched	M. arcticum (1) M. cancellatum (2) M. emodense (3) M. striatosporum (5) O. ambiguum (6) O. echinulatum (9) O. hughesii (14) O. muniellense (17) O. periconioides (19) O. pilicola (20) O. rhodogenum (21)

Character	Character State	Species
		O. setiferum (22) O. truncatum (24)
	Unbranched	O. flavum (11) O. fuscum (12) O. griseum (13) O. maius (15, 16) O. tenuissimum (23) M. setosum (4) O. cerealis (7)
	Variable	O. chlamydosporicum (8) O. fimicola (10)
Conidiophore pigmentation	Hyaline	M. setosum (4) O. cerealis (7)
	Variable	O. chlamydosporicum (8) O. fimicola (10)
	Melanized	All others
Conidiophore texture	Highly asperulate	O. fimicola (10)
	Smooth or minutely asperulate	All others
Colony surface colour	Yellow	M. setosum (4) O. maius var. citrinum (15)
	Off-white or grey	M. arcticum (1) M. cancellatum (2) M. emodense (3) O. ambiguum (6) O. fimicola (10) O. fuscum (12) O. griseum (13) O. maius var. maius (16) O. rhodogenum (21)
	Pale brown	O. echinulatum (9) O. flavum (11)
	Dark brown/green	M. striatosporum (5) O. cerealis (7) O. hughesii (14) O. muniellense (17) O. myxotrichoides (18) O. periconioides (19) O. setiferum (22) O. tenuissimum (23) O. truncatum (24)
	Variable	O. chlamydosporicum (8)
Optimal temperature	< 20 °C	M. cancellatum (2) M. setosum (4) O. hughesii (14) O. myxotrichoides (18) O. truncatum (24)
	> 20 °C	O. chlamydosporicum (8) O. muniellense (17) O. setiferum (22)
	20 °C	All others
Optimal pH	Basic (9–11)	M. setosum (4) O. echinulatum (9) O. truncatum (24)
	Acidic (3–5)	All others

Character	Character State	Species
Cellulose degradation	No	M. cancellatum (2) M. setosum (4) O. fuscum (12)
	Yes	All others
Lignin (wood guaiacol) degradation	Yes	O. echinulatum (9) O. maius var. citrinum (15)
	Variable	O. chlamydosporicum (8)
	No	All others
Lipid (TWEEN 20) degradation	Yes	M. setosum (4) O. echinulatum (9) O. flavum (11) O. fuscum (12) O. maius (15, 16) O. tenuissimum (23) O. truncatum (24)
	No	M. arcticum (1) M. cancellatum (2) O. cerealis (7) O. griseum (13) O. periconioides (19) O. rhodogenum (21) O. setiferum (22)
	Variable	O. chlamydosporicum (8)
Pectin degradation	No	<i>O. echinulatum</i> (9)
	Variable	O. periconioides (19)
	Yes	All others
Starch degradation	No	O. truncatum (24)
	Yes	All others
Tannic acid degradation	Yes	O. echinulatum (9) O. griseum (13) O. maius (15, 16) O. periconioides (19) O. setiferum (22)
	No	M. cancellatum (2) M. setosum (4) O. cerealis (7) O. flavum (11) O. fuscum (12) O. rhodogenum (21) O. tenuissimum (23) O. truncatum (24)
	Variable	M. arcticum (1) O. chlamydosporicum (8)

<b>Dichotomous Key to</b> <i>Oidiodendron</i> 1a Conidia produced on fertile hyphae arising laterally or terminally from the melanized branches of a reticuloperidium like conidiomaO. <i>myxotrichoides</i> (18)
1b Conidia produced on solitary conidiophores; conidiomata absent
<ul> <li>2a (1b) Conidiophores hyaline, in some isolates typically &lt; 5 μm long and in others typically &lt; 30 μm long (exceptional structures may be up to 130 μm long)</li></ul>
<ul> <li>3a (2a) Colonies cream to yellow. Conidia hyaline, subglobose to elongate</li></ul>
4a (2b) Conidiophores bearing melanized appendages at their apices
4a (2b) Conidiophores ocaring inclanzed appendages at their apices
(20) contaiophores not ocaring metainized appendages at their aprecision
5a (4a) Appendages highly branched and anastomosing to form a reticulate network, 60–300 μm diam. including peripheral spines. Conidia pale olive brown, produced <i>en masse</i> at the centre of the reticulum
hyphae arising from the conidiophore apex or from appendage branch points or tips
6a (5b) Appendages straight, up to 60 μm long. Conidia globose to subglobose, asperulate to echinulate
6b (5b) Appendages often recurved, up to 130 μm long. Conidia subglobose to elongate or irregular, with smooth
to faintly reticulate ornamentation
<ul> <li>7a (4b) Fertile hyphae swelling to form chains of vesicles, which form thick-walled, melanized, spiny, globose to ellipsoidal conidia, 3–6 × 2–4 μm</li></ul>
<ul> <li>8a (7b) Melanized chlamydospores present, 3–6 × 2–4 μm, borne on repent hyphae and conidiophores. Conidiophores 5–70 μm long (mean &lt; 20 μm). Conidia hyaline, 1.5–3 × 1–2 μmO. <i>chlamydosporicum</i> (8)</li> <li>8b (7b) Chlamydospores absent. Conidiophores typically longer than 20 μm. Conidia hyaline or melanized9</li> </ul>
9a (8b) Conidiophores asperulate under light microscopy. Conidia hyaline to pale brown, elongate to barrel- shaped or irregular, $3-6 \times 2-3 \mu m$
9b (8b) Conidiophores smooth under light microscopy. Conidia hyaline or melanized, subglobose to ellipsoidal,
elongate, barrel-shaped or irregular
<ul> <li>10a (9b) Conidia subglobose to barrel-shaped with truncate ends</li></ul>
11a (10a) Conidia melanized, produced either on conidiophores $< 200 \ \mu m$ long or directly from vegetative
hyphae
<ul> <li>12a (11a) Mature colonies olive-green with yellow margins. Conidia 2–7 × 1.5–2.5 μm, smooth to asperulate with distinct apical scars, produced on unbranched or dichotomously branched conidiophores &lt;100 μm long or directly from vegetative hyphae</li></ul>

13a (11b) Conidiophores dichotomously or trichotomously branched, 25–100  $\mu m$  long. Conidia 1.5–3.5  $\times$  1–2.5

13b	$\mu$ m, thick-walled, with reticulate ornamentation
	(10b) Conidia melanized
15a	(14a) Conidia globose to broadly ellipsoidal, warty. pH optimum > 7. Conidiophores dichotomously branched
15b	(14a) Conidia subglobose to elongate or irregular, with indistinct or asperulate ornamentation. pH optimum < 7. Conidiophores unbranched
16a	(15b) Colonies cream. Conidia subglobose, ellipsoidal, pyriform, or irregular, thick walled, smooth to asperulate. Conidiophores 25–80 µm long
16b	(15b) Colonies brown. Conidia subglobose to elongate, with indistinct to asperulate ornamentation. Conidiophores 30–250 μm long
17a	(14b) Colonies white to pale grey. Conidia produced in branching chains from fertile hyphae or in truncated chains (1-2 conidia) in whorls at the conidiophore apices. Conidia subglobose to elongate and irregular, $1.5-3.5 \times 1-2.5 \mu m$ . Conidiophores dichotomously branched
17b	(14b) Colonies off-white, grey, or yellow. Conidia produced only in branching chains from fertile hyphae. Conidia globose to ellipsoidal or subglobose to elongate. Conidiophores unbranched or dichotomously branched
18a	(17b) Colonies off-white to grey or green-grey. Conidiophores dichotomously branched. Conidia globose to ellipsoidal in some isolates and subglobose to elongate or irregular in others
18b	(17b) Colonies off-white to grey, or yellow. Conidiophores unbranched. Conidia subglobose, ellipsoidal or elongate
	(18a) Colonies off-white to grey, sometimes with diffusible red pigment. Conidiophores 30–85 $\mu$ m long. Fertile hyphae dichotomously branched. Conidia subglobose to elongate or irregular, $1.5-5 \times 1.5-2 \mu$ m, with indistinct ornamentation
19b	(18a) Colonies grey or green-grey, red pigment absent. Conidiophores up to 200 $\mu$ m long. Fertile hyphae often verticillate. Conidia globose to ellipsoidal, vertuculose and 3–4.5 × 2.5 $\mu$ m in some isolates and subglobose to short cylindrical, smooth and 1.5–3.5 × 1.5–2 $\mu$ m in others
20a	(19b) Colonies grey. Conidiophores 100–200 $\mu$ m long. Conidia globose to ellipsoidal, 3–4.5 × 2.5 $\mu$ m, verruculose
20b	(19b) Colonies grey or green-grey. Conidiophores 20–200 $\mu$ m long. Conidia subglobose, ellipsoidal or short cylindrical, 1.5–3.5 × 1.5–2 $\mu$ m, smooth
21a	(18b) Colonies off-white or yellow. Mean conidiophore length > 100 $\mu$ m. Conidia produced in long undulating chains
21b	(18b) Colonies off-white to grey or grey-brown. Mean conidiophore length $< 100 \ \mu\text{m}$ . Conidia produced in a dense head of non-undulating chains
22a	(21a) Colonies yellow to yellow-green. Conidia yellow <i>en masse</i> with a rugose perispore. Positive reaction in WDG test. Conidiophores 50, 230 µm long.
22b	WDG test. Conidiophores 50–230 μm long
23a	(21b) Colonies off-white to grey. Conidiophores 25–130 $\mu$ m long. Conidia subglobose to cylindrical, 1.5–5 ×1–2 $\mu$ m with an asperulate perispore. Degrades cellulose and tannic acid but not lipidO. griseum (13)
23b	$\times$ 1–2 µm with an asperulate perispore. Degrades certaiose and tannic acid but not lipid

 Table 2: Conidial shapes in Oidiodendron species.

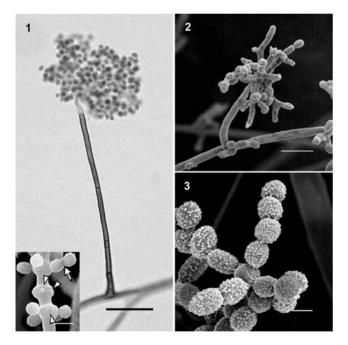
Conidial shape	Illustration	Species
Subglobose to elongate, thin-walled, with idistinct ornnamentation	$\square$	Myxotrichum arcticum, M. emodense, M. setosum, Oidiodendron chlamydosporicum, O. fuscum, O. griseum, O. maius, O. setiferum, O. rhodogenum
Barrel-shaped, truncate, with distinct dehiscence scars		<i>M. cancellatum, M. striatosporum, O. pilicola, O. truncatum</i>
Lens-shaped with a thickened ring	$\bigcirc$	O. cerealis
Globose to elliptical, thick-walled, with echinulate ornamentation	Stand Conners and Conners	O. echinulatum, O. muniellense, O. periconioides
Pyriform to irregular, thick-walled, with indistinct to asperulate ornamenta- tion (not discernible at this scale)	OD	O. fimicola, O. flavum
Subglobose to elongate, thick- walled, with indistinct to asperulate ornamentation (not discernible at this scale)		O. fimicola, O. flavum, O. hughesii, O. myxotrichoides, O. tenuissimum

#### **Species Descriptions**

**1.** *Oidiodendron* **anamorph of** *Myxotrichum arcticum* Udagawa, Uchiyama & Kamiya, Mycotaxon 52: 198–204. 1994. Figs 1–3.

Colonies on CMA 23-25 mm diam at 28 d, white to pale grey, appressed; reverse dark brown. Conidiophores abundant, bearing masses of white conidia, smooth, melanized, dichotomously branched at apex, 20-(75)- $215 \times 2-4 \mu m$ . Conidiophores in some cases showing "geniculate conidiogenesis" and terminating in whorls of truncated chains of 1-2 conidia that are borne perpendicular to the conidiogenous cell, and in other cases terminating in hyaline, dichotomously branched fertile hyphae, 2-3 µm diam, that fragment to form chains of conidia. Conidia thin-walled, hyaline, subglobose to elongate and irregular, 1.5-(2.4)-3.5 $\times 1$ –(1.9)–2.5 µm, asperulate to spinulose under SEM. Maximal growth at 20 °C and pH 3. Degrades cellulose, gelatin, pectin, and starch; UAMH 7565 also degrades tannic acid.

Specimens examined: U.S.A., George Parks Hwy Road, Willow, north of Wasilla, Alaska, forest soil,



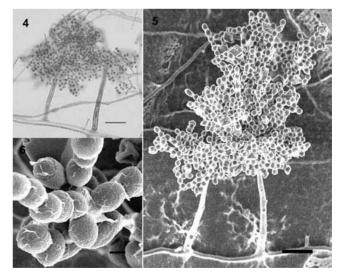
**Figs 1–3.** *Oidiodendron* state of *Myxotrichum arcticum*. 1. Small dense head of subglobose to elongate, hyaline conidia at the apex of a tall, erect, melanized conidiophore [University of Alberta Microfungus Collection and Herbarium (UAMH) 7565]. Bar = 20  $\mu$ m. Inset. "Geniculate conidiogenesis." Conidiophore apex bearing whorls of truncated chains of one to two conidia. Arrow indicates connective between chain of two conidia, arrowheads indicate scars from detached conidia. Bar = 2.5  $\mu$ m. Reproduced with permission from Tsuneda & Currah 2004, fig 28. 2. Branches of fertile hyphae fragmenting to form subglobose to elongate, asperulate to spinulose conidia (UAMH 9243). Bar = 10  $\mu$ m. 3. Chains of asperulate to spinulose, subglobose to elongate conidia with short connectives visible between them (UAMH 9243). Bar = 1  $\mu$ m.

1992, Udagawa, (UAMH 7565, ex-type). **Canada**, Mariana Lake, Alberta, decaying *Picea glauca*, 1997, Lumley (UAMH 9243).

Notes: The tall conidiophores and white conidia make this species superficially similar to *O. maius* var. *maius* but the smaller conidia and the shorter and less undulate conidial chains of the *M. arcticum* anamorph are distinct. The peridial elements of the teleomorph are morphologically similar to those of sterile gymnothecia produced by *O. maius* var. *maius* (Rice & Currah 2002). *Oidiodendron fuscum*, *O. griseum*, and *M. emodense* have similar conidiophore lengths and also have dense conidiogenous heads. However, geniculate conidiogenesis is unique to *M. arcticum*. Molecular evidence suggests a close relationship between *M. arcticum* and *O. griseum* (Hambleton *et al.* 1998, Sigler & Gibas 2005–this volume).

## **2.** *Oidiodendron* **anamorph of** *Myxotrichum cancellatum* Phillips, Grevillea 13:51–52. 1884. Figs 4–6.

Colonies on CMA 11–13 mm diam at 28 d, white to grey, appressed at margins; reverse purple to black. Aerial hyphae and conidiophores abundant. *Conidiophores* bearing masses of off-white to grey conidia, melanized, smooth, branched dichotomously or trichotomously at apex,  $25-(50)-100 \times 2-4 \mu m$ . *Conidia* thick-walled, hyaline to lightly melanized at maturity, subglobose to barrel-shaped,  $1.5-(2.6)-3.5 \times 1-(1.7)-2.5 \mu m$ , reticulately ornamented with a rugose perispore and bearing conspicuous intercalary connectives. Maximal growth at 15–20 °C and pH 5. Degrades gelatin, pectin, and starch.



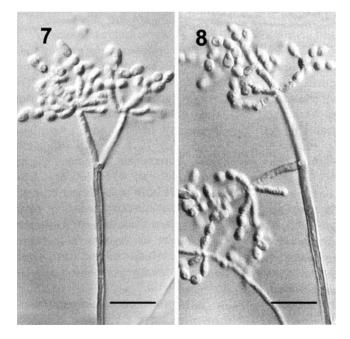
**Figs 4–6.** *Oidiodendron* state of *Myxotrichum cancellatum* (UAMH 1996). 4. Short, erect conidiophores bearing divergent chains of thick-walled, hyaline to lightly pigmented, barrel-shaped conidia. Bar =  $15 \mu m$ . 5. Conidiophores bearing long chains of subglobose to barrel-shaped conidia. Bar =  $10 \mu m$ . 6. Subglobose to barrel-shaped conidia with a rugose to reticulate perispore. Bar =  $1 \mu m$ .

Specimen examined: Japan, Tokyo, soil, 1959, Udagawa (UAMH 1996).

*Notes*: Dalpé (1991) noted that this species uses the cellulose in Czapek cellulose agar but in the present study, the cellulose azure test was negative. *Oidiodendron truncatum* is similar but differs in having melanized conidia and dichotomously branched conidiophores.

**3.** *Oidiodendron* anamorph of *Myxotrichum emodense* Udagawa & Uchiyama, Mycoscience 40: 292–296. 1999. Figs 7–8.

Colonies on oat agar (OA) 28-30 mm diam at 28 d at 25 °C, thin, with submerged vegetative mycelium, appearing granular due to the production of abundant ascomata intermixed with aerial hyphae and conidial heads; at first greyish yellow, becoming greenish grey or olivaceous black, with clear exudates; reverse dull green or grey olivaceous; conidiogenesis moderate. Colonies on potato carrot agar (PCA) 21-22 mm diam at 28 d at 25 °C, floccose, plane, with thin vegetative mycelium, producing abundant conidia, greenish grey or smoke grey; exudate absent; reverse uncoloured to brownish grey or smoke grey. Conidiophores erect, arising from vegetative mycelium or aerial hyphae, straight below, branching at the top to produce an arborescent, olivaceous brown head; conidiophores olivaceous brown to dark brown, 25-200 µm long  $\times$  1.5–2.5 µm diam, straight, septate, thick-walled,



**Figs 7–8.** *Oidiodendron* state of *Myxotrichum emodense*. Reproduced with permission from Udagawa & Uchiyama 1999, figs 13–14. 7. Dichotomously branched conidiophore bearing verticillate whorls of fertile hyphae that give rise to subglobose to ellipsoidal and elongate conidia. Bar = 20  $\mu$ m. 8. Divergent branches of a conidiophore give rise to verticils of fertile hyphae and thick-walled, subglobose to ellipsoidal conidia. Bar = 20  $\mu$ m.

smooth or sometimes with black nodes; branches hyaline to pale olivaceous brown,  $10-60 \times 2-2.5 \mu m$ , smooth-walled, repeatedly re-branched, frequently forming a verticillate whorl of 4–6 narrow fertile hyphae. Fertile hyphae hyaline, cylindrical, 1.2–1.5  $\mu m$  diam, fragmenting to form conidial chains. *Conidia* hyaline, pale greyish green in mass, subglobose, ovoid, ellipsoidal or short cylindrical, 1.5–3.5 × 1.5–2  $\mu m$ , almost smooth-walled, truncate at one or both ends. Connectives sometimes visible between conidia. Weakly cellulolytic. Reduced growth at 15 °C. Habitat: grassland soil, Nepal. Description is from Udagawa & Uchiyama (1999).

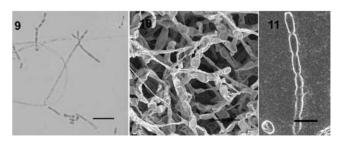
*Notes*: This species is morphologically similar to *O. fuscum*, *O. griseum*, and *M. arcticum* but *M. arcticum* has geniculate conidiogenesis and *O. griseum* and *O. fuscum* have unbranched conidiophores and dichotomously branched fertile hyphae that are distinct from the verticillate whorls formed in *M. emodense*.

**4.** *Oidiodendron* anamorph of *Myxotrichum setosum* (Eidam) Orr & Plunkett, Can. J. Bot. 41: 1470–1471. 1963. Figs 9–11.

Colonies on CMA 14–15 mm diam at 28 d, cream to pale yellow, appressed at margins; reverse cream to orange. Aerial conidia abundant, off-white to yellow *en masse.* Conidiophores typically less than 5  $\mu$ m long or absent, hyaline to lightly melanized. Hyaline conidiophores 30–140  $\mu$ m long were observed by Sigler & Carmichael (1976). Conidia hyaline, subglobose to elongate or irregular, 2–(3.6)–5 × 1.5– (2)–3  $\mu$ m, produced in dichotomously branched chains at the conidiophore apices of reduced conidiophores or directly from vegetative hyphae. Maximal growth at 15 °C and at alkaline pH. Degrades gelatin, pectin, lipid, and starch.

*Specimens examined*: **Canada**, Mt. Allen, Kananaskis, Alberta, soil, 1971, Bissett (UAMH 3835); washed mineral soil particle, 1971, Bissett (UAMH 4535).

Notes: The absence of melanized conidiophores is



**Figs 9–11.** *Oidiodendron* state of *Myxotrichum setosum* (UAMH 3835). 9. Short, sparingly branched chains of elongate conidia produced from vegetative hyphae. Bar =  $10 \mu m$ . 10. Chains of elongate conidia that collapse upon desiccation. Bar =  $5 \mu m$ . 11. Short, unbranched chain of elongate conidia. Bar =  $5 \mu m$ .

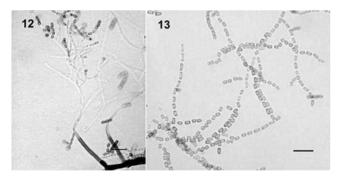
unusual in species of *Oidiodendron*. This character, along with the yellow colour of the colony, readily distinguishes the anamorph of *M. setosum* from other species. Molecular evidence supports a presumed relationship with other species of *Oidiodendron* (Hambleton *et al.* 1998). *Oidiodendron sulphureum* (Stalpers 1974), if it were to be re-collected and if it then turned out to be distinct from *O. flavum*, would be similar to *M. setosum*, but it could be distinguished based on its darker yellow colonies, the presence of some melanized conidiophores, and curved fertile hyphae. More details about *O. sulphureum* are found under *O. flavum*.

**5.** *Oidiodendron* anamorph of *Myxotrichum striatosporum* (Barron & Booth) Sigler, Mycotaxon 4: 385– 388. 1976. Figs 12–13.

 $\equiv$  Arachniotus striatosporus Barron & Booth fide von Arx

 $\equiv$  Byssoascus striatisporus (Barron & Booth) von Arx (1971) fide Sigler & Carmichael (1976)

Colonies 15–20 mm diam at 14 d at 25 °C on potato dextrose agar (PDA) and malt extract agar (MEA); 10 mm diam at 14 d and 25 °C on Czapek's synthetic agar. Colonies bright yellow at first, becoming dark olivaceous in the center, smooth to slightly floccose, becoming funiculose; when mature olive-green with yellow margins, weakly zonate, with edges slightly irregular to scalloped. A thick turf of conidia is eventually produced, which may crack irregularly in older cultures. Colony description is from Barron & Booth (1966). *Conidiophores* present or absent; when present, melanized in the lower one-fifth to one-third,  $[12–(35)–62.5 \times 2–3 \mu m]$ , unbranched or dichotomously branched, with upper portion



**Figs 12–13.** *Oidiodendron* state of *Myxotrichum striatosporum* (UAMH 3758). 12. Conidiophores arising from a melanized section of the vegetative hyphae. The melanized lower portions of the conidiophores are unbranched and give rise to much longer, hyaline upper portions that branch several times and bear fertile hyphae. The fertile hyphae fragment to form dark, smooth to asperulate, thick-walled, barrel-shaped, truncate conidia with apical scars. Bar = 15 µm. 13. Long chains of dark, smooth to asperulate, thickwalled, barrel-shaped to rectangular conidia with darker apical scars. Bar = 15 µm.

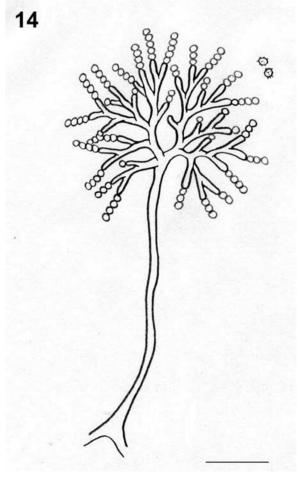
hyaline to subhyaline (up to 50  $\mu$ m long), branching dichotomously and producing fertile hyphae, 1–1.5  $\mu$ m diam, that fragment to form long, branched chains of conidia. *Conidia* barrel-shaped, smooth to asperulate, truncate with pigmented basal scars, hyaline to yellow when immature, yellow-brown to brown at maturity, 2–(4)–7 × 1.5–(2)–2.5  $\mu$ m.

*Specimen examined*: **Canada**, Bradford Marsh, Ontario, soil, 1960, Barron (UAMH 3758), ex-type *Arachniotus striatosporus*). Degenerate and no longer producing conidia. A permanent slide of the type was obtained from UAMH and used to obtain microscopic measurements.

*Notes*: This species is known only from the type but it is easily distinguished from other *Oidiodendron* species based on its olive-green colonies with yellow margin and by its yellow to brown, truncate, asperulate conidia.

**6.** *Oidiodendron ambiguum* (Peyronel) Malan, Nuovo Giornale Botanico Italiano 56: 735–737. 1949. Fig 14.

 $\equiv$  Dicyma ambigua Peyronel fide Malan (1949)



**Fig. 14.** *Oidiodendron ambiguum.* Reconstructed from the descriptions of Peyronel (1914) and Malan (1949). Tall conidiophore bearing branched fertile hyphae and verruculose, subglobose to ellipsoidal conidia. Bar =  $20 \mu m$ .

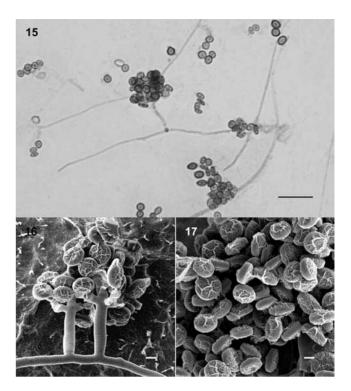
Colonies "large" (quote from the original description; dimensions not specified), round, initially ash grey, later darkening to an intermediate mouse grey. Vegetative hyphae septate, mostly hyaline and 1-2.5 µm diam, some melanized and 3-7 µm diam. Conidiophores arising from areas of dark hyphal growth that are spaced at relatively regular intervals in the predominantly hyaline mycelium, erect, rigid, septate, melanized at maturity,  $100-200 \times 2-4 \mu m$ , with apices bearing dichotomous primary branches with many dichotomous, verticillate, or sympodial sub-branches. Conidia formed in branched chains along swollen terminal branches, hyaline, globose to ellipsoidal, minutely vertuculose,  $3-4.5 \times 2.5 \ \mu m$ , grey en masse, giving the colony its characteristic colour. Source of isolation: air samples from an alpine forest. Description is from Peyronel (1914) and Malan (1949), translated from Italian. [UAMH 8443 (=ATCC 36256) from Italy, soil of snow valley, Mosca (received from ATCC as O. ambiguum) was reidentified as O. truncatum].

*Notes*: Peyronel (1914) was uncertain about the mode of conidial development and, as a consequence, his description and figures are unclear. Malan (1949) considered development to be arthroconidial, and placed this species within Oidiodendron. Improved illustrations were provided, but little was added to the written description. The illustrations provided by Malan (1949) coupled with isolation data, suggest that this is likely to be an Oidiodendron species. Neither Peyronel nor Malan, however, specified a type or deposited specimens. The only record of O. ambiguum since Malan is UAMH 8443, which was reidentified by us as O. truncatum on the basis of its dark, barrel-shaped conidia with reticulate ornamentation. If encountered again, O. ambiguum would be distinguished by its verruculose, hyaline, globose to ellipsoidal conidia.

7. *Oidiodendron cerealis* (Thüm.) Barron, Can. J. Bot. 40: 594–595. 1962. Figs 15–17.

- *≡ Trichosporium cerealis* Thüm. *fide* Barron (1962)
- ≡ *Stephanosporium cereale* (Thüm.) Swart *fide* Swart (1965)
- = Oidiodendron nigrum Robak fide Barron (1962)

Colonies on CMA 30–34 mm diam at 28 d, greengrey (CBS 349.62) or pale with clumps of brown to black conidia (UAMH 504, UAMH 1522), reverse green-grey to black (CBS 349.62) or dark brown to black beneath areas of heavy sporulation (UAMH 504, UAMH 1522). Aerial hyphae abundant and hyaline in UAMH 504 and UAMH 1522 but scarce in CBS 349.62. *Conidiophores* short, branched, hyaline to lightly melanized, 5–(15)–28 × 2–3  $\mu$ m. *Conidia* melanized, in short chains or appearing to be clumped at conidiophore apex, subglobose to lens-shaped with a



**Figs 15–17.** *Oidiodendron cerealis.* (UAMH 1522). 15. Dark, lens-shaped conidia produced in clusters at the apices of short, hyaline to lightly pigmented conidiophores. Bar =  $10 \mu m$ . 16. Short conidiophores branched at the apices and supporting chains of lens-shaped conidia with an extremely rugose perispore. Bar =  $1 \mu m$ . 17. Lens-shaped conidia with a rugose perispore. Bar =  $1 \mu m$ .

thickened ring and highly rugose (wrinkled) perispore, 2.5–(3.3)–4 × 2–(2.8)–4  $\mu$ m. Maximal growth at pH 3–5 and 20 °C. Degrades cellulose, gelatin, pectin, and starch.

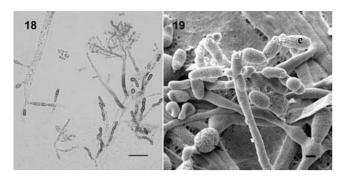
*Specimens examined*: **Italy**, Piedmont, alpine meadow soil, 1962, Dal Vesco (CBS 349.62); **Canada**, Edmonton, Alberta, human hair, 1956, Carmichael (UAMH 504); Bradford Marsh, Ontario, peat soil, 1960, Barron (UAMH 1522).

*Notes*: This species is unique because of its hyaline conidiophores and lens-shaped arthroconidia with thickened rings of cell wall material. These features led to its placement outside of the genus *Oidiodendron*. Molecular analyses, however, support its placement within *Oidiodendron* (Hambleton *et al.* 1998). Its morphological distinction is significant only at the species level.

**8.** *Oidiodendron chlamydosporicum* Morrall, Can. J. Bot. 46: 205–206. 1968. Figs 18–19.

= Oidiodendron scytaloides Gams & Söderström (1983)

*Colonies* on CMA 9–16 mm diam at 28 d, cream or pale grey to green-grey or brown, darker at margins, appressed; reverse cream near margin, becoming dark brown at centre. Conidia and chlamydospores pale to



**Figs 18–19.** *Oidiodendron chlamydosporicum*. 18. Elongate, hyaline conidia produced in short chains at the apices of short, dark conidiophores and lateral, terminal, and intercalary dark, subglobose to elongate or irregular chlamydospores produced singly or in short chains from vegetative hyphae (UAMH 9751). Bar = 10  $\mu$ m. 19. Asperulate, elongate conidia (C) in short chains at a conidiophore apex, intercalary, pitted chlamydospore (arrowhead) borne on a vegetative hypha (UAMH 6520). Bar = 1  $\mu$ m.

brown en masse, produced on repent hyphae at the surface of the agar or on well developed conidiophores that are mainly found near the centres of colonies. Conidiophores (2-3.5 µm diam) intergrading between structures that are short  $[3-(10)-17 \mu m long]$ , branched, and lightly pigmented to melanized, and structures that are erect, melanized and 5-(35)-70 µm long; short and long types both bear chains of hyaline conidia interspersed with melanized chlamydospores. Conidia thin-walled, hyaline, globose, subglobose or elongate,  $1.5-(2.5)-5 \times 1-(1.7)-2.5 \mu m$ , produced in chains arising from vegetative hyphae or from conidiophores. Chlamydospores subglobose to barrelshaped or pyriform, thick-walled, melanized, 3-(4)-7  $\times$  2–(3.5)–4µm, abundant, arising singly or in short chains from vegetative hyphae or conidiophores. In SEM, conidia minutely asperulate and chlamydospores pitted. Maximal growth at 20-25 °C and pH 3. All isolates tested degrade cellulose, gelatin, pectin and starch; UAMH 6520, UAMH 8510, and UAMH 9751 degrade lipid; UAMH 6520 and UAMH 6521 degrade lignin; and UAMH 9751 degrades tannic acid.

Specimens examined: Canada, Candle Lake, Saskatchewan, boreal forest soil, 1964, Morrall (UAMH 6520, ex-type); Perryvale, Alberta, Sphagnum *fuscum* (Schimp.) Klinggr., bog, Thormann (UAMH 9751, as *O. scytaloides*); Sweden, humus, *Picea abies* (L.) Karst. forest, 1973, Söderström & Bååth (UAMH 6521, ex-type of *O. scytaloides*); Kongalund, illuvial soil, *Picea abies* forest, 1973, Söderström & Bååth (UAMH 6527, as *O. scytaloides*); Germany, Freiberg, roots of dying *Abies alba* Miller, 1981, Schuler (UAMH 8510, as *O. scytaloides*).

*Notes*: *Oidiodendron chlamydosporicum* was described as having subglobose to globose, terminal or intercalary chlamydospores,  $4-9 \mu m$  diam, and subglobose, ellipsoidal or cylindrical conidia, 2-6

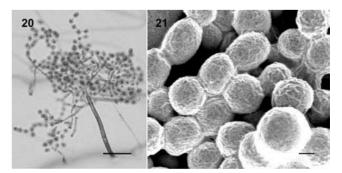
×1.2–2 µm (Morrall 1968). Oidiodendron scytaloides was described as having smaller  $(3-5 \times 2.5-3 \text{ }\mu\text{m})$ ellipsoidal chlamydospores formed in short, terminal, lateral, or intercalary chains and as having relatively short  $(2-4 \times 1-2 \mu m)$  cylindrical or ellipsoidal conidia (Gams & Söderström 1983). The ex-type specimens of the two species, however, are indistinguishable in terms of chlamydospore shape and size: the shape ranges from subglobose to barrel-shaped or pyriform and the size is within the range  $3-7 \times 2-4 \mu m$  in each isolate. Moreover, conidial size, which overlapped in the original descriptions, is  $1.5-5 \times 1-2.5 \ \mu m$  in all isolates. Oidiodendron chlamydosporicum has priority over O. scytaloides, which is here relegated to synonymy. Molecular analyses support their conspecificity (Hambleton et al. 1998, Calduch et al. 2004).

**9.** *Oidiodendron echinulatum* Barron, Can. J. Bot. 40: 595–597. 1962. Figs 20–21.

Colonies on CMA 35–37 mm diam at 28 d, offwhite to tan, floccose, with brown exudate; reverse dark brown. Aerial hyphae abundant, hyaline. *Conidiophores* abundant, bearing masses of brown conidia, dichotomously branched, melanized, smooth,  $12-(35)-88 \times 2-5 \mu m$ . Additional conidiogenous branches arising directly from vegetative mycelium, hyaline, 2–3  $\mu m$  diam, dichotomously branched, fragmenting into chains of conidia. *Conidia* thickwalled, melanized, globose, subglobose or ellipsoidal, warted at maturity, 2–(3)–4 × 2–(2.6)–3  $\mu m$ . Growth is suppressed by daylight. Maximal growth at pH 11 and 20 °C. Degrades cellulose, gelatin, lipid, starch, tannic acid and lignin.

*Specimen examined:* **Canada**, Ontario, peat soil, cedar bog, Barron (UAMH 8467, authentic).

*Notes: Oidiodendron echinulatum* can be distinguished from other species in the genus by its branched conidiophores, warted conidia, growth suppression by



**Figs 20–21.** *Oidiodendron echinulatum* (UAMH 8467). 20. Erect conidiophore bearing divergent, branched chains of thick-walled, warty, dark, subglobose to ellipsoidal conidia. Bar = 15  $\mu$ m. 21. Subglobose to ellipsoidal, warty or pitted conidia. Short connectives are visible between some conidia. Bar = 1  $\mu$ m.

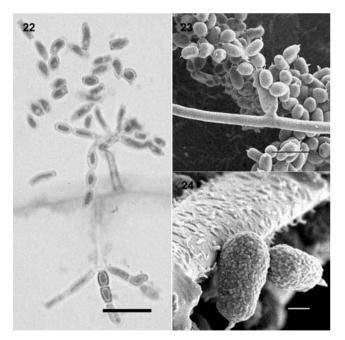
light, maximal growth at pH 11, and positive WDG reaction. *Oidiodendron periconioides* is similar but has spiny, globose conidia, is WDG negative, and is not inhibited by light.

**10.** *Oidiodendron fimicola* Rice & Currah (2005–this volume), Figs 22–24.

= *Oidiodendron sindenia* nomen invalidum *fide* Rice & Currah (2005)

Colonies on CMA 19–26 mm diam at 28 d, off-white to beige or pale grey, appressed with concentric rings of abundant conidiophores bearing masses of off-white to beige conidia; reverse olivaceous. *Conidiophores* present or absent, branched or unbranched, melanized, asperulate to scaly, 20–(50)–100 × 2–4 µm. Fertile hyphae hyaline, 2 µm diam, fragmenting to form short, dichotomously branched chains of arthroconidia. *Conidia* thick-walled, hyaline to light brown, barrelshaped to elongate or irregular, more or less truncate at one or both ends, asperulate, 3–(4.9)–6 × 2–(2.4)–3 µm.

*Specimens examined*: U.S.A., St. Louis, Missouri, mushroom compost, 1976, Beyer (UAMH 10459 = DC 60, as *Oidiodendron* sp., ex-type); California, mushroom compost, 1976, Beyer (UAMH 10523 = DC 61, as *Oidiodendron* sp.).



**Figs 22–24.** *Oidiodendron fimicola* (UAMH 10459). 22. Short, asperulate conidiophores bearing short chains of thick-walled, lightly pigmented to dark, barrel-shaped to elongate or irregular conidia. Bar = 15  $\mu$ m. 23. Portion of fertile hypha bearing chains of asperulate, subglobose to elongate or barrel-shaped conidia with long, thin connectives visible between conidia. Bar = 5  $\mu$ m. 24. Fragment of scaly conidiophore and asperulate, elongate to irregular conidia with the remnants of connectives remaining at their apices. Bar = 1  $\mu$ m.

*Notes*: D. M. Beyer labelled material he sent for deposit in ATCC in 1976 "*O. sindenia*", but never validly published the name. The material deposited at ATCC was listed in the catalogue under *O. sindenia* but it has since died (ATCC, pers. comm.). Beyer sent us cultures from the Pennsylvania State Mushroom Spawn Laboratory. One of these, DC 60 (= UAMH 10459), is reportedly from the same collection as the material deposited in ATCC. *Oidiodendron fimicola* is the only *Oidiodendron* species that has consistently asperulate conidiophores, a character that distinguishes it from the morphologically similar *O. flavum*.

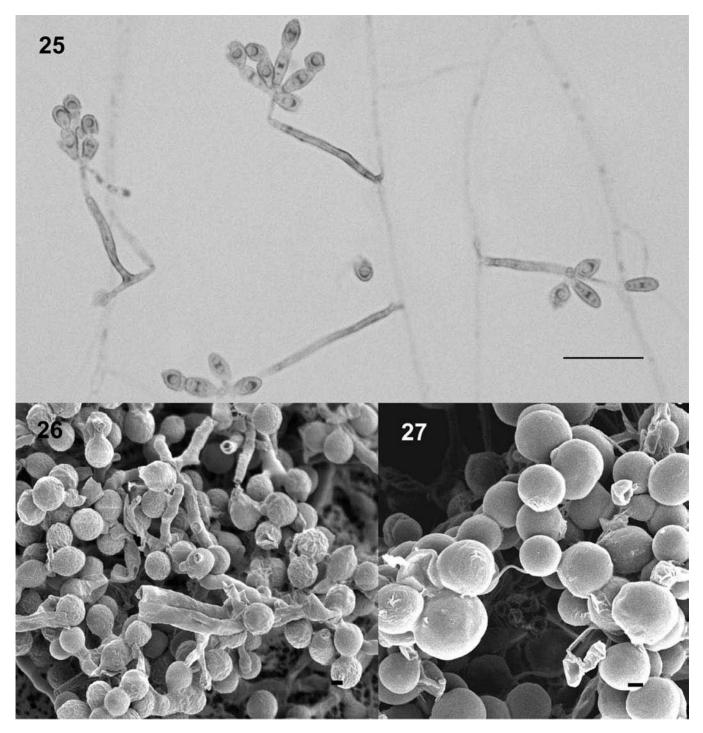
**11.** *Oidiodendron flavum* von Szilvinyi, Zbl. Bakt. Abt. II, 103: 179. 1941. Figs 25–27.

Colonies on CMA 27–28 mm diam at 28 d, cream to yellow-brown, appressed; reverse dark brown. Hyphae submerged at colony margins. Conidiophores abundant, bearing masses of brown to grey conidia, smooth, unbranched, melanized,  $25-(45)-80 \times 2-4$  µm. Fertile hyphae hyaline, 2-3 µm diam, 2-4 times dichotomously branched, fragmenting into short chains of 2–10 conidia. Conidia thin-walled, hyaline and elongate when immature, becoming globose to irregular, barrel-shaped, ellipsoidal or pyriform, thick-walled, melanized, smooth to asperulate or dimpled,  $2.5-(3.3)-4 \times 2-(2.8)-3\mu m$  at maturity. Maximal growth at pH 3 and 20 °C. Degrades cellulose, gelatin, lipid, pectin, and starch.

*Specimen examined*: **Canada**, Aberfoyle, Ontario, peat soil, cedar bog, Barron (UAMH 1524, authentic).

*Notes*: *Oidiodendron flavum* is distinguished by the wide variation in the shape of mature melanized conidia and by the changes in the shape and pigmentation of conidia during maturation. *Oidiodendron fimicola* is similar in displaying a range of conidial shapes and pigmentation, but *O. flavum* is distinct in having smooth conidiophores and relatively round and smooth conidia. Molecular evidence suggests a close relationship between *O. flavum* and *O. griseum* (Hambleton *et al.* 1998, Lacourt *et al.* 2001, Sigler & Gibas 2005–this volume). However, the consistency of the phenotypic differences between the authentic strains of the two species merits maintenance of the two names.

Stalpers (1974) transferred *Oedocephalum* sulphureum to *Oidiodendron* as *Oidiodendron* sulphureum and suggested that it was similar or identical to *O. flavum* because the conidial dimensions, given as  $3.8-5 \times 2.5-3.3 \mu m$ , are similar to those noted by von Szilvinyi (1941) ( $3.4-5.7 \times 2.5-3.4 \mu m$ ) and because the curved branches on the fertile hyphae of *O. sulphureum* were also mentioned by Barron (1962) in connection with *O. flavum*. The brief description provided by Stalpers (1974) does

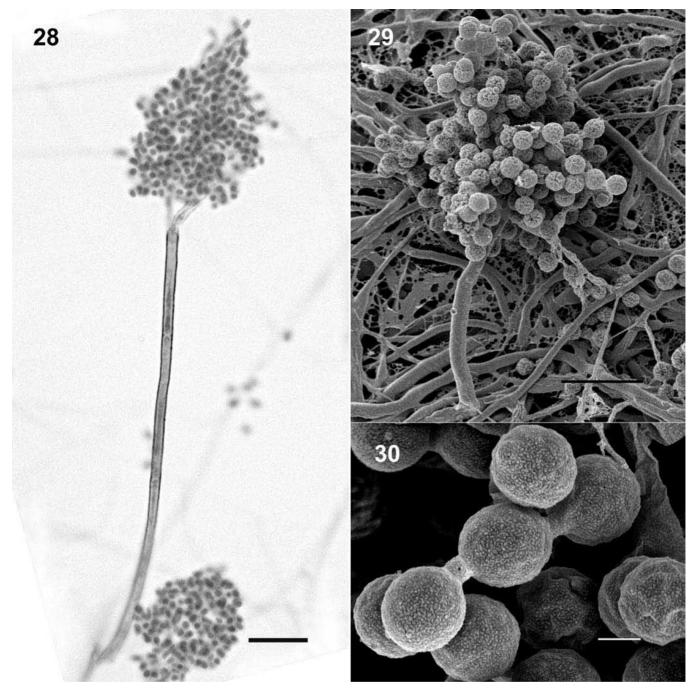


Figs 25–27. Oidiodendron flavum (UAMH 1524). 25. Erect conidiophores bearing short chains of thick-walled, dark, pyriform to irregular conidia. Bar = 15  $\mu$ m. 26. Smooth to pitted, subglobose to pyriform conidia borne on fertile hyphae. Bar = 1  $\mu$ m. 27. Smooth to pitted, subglobose to pyriform or irregular conidia. Bar = 1  $\mu$ m.

not provide measurements for conidiophore length, but instead describes the conidiophores as "rather short or absent, to 3.5 µm wide, with a pigmented, sometimes roughened basal part and a hyaline repeatedly branched upper part." The conidiophore is not shown in his illustration. No cultures are available and we have not examined the type so we are unable to ascertain the precise placement of this species. Based on Stalpers' brief description and illustrations, we are including it under O. flavum. If encountered again, O. sulphureum would be distinguishable by virtue of its short conidiophores, sulphur-yellow colonies and curved fertile hyphae.

12. Oidiodendron fuscum Robak, Saertryk av Nyt Mag. Naturvidensk. 71: 249–251.1932. Figs 28–30.

Colonies on CMA 24-26 mm diam at 28 d, offwhite to pale grey, appressed; reverse grey-brown to black. Conidiophores abundant, bearing masses of off-white to grey conidia, smooth, unbranched, melanized,  $15-(25)-40 \times 2-3$  µm. Fertile hyphae



**Figs 28–30.** *Oidiodendron fuscum* (UAMH 8511). 28. Tall, erect conidiophore bearing a dense head of thin-walled, subglobose to ellipsoidal conidia. Bar = 15  $\mu$ m. 29. Conidiophore bearing a large, dense head of dimpled, asperulate, subglobose conidia. Bar = 10  $\mu$ m. 30. Short chain of subglobose to ellipsoidal, dimpled, asperulate to minutely vertuculose conidia. Long connectives are visible between conidia. Bar = 1  $\mu$ m.

hyaline, dichotomously branched, fragmenting to form chains of conidia in a dense head. *Conidia* thin-walled, hyaline to lightly pigmented, dimpled, subglobose to ellipsoidal with an asperulate to minutely verruculose perispore,  $1.5-(2)-3 \times 1-(1.5)-2 \mu m$ . Maximal growth at pH 3 and 20 °C. Degrades gelatin, lipid, pectin, and starch.

*Specimen examined*: **Norway**, wood pulp, Robak (UAMH 8511, ex-type).

Notes: Robak (1932) described O. fuscum as having 106

grey-brown to brown colonies, featuring smooth, branched or unbranched conidiophores 60–265  $\mu$ m long, averaging 110–120  $\mu$ m, as well as hyaline to greenish brown conidia 1.6–3.6 × 1.2–2.2  $\mu$ m, averaging 2.4 × 1.7  $\mu$ m. Barron (1962) made *O*. *fuscum* a synonym of *O*. *tenuissimum* and described *O*. *tenuissimum* as a variable species with off-white to grey or brown colonies and hyaline to pigmented conidia. Nuclear ribosomal sequence analyses indicated that *O*. *tenuissimum sensu* Barron comprises two distinct lineages. The first, containing UAMH 8511, was designated "O. tenuissimum" and the other lineage was called "O. sp. nov" (Hambleton et al. 1998). SEM examination of the conidia of UAMH 8511, UAMH 8513 ("O. sp. nov"), and the type specimen of Periconia tenuissima, showed that UAMH 8511 was distinct, while UAMH 8513 looked the same as the type of *P. tenuissima*. UAMH 8511 also differs in cultural morphology from the type of *P. tenuissima* (Hambleton, pers. comm.). We regard O. *fuscum* as a distinct species on the basis of these morphological and molecular differences.

*Oidiodendron fuscum* is morphologically similar to the anamorphs of *M. arcticum* and *M. emodense*, as well as to *O. griseum* and *O. maius* var. *maius*. It lacks the geniculate conidiogenesis of *M. arcticum* and the verticillate fertile hyphae of *M. emodense*. On average, the conidia and conidiophores of *O. fuscum* are shorter than those of *O. maius* var. *maius* and *O. griseum*. Morphological differences between the conidia of *O. fuscum* and *O. griseum* are best observed using SEM. *Oidiodendron fuscum* produces subglobose to ellipsoidal, dimpled, minutely verruculose conidia while *O. griseum* has subglobose to cylindrical, asperulate conidia.

**13.** *Oidiodendron griseum* Robak, Saertryck ur Svensk. Skogvårdsföreningens. Tidskr. 3–4: 440. Figs 31–33.

Colonies on CMA 26–32 mm diam at 28 d, off-white to pale grey, appressed; reverse dark green-grey to black. Conidiophores abundant, bearing masses of offwhite to grey conidia, smooth, unbranched, melanized,  $25-(60)-130 \times 2-5 \mu m$ . Fertile hyphae hyaline, 2–3  $\mu m$  diam, dichotomously branched with acute branch angles, fragmenting to form long chains, of up to 30 conidia, in a dense fertile head. Conidia thin-walled, hyaline, subglobose to elongate or cylindrical, 1.5–  $(2.5)-5 \times 1-(1.5)-2 \mu m$ , with an asperulate perispore. Maximal growth at pH 3 and 20 °C. Degrades cellulose, gelatin, pectin, starch, and tannic acid.

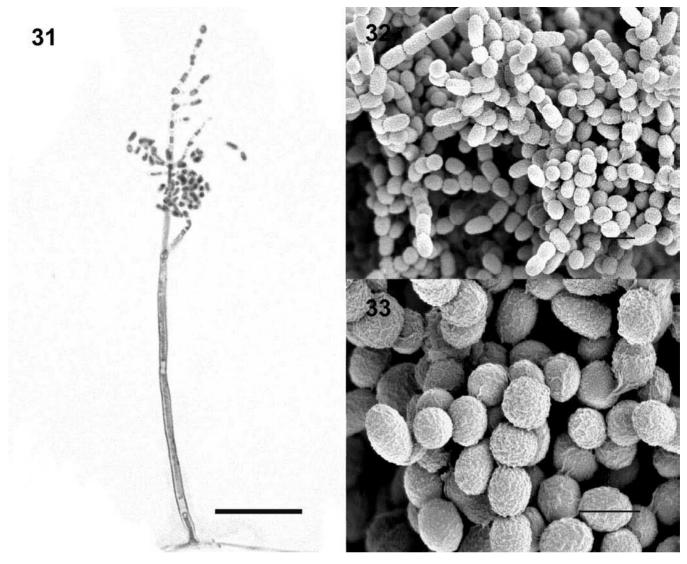
Specimens examined: Sweden, wood pulp, 1960, Melin (UAMH 1403, authentic). Canada, Westlock, Alberta, wood chips and bark, ex logging truck, Sigler (UAMH 4080); Slave Lake, Alberta, roots of Vaccinium myrtilloides, Pinus banksiana stand, sand dune, Hambleton (UAMH 8925).

*Notes: Oidiodendron griseum* is morphologically similar to the anamorphs of *M. arcticum* and *M. emodense*, as well as to *O. maius* var. *maius*, and *O. fuscum*. It lacks the geniculate conidiogenesis of *M. arcticum* and has unbranched conidiophores and dichotomously branched fertile hyphae as opposed to the branched conidiophores and verticillate fertile hyphae of *M. emodense*. Historically, there have

been problems distinguishing isolates of *O. griseum* with longer-than-average conidiophores from isolates of *O. maius* var. *maius* (Hambleton & Currah 1997, Hambleton *et al.* 1998). However, the fertile hyphae of *O. griseum* have narrower branch angles and are less undulate than those of *O. maius* var. *maius*. The average conidiophore length in *O. griseum*, < 100  $\mu$ m, is less than in *O. maius* var. *maius*, where the average is > 100  $\mu$ m. Conidia of *O. griseum* are shorter on average (< 3  $\mu$ m) than those of *O. maius* var. *maius* (> 3  $\mu$ m).

Molecular studies have indicated a complex relationship between O. griseum and the polyphyletic O. tenuissimum sensu Barron (Hambleton et al. 1998, Lacourt et al. 2001, Hambleton, unpubl. data). Hambleton et al. (1998) found that isolates of O. griseum and O. tenuissimum produced indistinguishable RFLP patterns but formed distinct clusters based on ITS sequence data. A similar study (Lacourt et al. 2001), based on a different set of isolates, found no ITS differences between the two species. Hambleton (unpublished) has found that a clade encompassing all sequenced isolates ever identified as O. griseum and O. tenuissimum sensu Barron is so broad that it encompasses isolates of all the other sequenced Oidiodendron species. However, with the division of O. tenuissimum sensu Barron into O. fuscum and O. tenuissimum sensu stricto, the similarities between O. griseum and O. tenuissimum are minimal.

Oidiodendron griseum is morphologically and physiologically most similar to O. fuscum. According to Robak's original descriptions of O. griseum (Melin & Nannfeldt 1934) and O. fuscum (Robak 1932), the two differ primarily in colony morphology and show only slight differences in conidiophore lengths and conidial dimensions. Robak described the colonies of O. griseum as green-grey with a dark green-black reverse (Melin & Nannfeldt 1934) and the colonies of O. fuscum as brown or grey-brown with a brownblack reverse (Robak 1932). We did not observe these cultural differences, possibly because different growth media were used. Both O. griseum and O. fuscum were similar in having off-white to grey colonies with a dark grey to black reverse. Furthermore, conidiophore lengths and conidial dimensions given for the two species overlap. In O. griseum, the conidiophores range in length from 40 to 150 µm, averaging 90–100 um (Melin & Nannfeldt 1934), while those of O. fuscum range from 60 to 265 µm, averaging 110–120 µm (Robak 1932). Conidia of O. griseum are 2.0- $3.6 \times 1.6$ – $2.0 \mu m$ , averaging  $2.6 \times 1.8 \mu m$  (Melin & Nannfeldt 1934), while those of O. fuscum are 1.6-3.6  $\times$  1.2–2.2 µm, averaging 2.4  $\times$  1.7 µm (Robak 1932). The range in length of conidiophores we observed  $(25-130 \ \mu m)$  is smaller than that recorded by Robak although there is considerable overlap. These different



**Figs 31–33**. *Oidiodendron griseum*. 31. Conidiophore bearing long chains of elongate to cylindrical conidia (UAMH 1403). Bar = 15  $\mu$ m. 32. Chains of asperulate, subglobose to elongate or cylindrical conidia with short connectives visible between some of the conidia (UAMH 4080). Bar = 5  $\mu$ m. 33. Asperulate, subglobose to elongate to cylindrical conidia with intervening connectives sometimes visible (UAMH 4080). Bar = 5  $\mu$ m.

ranges might be explained by our use of slide cultures and different media. Our measurements of mean conidiophore length (60  $\mu$ m) were less than Robak's (Melin & Nannfeldt 1934). We observed a wider range of conidial lengths (1.5–5  $\mu$ m) but mean dimensions (2.5–1.5  $\mu$ m) were similar to Robak's (Melin & Nannfeldt 1934). Our measurements for *O. griseum* fall between the measurements we obtained for *O. fuscum* and those given in the original description (Robak 1932).

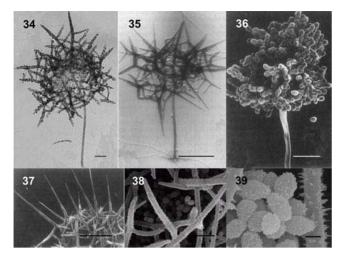
In general, the isolates of *O. griseum* have longer conidiophores (25–130  $\mu$ m) than the ex-type of *O. fuscum* (15–40  $\mu$ m). Conidia of *O. griseum* also differ from those of *O. fuscum* under SEM. Our isolates of *O. griseum* have relatively long (1.5–5  $\mu$ m), cylindrical conidia with an asperulate perispore while *O. fuscum* has relatively short (1.5–3  $\mu$ m), subglobose to ellipsoidal, dimpled conidia with an asperulate to minutely verruculose perispore. Additional cultural

and molecular differences between *O. fuscum* and *O. griseum* (Sigler & Gibas 2005–this volume) support recognizing them as distinct.

**14.** *Oidiodendron hughesii* Udagawa & Uchiyama, Can. J. Bot. 76: 1641–1643. 1998. Figs 34–39.

= Oidiodendron reticulatum Calduch et al. (2004)

Colonies on PCA 12–13 mm diam at 21 d at 15 °C, 3–4 mm diam at 21 d at 25 °C, green-grey, becoming dark green to olivaceous black with age, appressed; reverse uncoloured to brown-grey; exudates absent. Conidia abundant after 14 d. Colonies on OA growing more slowly than on PCA, bearing conidiophores in dense stands; reverse red-brown. *Conidiophores* erect,  $60–100 \times 2.5–3 \mu m$ , melanized, unbranched and smooth-walled below and asperulate and darkened above, branched and anastomosed to form a globose to subglobose reticulate network ( $60–160 \mu m$  diam; 250– 280 µm diam when peripheral spines are included).



Figs 34-39. Oidiodendron hughesii. Reproduced with permission from Udagawa & Uchiyama 1998 and Calduch et al. 2004. Conidiophore and reticulum of asperulate appendages surrounding a conidial mass (O. reticulatum; Calduch et al. 2004, fig. 24). Bar = 30  $\mu$ m. 35. Conidiophore and reticulum of smooth to asperulate appendages surrounding a conidial mass (O. hughesii; Udagawa & Uchiyama 1998, fig. 11). Bar = 50 µm. 36. Simple conidiophore bearing chains of asperulate to spinulose, ellipsoidal conidia (O. hughesii; Udagawa & Uchiyama 1998, fig. 17). Bar = 10 µm. 37. Appendages of the reticulum surrounding the conidial mass. Note that the asperulate ornamentation does not extend to the apices (O. hughesii; Udagawa & Uchiyama 1998, fig. 14). Bar = 50 μm. 38. Asperulate hyphae of the reticulum surrounding the conidial mass. Note that the asperulate ornamentation of the hyphae extends almost to the apices, but that the tips of the hyphae are smooth (O. reticulatum; Calduch et al. 2004, fig. 27). Bar = 10  $\mu$ m. 39. Ellipsoidal, asperulate to spinulose conidia (O. reticulatum; Calduch et al. 2004, fig. 31). Bar  $= 2 \, \mu m.$ 

Peripheral spines appendage-like, septate, dark olive brown, basally asperulate, with 1–2 branchlets arising near base; apices pointed, lighter in colour and smoother than the basal region. Fertile hyphae,  $1.5-2.5 \mu m$  diam, arising from lateral branches of reticulum elements, verticillate, hyaline, smooth-walled, fragmenting to produce conidia. *Conidia* hyaline to pale olivebrown *en masse*, oval to ellipsoidal, thick-walled, asperulate, 2–4 × 1.5–2.5  $\mu m$ . Simple conidiophores also produced, melanized, smooth, branched at apex to produce a dense head of fertile hyphae. Optimal growth at 15 °C. Habitat: forest soil. Description is from Udagawa & Uchiyama (1998).

*Notes*: Calduch *et al.* (2004) distinguish *O. reticulatum* from *O. hughesii* on the basis of appendage ornamentation, conidial colour, and temperature

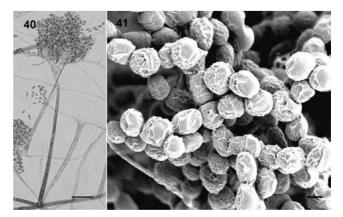
**Figs 40–41.** *Oidiodendron maius* var. *citrinum* (UAMH 1525). 40. Tall, erect conidiophore bearing a branched head of fertile hyphae that fragment to form long chains of subglobose to elongate conidia. Bar =  $15 \mu m. 41$ . Subglobose to elongate conidia with a rugose perispore. Bar =  $1 \mu m$ .

optima. In O. reticulatum, the appendages are verruculose along their entire length while in O. hughesii they are smooth at their apices. The conidia of O. reticulatum are described as pale brown to olivaceous (Calduch et al. 2004) while those of O. hughesii are described as hyaline to pale olive brown en masse (Udagawa et al. 1998). These differences are slight in light of the similarities between the two species in colony morphology, reticulum dimensions, and conidial size, shape, and ornamentation (Udagawa et al. 1998, Calduch et al. 2004). These minor differences become even less credible considering that both species are monotypic. Differences in appendage ornamentation and conidial size could reflect either intraspecific variation among isolates or differences in developmental stage. Calduch et al. (2004) report that O. reticulatum grows optimally at 25 °C while O. hughesii grows optimally at 15 °C. However, they also note that, on some media, growth of O. reticulatum is similar at 15 and 25 °C (Calduch et al. 2004). It is plausible that this physiological difference has been overstated and is due to ecological rather than phylogenetic differences. Udagawa et al. (1998) isolated O. hughesii from a cool, temperate, alpine site while Calduch et al. (2004) isolated O. reticulatum from a warm, subtropical site in Spain. We feel that the differences between O. hughesii and O. reticulatum are not significant at the species level and suggest they are synonymous. There are no sequence data for O. hughesii.

*Oidiodendron hughesii*, *O. muniellense*, and *O. setiferum* are the only species bearing appendages at the apex of the conidiophore. In *O. hughesii*, the appendages are highly branched and anastomose to form a reticuloperidium-like structure that encloses the arthroconidial mass, while in the other two species appendages are more sparsely branched and antler-like.

**15.** *Oidiodendron maius* var. *citrinum* (Barron) Rice & Currah, stat. nov., MycoBank MB500256, Figs 40–41.

 $\equiv$  *Oidiodendron citrinum* Barron, Can. J. Bot. 40: 597. 1962 (basionym).



Colonies on CMA 30–36 mm diam at 28 d, yellowgreen, appressed; reverse pale brown to dark brown in the centre. Conidiophores abundant, bearing masses of yellow conidia, tall, unbranched, melanized, smooth,  $50-(120)-230 \times 2-4 \mu m$ . Fertile hyphae hyaline,  $2-3 \mu m$  diam, dichotomously branched, fragmenting to form long, undulating chains of conidia. Conidia thinwalled, hyaline, subglobose to elongate,  $1.5-(2.8)-5 \times 1-(1.8)-2.5 \mu m$ , with a rugose perispore. Maximal growth at pH 3–5 and 20 °C. Degrades cellulose, gelatin, lipid, pectin, starch, tannic acid, and lignin.

Specimens examined: Canada, Guelph, Ontario, soil, cedar bog, Barron (UAMH 1525, ex-type *O. citrinum*); 6 Mile Lake, Muskoka District, Ontario, *ex* black sclerotia in stream drift, March 1991, Malloch (UAMH 7089); Slave Lake, Alberta, *ex* black mycorrhizal root tip (*Cenococcum* Moug. & Fr. sp.) of *Arctostaphylos uva-ursi*, *Pinus banksiana* stand on sand dune, 1998, Hambleton (UAMH 9275).

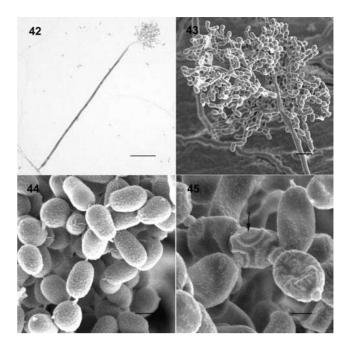
*Notes*: *Oidiodendron citrinum* is sufficiently similar to *O. maius* that it can be considered a subspecific taxon within *O. maius*, which was described in the same publication (Barron 1962). *Oidiodendron maius* is much more common in the literature and is given priority. These two taxa are recognized at the varietal level, rather than as subspecies, because the latter term implies the existence of intermediate forms and differences in distribution (Hawksworth 1974). There are few data concerning the distribution and/or possible intergradation of these taxa that would support designating them as subspecies.

The conidiophores and conidia are similar to O. maius var. maius but the two can be distinguished on the basis of colony colour, conidial ornamentation under SEM, and WDG reaction. Oidiodendron maius var. citrinum has yellow colonies, conidia with a rugose perispore, and a positive WDG reaction while O. maius var. maius has white colonies, conidia with an asperulate perispore, and a negative WDG reaction. Molecular analyses indicate that these differences are probably not significant at the species level leading to the suggestion that O. citrinum and O. maius are conspecific or that O. citrinum is a subspecies of O. maius (Hambleton et al. 1998, Lacourt et al. 2001, Sigler & Gibas 2005-this volume). Additional morphological (Sigler & Gibas 2005-this volume) and physiological (Rice & Currah 2005-this volume) characters support a close relationship between these taxa.

# **16.** *Oidiodendron maius* var. *maius* (Barron) Rice & Currah, Figs 42–45.

 $\equiv$  *Oidiodendron maius* Barron, Can. J. Bot. 40: 600–602. 1962.

*Colonies* on CMA 29–38 mm diam at 28 d, off-white to grey, appressed; reverse pale grey to dark brown in



**Figs 42–45.** *Oidiodendron maius* var. *maius*. 42. Extremely tall conidiophore bearing a head of divergent, branched, undulating chains of thin-walled, subglobose to elongate or cylindrical conidia (UAMH 9749). Bar = 40  $\mu$ m. 43. Conidiophore apex branching to form fertile hyphae that fragment to form chains of subglobose to elongate conidia (UAMH 10460). Bar = 10  $\mu$ m. 44. Chains of asperulate, elongate conidia with connectives visible between the conidia (UAMH 8920). Bar = 1  $\mu$ m. 45. Branching chain of asperulate conidia with scars (arrow) showing position of side branches that have broken free (UAMH 8920). Bar = 1  $\mu$ m.

centre. *Conidiophores* abundant, tall, dark, bearing masses of white conidia, unbranched, smooth, 70–(185)–390 × 2–4 µm. Fertile hyphae hyaline, 2–3 µm diam, dichotomously branched, fragmenting into long, undulating chains of conidia. *Conidia* thin-walled, hyaline, subglobose to elongate, 2–(3.3)–5 × 1–(1.7)–2.5 µm, with an asperulate perispore. Maximal growth at pH 3 and 20 °C. Degrades cellulose, gelatin, lipid, pectin, starch, and tannic acid.

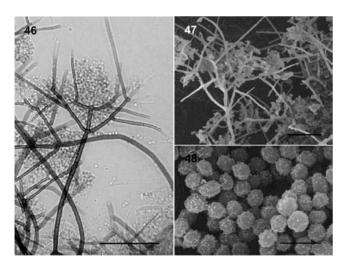
Specimens examined: Canada, Ontario, soil, cedar bog, Barron (UAMH 1540, ex-type); Alberta, roots Oxycoccus quadripetalus Gilib, Picea mariana Miller bog, Hambleton (UAMH 8920); Perryvale, Alberta, decomposing Sphagnum fuscum, bog, Thormann (UAMH 9749); Fort McKay, Alberta, roots Vaccinium myrtilloides, disturbed sand hill, Hill-Rackette (UAMH 10460). Finland, Kevo, Research Station, roots Vaccinium vitis-idaea L., Betula L.-dominated fjell, Currah (UAMH 10461).

*Notes: O. maius* var. *maius* is the only species in the genus confirmed to act as an ericoid mycorrhizal partner in nature. It can be distinguished from morphologically similar species, including *O. fuscum, O. griseum*, and the anamorphs of *M. arcticum* and *M. emodense*, by

its loose head of highly undulating chains of white conidia, and its long conidiophores (mean >100). The other species have less undulant fertile hyphae that branch at more acute angles, resulting in denser conidial heads, and mean conidiophore lengths less than 100  $\mu$ m.

**17.** *Oidiodendron muniellense* Calduch, Stchigel, Gené & Guarro, Stud. Mycol. 50: 161–163. 2004. Figs 46–48.

Colonies on decaying basidiome effuse, hairy, greenish brown, with the melanized mycelium (hyphae 1-2 um wide, septate) partially immersed in the substrate. Colonies on OA 30-35 mm diam at 4 wk at 25 °C, brownish beige to brown, flat, velvety, irregularly folded; reverse dark brown; brownish orange diffusible pigment produced. Colonies on PCA 26-30 mm at 4 wk at 25 °C, olive-brown, flat; reverse olive-brown. Colonies on PDA 37-40 mm diam at 4 wk at 25 °C, greyish orange to greyish brown, slightly funiculose at centre, radially folded; reverse brownish orange to yellowish brown. Conidiophores erect, melanized, up to 200 µm long, 2-3.5 µm wide; upper part bearing 4-6 verticillate appendages. Appendages several times dichotomously or trichotomously branched, straight, up to 60 µm long, 1.5-2.5 µm wide at the base, melanized, thick-walled, septate, and smooth at the base, becoming pale, thin-walled, and roughened at the pointed tips. Fertile hyphae terminal or lateral on the conidiophore apex and appendages, branched, hyaline, smooth-walled, 1–2.5 µm wide, fragmenting to form chains of conidia. Conidia globose to subglobose, ochraceous, 1.5-2.5 µm diam, covered with



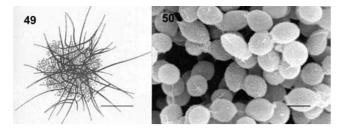
**Figs 46–48.** *Oidiodendron muniellense*. Reproduced with permission from Calduch *et al.* 2004. 46. Conidiophore bearing straight, branched, melanized appendages and a conidial mass. Bar = 50  $\mu$ m. 47. Conidiophores bearing branched, melanized, fertile appendages. Bar = 40  $\mu$ m. 48. Globose to subglobose conidia with a reticulate network of spines. Bar = 5  $\mu$ m.

a reticulate network of spines as seen under SEM. Optimal growth at 25 °C. Habitat: decaying basidiome, Spain. Description is from Calduch *et al.* (2004).

*Notes*: This species is morphologically most similar to O. setiferum but the appendages of O. muniellense are straighter than those of O. setiferum and are rough at the tips while those of O. setiferum are smooth. The conidia of O. muniellense are globose to subglobose and covered by a reticulate network of spines, causing them to appear asperulate to echinulate under light microscopy while those of O. setiferum are subglobose to ovoid or elongate with a central dimple and covered with a rugose perispore that causes them to appear faintly ornamented to smooth under light microscopy. Notably, the conidia of O. tenuissimum, a species suggested by molecular evidence to be closely related to O. muniellense, are very similar to those of that species: melanized, subglobose, and covered with a reticulate network of spines.

## **18.** *Oidiodendron myxotrichoides* Calduch, Gené & Guarro, Stud. Mycol. 47: 217–218. 2002. Figs 49–50.

Colonies on beech leaves effuse, greenish-brown, forming patches. Hyphae pale brown to brown, septate, branched, 1.5-2.5 µm wide. Colonies on OA 30-35 mm diam at 4 wk at 15 °C, grey-violet to violet, flat, granulose; reverse dull violet to dark violet. Colonies on PCA 20-28 mm diam at 4 wk at 15 °C, green-grey at the center with white to grey-white margins; reverse green-grey to dark green. Colonies on MEA 21-29 mm diam at 4 wk at 15 °C, violet-grey to dark violet, velvety and radially folded, reverse violet-grey to dark violet. Colonies on PDA 28-35 mm diam at 4 wk at 15 °C, grey-green, fasciculate, producing a light orange to grey-orange diffusible pigment; reverse dark brown. Conidiomata grey-green to olive, abundant, arranged in concentric circles on OA and PCA, towards the periphery on MEA, absent on PDA. Conidiomata superficial, solitary, confluent, brown to dark brown, spherical to subspherical, up to 490 µm diam, consisting of a reticulate network of septate, brown, thick- and smooth- walled, branched and anastomosed hyphae up to 4.5 µm wide, radially disposed, from which fertile hyphae are produced. Peripheral hyphae up to 250 µm long, spine-like, straight, usually with shorter and deflected lateral branches, brown to dark brown, paling towards the apex, smooth- and thickwalled, 2-4 µm wide. Conidiophores of arborescent fertile hyphae that arise laterally or terminally from the melanized hyphae of the reticulum, subhyaline, 2-3 µm wide, smooth- and thin- walled. Conidia globose, subglobose, or broadly ellipsoidal, pale brown, smooth-walled or very finely rugose and thickwalled at maturity,  $2-3 \times 1.5-2.5 \mu m$ . Optimal growth at 15 °C; growth and sporulation reduced at 25 °C; no



**Figs 49–50.** *Oidiodendron myxotrichoides*. Reproduced with permission from Calduch *et al.* 2002. 49. Sessile, reticuloperidium-like conidioma supporting fertile hyphae that fragment to produce ellipsoidal conidia. Bar = 50  $\mu$ m. 50. Ellipsoidal conidia with a rugose perispore with connectives visible between some of the conidia. Bar = 2  $\mu$ m.

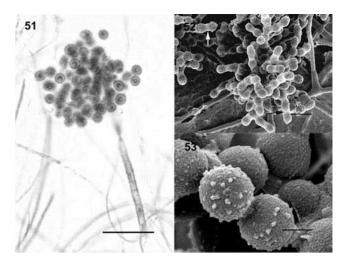
growth at 37 °C. Habitat: *Fagus sylvatica* leaf, Santa Fe del Montseny, Montseny Natural Park, Catalonia, Spain. Description from Calduch *et al.* (2002). The description of *O. myxotrichoides* appeared while this manuscript was nearly complete and isolates were not examined.

*Notes*: The conidiomata of *O. myxotrichoides* are described as sporodochia by Calduch *et al.* (2002); however, this term is inappropriate because the conidiomata lack basal pads of pseudoparenchyma and do not consist of masses of short conidiophores (Hawksworth *et al.* 1995). The structure is probably best referred to simply as a conidioma. *Oidiodendron myxotrichoides* is similar to *O. hughesii* in producing conidia within a reticuloperidium-like structure but in *O. hughesii* the reticulum forms from anastomosed appendages at the apex of a solitary conidiophore.

**19.** *Oidiodendron periconioides* Morrall, Can. J. Bot. 46: 204–205. 1968. Figs 51–53.

Colonies on CMA 11–18 mm diam at 28 d, dark greengrey to brown; reverse dark red-brown. Orange-brown exudate produced. Aerial hyphae and conidiophores abundant. Conidia green-grey to brown *en masse*. *Conidiophores* smooth, melanized and unbranched at base becoming hyaline and branched at apex, 25– (85)–175 × 2–4  $\mu$ m. Fertile hyphae hyaline, branched, swollen to form chains of vesicles that fragment to become chains of conidia arising at the conidiophore apices or laterally from vegetative hyphae. *Conidia* thick-walled, dark, spiny at maturity, globose to ellipsoidal, 3–(3.7)–6 × 2–(3.1)–4  $\mu$ m. Maximal growth at pH3 and 20 °C. Degrades cellulose, gelatin, pectin (UAMH 6084, UAMH 8527), starch and tannic acid.

*Specimens examined*: **Canada**, Candle Lake, Saskatchewan, boreal forest soil, 1964, Morrall (UAMH 8527, ex-type); Nichol Springs, Cypress Hills, Alberta, root endophyte, *Calypso bulbosa* (L.) Oakes, May 1987, Hambleton (UAMH 6084). **Japan**, humus, Currah (UAMH 7289).



**Figs 51–53.** *Oidiodendron periconioides* (UAMH 8527). 51. Erect conidiophore bearing a dense head of dark, spinulose, subglobose to ellipsoidal conidia. Bar =  $20 \ \mu m$ . 52. Short chains of spinulose, subglobose to ellipsoidal conidia forming from swollen vesicles (arrows). Bar =  $5 \ \mu m$ . 53. Spinulose, globose to ellipsoidal conidia. Bar =  $1 \ \mu m$ .

*Notes*: *Oidiodendron periconioides* is unique in the genus because it produces chains of globose, vesiclelike swellings that precede the appearance of conidia in short conidiogenous branches. It is also the only species of *Oidiodendron* that consistently produces dark, spiny, globose to ellipsoidal conidia. *Oidiodendron echinulatum* is similar but has more ellipsoidal conidia with rounded warts on the perispore; it is also WDG positive while *O. periconioides* is WDG negative.

**20.** *Oidiodendron pilicola* Kobayasi, Bull. Natl. Sci. Mus. (Tokyo) 12: 424–425. 1969. Fig. 54.

*Conidiophores* simple, erect, septate, thick-walled, pale olivaceous brown,  $100-150 \times 2.5-4 \mu m$ . Upper part branched monopodially (laterally and oppositely) into fertile hyphae. Fertile hyphae (1.5–2.5  $\mu m$  diam), 2–3 × branched, hyaline, fragmenting to form conidia. *Conidia* hyaline, barrel-shaped, truncate with frills at both ends, smooth, catenate, apically or laterally produced, forming dense clusters,  $3-3.5 \times 1.5-2 \mu m$ . Habitat: decaying human hair; soil. Description from Kobayasi (1969).

*Specimen examined*: **Sweden**, forest soil, 1972, Nylund (UAMH 7526). Degenerate and not producing conidia.

Notes: Oidiodendron pilicola resembles O. truncatum, and the anamorphs of M. cancellatum and M. striatosporum, in producing conidia that are truncate at both ends. Conidia of O. pilicola are hyaline, while those of O. truncatum and M. striatosporum are dark. Oidiodendron truncatum and M. cancellatum conidia differ by being reticulate, not smooth, and M. striatosporum conidia differ by being asperulate.

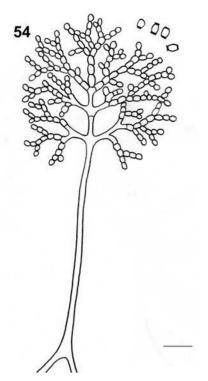


Fig. 54. Oidiodendron pilicola. Reconstructed from descriptions and illustrations given by Kobayasi (1969). A tall conidiophore bears oppositely branched, fertile hyphae that fragment to form branched chains of hyaline, smooth, barrel-shaped conidia with apical frills. No information was given to allow placement of septa in the conidiophore stipe in this conceptual drawing. Bar =  $15 \mu m$ .

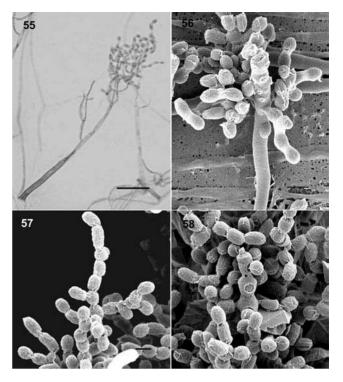
Molecular evidence suggests that this species is distinct but close to *O. chlamydosporicum* (Hambleton, unpubl. data).

**21.** *Oidiodendron rhodogenum* Robak, Saertryk av Nyt Mag. Naturvidensk. 71: 251–255. 1932. Figs 55–58.

Colonies on CMA 31–34 mm diam at 28 d, off-white to grey, appressed; reverse brown to grey-brown. Red diffusible pigment absent on CMA but produced by UAMH 1405 on OA. Conidiophores abundant, bearing masses of off-white conidia, smooth, branched, melanized,  $30-(50)-85 \times 3-6 \mu m$ . Fertile hyphae hyaline,  $2-5 \mu m$  diam, dichotomously branched, fragmenting into long chains of conidia. Conidia hyaline to lightly melanized, subglobose to elongate and irregular,  $1.5-(2.5)-5 \times 1.5-(1.6)-2 \mu m$ , with a rugose perispore. Maximal growth at pH3 and 20 °C. Degrades cellulose, gelatin, pectin, and starch.

*Specimens examined*: **Norway**, Kistefoss Mills, sludge in pulp strainers, 1929, H. Robak (UAMH 1405, authentic). **Canada**, Ontario, forest soil, 1969, Barron (CBS 401.69 = UAMH 8508).

*Notes: O. rhodogenum* has been identified traditionally on the basis of a red diffusible pigment in culture but this character is unreliable; pigment production is



**Figs 55–58.** *Oidiodendron rhodogenum* (UAMH 1405). 55. Erect, dichotomously branched conidiophore bearing divergent, branched chains of thin-walled, subglobose to elongate or cylindrical conidia. Bar =  $15 \,\mu\text{m}$ . 56. Short chains of ellipsoidal to elongate conidia branching off a portion of the conidiophore. Conidia have a rugose perispore. Bar =  $5 \,\mu\text{m}$ . 57. Chains of ellipsoidal to elongate or cylindrical conidia to elongate or cylindrical conidia with a rugose perispore and connectives visible between conidia. Bar =  $1 \,\mu\text{m}$ . 58. Rugose, ellipsoidal to elongate conidia to elongate to elongate conidi

inconsistent within and among isolates. In the absence of the red pigment, *O. rhodogenum* is difficult to identify because the species is not distinctive morphologically or physiologically. *Oidiodendron fuscum* and *O. griseum* are similar but have unbranched conidiophores. In addition, the conidia of *O. rhodogenum* are elongate to cylindrical with a rugose perispore while those of *O. griseum* are asperulate and those of *O. fuscum* are dimpled, asperulate, and subglobose to ellipsoidal.

**22.** *Oidiodendron setiferum* Udagawa & Toyazaki, Mycotaxon 28: 234–238. 1987. Figs 59–65.

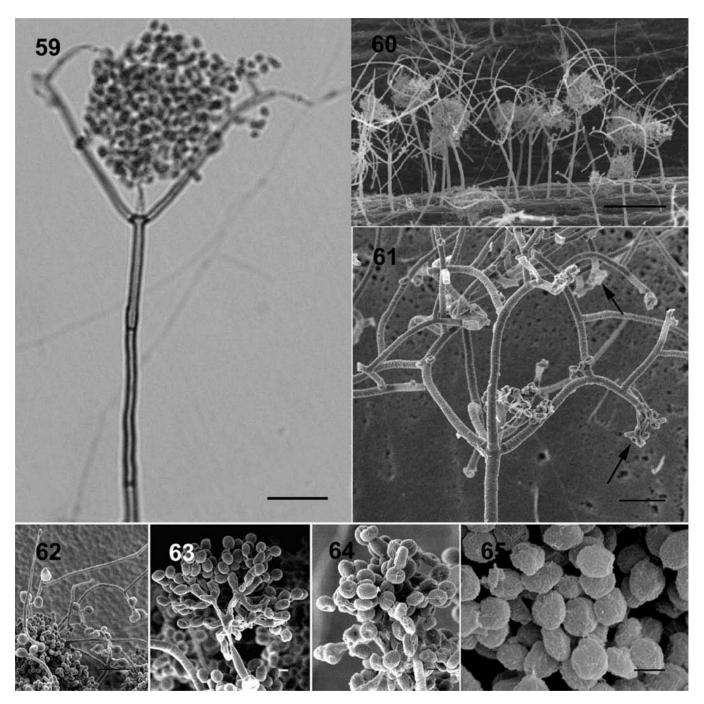
= Oidiodendron ramosum Calduch et al. (2004)

Colonies on CMA 23–25 mm diam at 28 d, brown, appressed; reverse green-grey to black (darkest under areas of conidial production). Conidiophores abundant, bearing brown masses of conidia and appendages, smooth, melanized, branching at apex to form appendages and fertile hyphae,  $40-(80)-180 \times 2-3 \mu m$ . Fertile hyphae hyaline, penicillate, borne either at the conidiophore apex or at the tips or branching points of the appendages (2–4 per conidiophore) produced at the apices of the conidiophores and subtending masses

of conidia, dichotomously branched, melanized, with tapered apices,  $20-100 \times 2-3 \mu m$ . *Conidia* thin-walled, hyaline to lightly pigmented, subglobose to elongate or irregular,  $1.5-(2.5)-4 \times 1-(1.5)-2.5 \mu m$ , with a rugose perispore and a central dimple under SEM. Maximal

growth at 25 °C and pH 3. Degrades cellulose, gelatin, pectin, starch and tannic acid.

*Specimen examined*: Japan, Kobe, house dust, Udagawa (UAMH 5715, ex-type).



**Figs 59–65.** *Oidiodendron setiferum* (UAMH 5715) or reproduced with permission from Calduch *et al.* 2004. 59. Erect conidiophore bearing two dichotomously branched appendages and a dense head of thin-walled, hyaline to lightly pigmented, subglobose to elongate or irregular conidia (UAMH 5715). Bar  $15 = \mu m$ . 60. Conidiophores bearing long, branched, recurved appendages subtending central conidial masses (*O. ramosum*; Calduch *et al.* 2004, fig. 12). Bar = 100 µm. 61. Apex of conidiophore bearing four dichotomously branched, recurved, fertile appendages and a small central conidial mass. Arrows indicate fertile hyphae arising from the appendages (UAMH 5715). Bar = 10 µm. 62. Fertile appendages with conidia arising from branching points and apices (UAMH 5715). Bar = 10 µm. 63. Penicillate head of fertile hyphae fragmenting to form short chains of subglobose to ellipsoidal or elongate conidia with a rugose perispore. Connectives are visible between the conidia (UAMH 5715). Bar = 1 µm. 64. Chains of subglobose to ellipsoidal conidia with a rugose perispore and central dimple visible on some conidia (*O. ramosum*; Calduch *et al.* 2004, fig. 18). Bar = 1.75 µm.

Notes: Calduch et al. (2004) distinguished O. ramosum from O. setiferum on the basis of the fertility of the appendages and conidial ornamentation. Oidiodendron setiferum was described as having sterile appendages surrounding the fertile head (Udagawa & Toyazaki 1987) while in O. ramosum, the appendages often give rise to fertile hyphae from their branching points or apices (Calduch et al. 2004). Although the matter is not noted in the original description of O. setiferum, our SEM observations of the ex-type show that fertile hyphae and conidia arise from the branching points and apices of the appendages. The conidia of O. ramosum are described as smooth to slightly roughened (Calduch et al. 2004) and those of O. setiferum are smooth (Udagawa & Toyazaki 1987). However, SEM examination of O. setiferum shows that the conidia have a rugose perispore and are no less roughened than the O. ramosum conidia depicted in the SEM images of Calduch et al. (2004). Thus, the differences noted by Calduch et al. (2004) between the original description of O. setiferum and the features of their taxon, O. ramosum, cannot be substantiated and O. ramosum is here considered a synonym of O. setiferum. The two taxa group together with low to moderate bootstrap support (54) based on ITS sequence data, suggesting a close relationship rather than confirming their distinctness as suggested by Calduch et al. (2004).

*Oidiodendron setiferum, O. muniellense* and *O. hughesii* can be distinguished from others in the genus by the melanized appendages that subtend the arthroconidia. See comments under *O. hughesii* and *O. muniellense*.

**23.** *Oidiodendron tenuissimum* (Peck) Hughes, Can. J. Bot 36: 790. 1958. Figs 66–69.

 $\equiv$  Periconia tenuissima Peck fide Hughes (1958).

Colonies on CMA 18–22 mm diam at 28 d, pale brown, appressed; reverse dark grey-brown to black. Conidiophores abundant, arranged in concentric rings, bearing masses of brown conidia, unbranched, melanized,  $30-(95)-240 \times 2-4 \mu m$ . Fertile hyphae hyaline, dichotomously branched, fragmenting to form chains of conidia. Conidia melanized at maturity, faintly ornamented, subglobose to elongate,  $2-(2.5)-4 \times 1-(2.1)-3 \mu m$ . Conidia covered by a reticulate network of spines as revealed by SEM. Maximal growth at pH 3–5 and 20 °C. Degrades cellulose, gelatin, lipid, pectin, and starch.

*Specimens examined*: **Spain**, La Gomera, Canary Islands, leaf litter, 1995, Castañeda (UAMH 8513). **Canada**, Guelph, Ontario, soil, mixed deciduous forest, 1960, Barron (UAMH 1523).

*Notes*: See also discussions under *O. fuscum* and *O. griseum*. Both UAMH 8513 and 1523, the two strains listed above, had previously been identified as *O.* 

tenuissimum sensu Barron, but were subsequently considered distinct from that species on the basis of ITS sequences and were labelled "O. sp. nov" (Hambleton et al. 1998). Closer comparison of these isolates with the type material of Periconia tenuissima shows that they are indistinguishable from it and are best accommodated under the name O. tenuissimum. Oidiodendron tenuissimum has brown colonies, conidiophores that may exceed 200 µm, and dark, spinulose conidia as opposed to the off-white or pale grey colonies, shorter conidiophores (typically less than 100 µm long), and hyaline, minutely vertuculose to asperulate conidia of O. fuscum. It can be distinguished from other species of Oidiodendron by the dark, subglobose to ellipsoidal or elongate conidia with a reticulate network of spines.

**24.** *Oidiodendron truncatum* Barron, Can. J. Bot. 40: 602–604. 1962. Figs 70–72.

Colonies on CMA 30–32 mm diam (UAMH 8443), 38–42 mm diam (UAMH 1399, UAMH 10464), brown to green-grey, appressed; reverse green-grey to brown. *Conidiophores* abundant, clumped, bearing masses of brown conidia, smooth, branched at apex, more or less melanized,  $18-(75)-180 \times 2-4 \mu m$ . *Conidia* dark at maturity, produced in branched chains at the conidiophore apices or from vegetative hyphae, barrelshaped to irregular, truncate with distinct apical scars and reticulate ornamentation,  $2-(3.6)-5 \times 1-(2.5)-3.5 \mu m$ . Maximal growth at 15–20 °C and pH >7. Degrades cellulose, gelatin, lipid, and pectin.

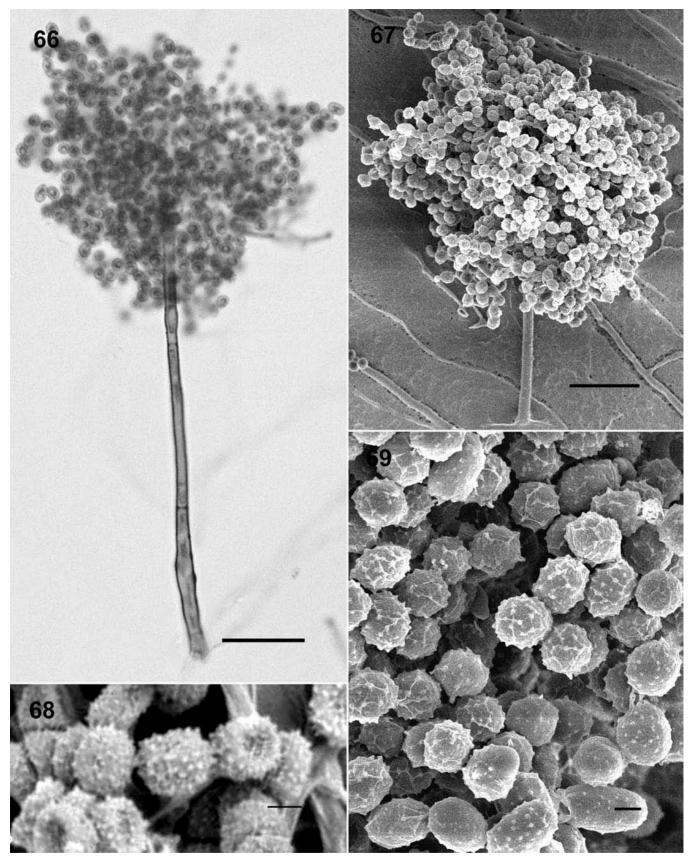
*Specimens examined*: **Canada**, Guelph, Ontario, soil, mixed forest, 1960, Barron (UAMH 1399, ex-type); Slave Lake, Alberta, decaying spruce wood, Lumley (UAMH 10464). **Italy**, soil of snow valley, Mosca (UAMH 8443 = ATCC 36256, as *O. ambiguum*).

*Notes*: This species can be readily distinguished from others in the genus because of its dark, reticulate, truncate conidia and its inability to degrade starch.

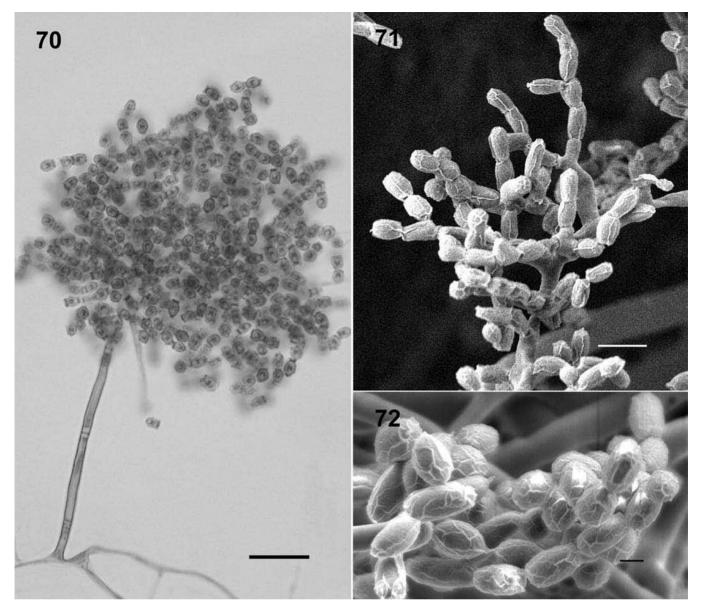
#### **Excluded Species**

*Oidiodendron robustum* Mercado Sierra & Castañeda Ruiz, Acta Bot. Cubana 33: 3–4. 1985.

The type specimen for this species was not examined but its description lists conidiophores that are 250–  $870 \times 7.5$ –10.5 µm and conidia 5–11 × 2.5–3.2 µm (Mercado Sierra & Castañeda Ruiz 1985). Both are much larger than all other species of *Oidiodendron* and are more reminiscent of species of *Oidiodendron*. From the original illustrations and description it is impossible to determine whether the chains of conidia are forming by basipetal fragmentation or acrogenous budding. Based on these ambiguities, this taxon is excluded from the genus.



**Figs 66–69.** *Oidiodendron tenuissimum.* 66. Erect conidiophore bearing a dense head of thick-walled, dark, subglobose to elongate conidia (UAMH 8513). Bar = 15  $\mu$ m. 67. Short conidiophore bearing a large, dense head of long chains of spinulose, subglobose conidia (UAMH 8513). Bar = 10  $\mu$ m. 68. Spinulose, subglobose to ellipsoidal conidia of dried type material (NYS). Bar = 2  $\mu$ m. 69. Subglobose to ellipsoidal conidia with a reticulate network of spines (UAMH 8513). Bar = 1  $\mu$ m.



**Figs 70–72.** *Oidiodendron truncatum*. 70. Erect conidiophore bearing a large, dense head of thick-walled, truncate, dark, barrel-shaped conidia with apical frills (UAMH 1399). Bar = 15  $\mu$ m. 71. Branched chains of barrel-shaped conidia with a rugose (reticulate) perispore (UAMH 10464). Bar = 5  $\mu$ m. 72. Barrel-shaped conidia with a reticulate perispore (UAMH 10464). Bar = 1  $\mu$ m.

*Oidiodendron terrestre* Roy & Singh, J. Indian Bot. Soc. 48: 158–159. 1969.

This species is described as having rapid growth (90 mm in 3 d), hyaline conidiophores, chlamydospores  $4.5-14 \times 3.5-12.5 \mu m$  and ellipsoidal to cylindrical, one-to two-celled conidia  $4-15 \times 3-13 \mu m$  (Roy & Singh 1969). This growth rate is much greater, and conidia much larger than observed in other *Oidiodendron* species. In addition, two-celled conidia are inconsistent with the generic diagnosis. Conidial ontogeny is unclear from the original description and illustrations but appears blastic and acropetal rather than basipetal. The absence of definitive *Oidiodendron* characters, along with the large, two-celled conidia, rapid growth, and hyaline conidiophores, easily exclude this species from *Oidiodendron*.

#### ACKNOWLEDGEMENTS

We thank David Beyer and Joost Stalpers for providing information on "O. sindenia" and O. sulphureum, respectively. George Braybrook assisted with SEM. Sarah Hambleton sequenced several isolates and kindly shared unpublished phylogenetic trees and SEM images. Lynne Sigler provided UAMH cultures and permanent slides and commented on an early ms. draft. Lindsay Elliott, Melissa Day, Ben Wilson, and Marcie Plishka provided laboratory assistance. Funding was provided to AVR by a Canadian Circumpolar Institute C/BAR grant, an Alberta Conservation Association Challenge Grant in Biodiversity, a Natural Sciences and Engineering Research Council of Canada (NSERC) PGS-A and NSERC PGS-B scholarship, and a University of Alberta Dissertation Fellowship. Additional support from the NSERC Discovery Grants Programme is gratefully acknowledged.

### REFERENCES

- Barron GL (1962). New species and new records of *Oidiodendron. Canadian Journal of Botany* **40**: 589–607.
- Barron GL, Booth C (1966). A new species of *Arachniotus* with an *Oidiodendron* conidial state. *Canadian Journal of Botany* **44**: 1057–1061.
- Bending GD, Read DJ (1997). Lignin and soluble phenolic degradation by ectomycorrhizal and ericoid mycorrhizal fungi. *Mycological Research* **101**: 1348–1354.
- Calduch M, Gené J, Cano J, Guarro J (2002). A new species of *Oidiodendron* with gymnothecium-like sporodochia. *Studies in Mycology* **47**: 211–216.
- Calduch M, Gené J, Cano J, Stchigel AM, Guarro J (2004). Three new species of *Oidiodendron* Robak from Spain. *Studies in Mycology* **50**: 159–170.
- Couture M, Fortin JA, Dalpé Y (1983). *Oidiodendron* griseum Robak: an endophyte of ericoid mycorrhiza in *Vaccinium* spp. *New Phytologist* **95**: 375–380.
- Currah RS (1985). Taxonomy of the *Onygenales*: *Arthrodermataceae*, *Gymnoascaceae*, *Myxotrichaceae* and *Onygenaceae*. *Mycotaxon* 24: 1–216.
- Currah RS (1994). Peridial morphology and evolution in the prototunicate ascomycetes. In: Hawksworth DL (ed.) *Ascomycete Systematics: Problems and Perspectives in the Nineties.* Plenum Press, New York. pp 281–293.
- Currah RS, Niemi M, Huhtinen S (1999). *Oidiodendron maius* and *Scytalidium vaccinii* from the mycorrhizas of *Ericaceae* in northern Finland. *Karstenia* **39**: 65–68.
- Currah RS, Tsuneda A, Murakami S (1993). Conidiogenesis in *Oidiodendron periconioides* and ultrastructure of ericoid mycorrhizas formed with *Rhododendron brachycarpum*. *Canadian Journal of Botany* **71**: 1481– 1485.
- Dalpé Y (1986). Axenic synthesis of ericoid mycorrhiza in *Vaccinium angustifolium* Ait. by *Oidiodendron* species. *New Phytologist* **103**: 391–396.
- Dalpé Y (1989). Ericoid mycorrhizal fungi in the Myxotrichaceae and Gymnoascaceae. New Phytologist 113: 523–527.
- Dalpé Y (1991). Statut endomycorrhizien du genre Oidiodendron. Canadian Journal of Botany 69: 1712– 1714.
- Delamarre S, Batt CA (1999). The microbiology and historical safety of margarine. *Food Microbiology* **16**: 327–333.
- Domsch KH, Gams W, Anderson T-H (1980). Compendium of Soil Fungi. Academic Press, U.K.
- Douglas GC, Heslin MC, Reid C (1989). Isolation of *Oidiodendron maius* from *Rhododendron* and ultrastructural characteristics of synthesized mycorrhizas. *Canadian Journal of Botany* **67**: 2206–2212.
- Ellis MB (1971). *Dematiaceous Hyphomycetes*. Commonwealth Agricultural Bureaux, U.K.
- Ellis MB (1976). *More dematiaceous hyphomycetes*. Commonwealth Agricultural Bureaux, U.K.
- Gams W, Söderström BE (1983). *Oidiodendron scytaloides* n. sp. *Cryptogamie*, *Mycologie* **4**: 239–243.
- Gibas CFC, Sigler L, Summerbell RC, Currah RS (2002). Phylogeny of the genus *Arachnomyces* and its

anamorphs and the establishment of *Arachnomycetales*, a new eurotiomycete order in the *Ascomycota*. *Studies in Mycology* **47**: 131–139.

- Greif MD, Currah RS (2003). A functional interpretation of the role of the reticuloperidium in whole-ascoma dispersal by arthropods. *Mycological Research* **107**: 77–81.
- Hambleton S, Currah RS (1997). Fungal endophytes from the roots of alpine and boreal *Ericaceae*. *Canadian Journal of Botany* **75**: 1570–1581.
- Hambleton S, Egger KN, Currah RS (1998). The genus Oidiodendron: species delimitation and phylogenetic relationships based on nuclear ribosomal DNA analysis. Mycologia 90: 854–869.
- Hawksworth DL (1974). *Mycologist's handbook*. Commonwealth Agricultural Bureaux, Farnam Royal, Slough, U.K.
- Hawksworth DL, Kirk PM, Sutton BC, Pegler DN (1995). Ainsworth & Bisby's dictionary of the fungi. 8th edn. University Press, U.K.
- Horak B, Dutkiewicz J, Solarz K (1996). Microflora and acarofauna of bed dust from homes in Upper Silesia, Poland. Annals of Allergy Asthma and Immunology 76: 41–50.
- Hughes SJ (1958). Revisiones hyphomycetum aliquot cum appendice de nominibus rejiciendis. *Canadian Journal* of Botany **36**: 727–836.
- Hutchison LJ (1990). Studies on the systematics of ectomycorrhizal fungi in axenic culture. II. The enzymatic degradation of selected carbon and nitrogen compounds. *Canadian Journal of Botany* **68**: 1522–1530.
- Johansson M (2001). Fungal associations of Danish *Calluna vulgaris* roots with special reference to ericoid mycorrhiza. *Plant and Soil* **231**: 225–232.
- Kobayasi Y (1969). Mycological flora of the Alaskan Arctic. Bulletin of the National Science Museum (Tokyo) 12: 424–425.
- Krysińska-Traczyk E, Kiecana I, Perkowski J, Dutkiewicz J (2001). Levels of fungi and mycotoxins in samples of grain and grain dust collected on farms in eastern Poland. *Annals of Agricultural and Environmental Medicine* 8: 269–274.
- Lacourt I, Girlanda M, Perotto S, Del Pero M, Zuccon D, Luppi AM (2001). Nuclear ribosomal sequence analysis of *Oidiodendron*: towards a redefinition of ecologically relevant species. *New Phytologist* **149**: 565–576.
- Lumley TC, Gignac LD, Currah RS (2001). Microfungus communities of white spruce and trembling aspen logs at different stages of decay in disturbed and undisturbed sites in the boreal mixed wood region of Alberta. *Canadian Journal of Botany* **79**: 76–92.
- Malan CE (1949). Su un nuovo reperto di *Dicyma ambigua* Peyronel e sulla posizione sistematica di questa specie. *Giornale Botanico Italiano* **56**: 735–738.
- Melin E, Nannfeldt JA (1934). Researches into the blueing of ground wood pulp. *Saertryck ur Svenska Skogsvårdsföreningens Tidskrift Hafte* **3-4**: 397–616.
- Mercado Sierra A, Castañeda Ruiz RF (1985). Nuevos hifomicetes tálicos de Cuba. *Acta Botanica Cubana* **32**: 1–10.
- Miyamoto T, Igarashi T, Takahashi K (2000). Lignin-

degrading ability of litter-decomposing basidiomycetes from Picea forests of Hokkaido. Mycoscience 41: 105-110.

- Mori Y, Sato Y, Takamatsu S (2000). Molecular phylogeny and radiation time of Erysiphales inferred from the nuclear ribosomal DNA sequences. Mycoscience 41: 437-447.
- Morrall RAA (1968). Two new species of Oidiodendron from boreal forest soils. Canadian Journal of Botany 46: 203-206.
- Orr GF, Kuehn HH (1964). A re-evaluation of Myxotrichum spinosum and Myxotrichum cancellatum. Mycologia 56: 473-481.
- Orr GF, Kuehn HH, Plunkett OA (1963). The genus Myxotrichum Kunze. Canadian Journal of Botany 41: 1457-1480.
- Perotto S, Perotto R, Faccio A, Schubert A, Varma A, Bonfante P (1995). Ericoid mycorrhizal fungi: cellular and molecular bases of their interactions with the host plant. Canadian Journal of Botany 73: S557-S568.
- Peyronel B (1914). Osservazioni critiche e sperimentali su alcune specie del genere Dicvma Boul. e sui loro stati ascofori. Annales Mycologici 12: 459-470.
- Piercey MM, Thormann MN, Currah RS (2002). Saprobic characteristics of three fungal taxa from ericalean roots and their associations with the roots of Rhododendron groenlandicum and Picea mariana in culture. Mycorrhiza 12: 175-180.
- Pivkin MV (2000). Filamentous fungi associated with Holothurians from the Sea of Japan, off the Primorye Coast of Russia. Biological Bulletin 198: 101-109.
- Reiman M, Uitti J (2000). Exposure to microbes, endotoxins, and total dust in cigarette and cigar manufacturing: an evaluation of health hazards. Annals of Occupational Hygiene 44: 467-473.
- Rice AV, Currah RS (2001). Physiological and morphological variation in Oidiodendron maius. Mycotaxon 79: 383-396.
- Rice AV, Currah RS (2002). New perspectives on the niche and holomorph of the myxotrichoid hyphomycete, Oidiodendron maius. Mycological Research 106: 1463-1467.
- Rice AV, Currah RS (2005). A new species of Oidiodendron and a preliminary evaluation of Biolog FF microplates for distinguishing among Oidiodendron species. Studies in Mycology 53: 75-82.
- Rice AV, Currah RS (in press). Oidiodendron maius: saprobe in Sphagnum peat, mutualist in ericaceous roots. In: Schulz B, Boyle C, Sieber T (eds) Microbial Root Endophytes. Springer-Verlag, Heidelberg: In Press.
- Robak H (1932). Investigations regarding fungi on Norwegian ground wood pulp and fungal infections at wood pulp mills. Saertrykk av Nyt Magazin for Naturvidenskaberne 71: 185–330.
- Roose-Amsaleg C, Brygoo Y, Harry M (2004). Ascomycete diversity in soil-feeding termite nests and soils from a tropical rainforest. Environmental Microbiology 6: 462-469.
- Roy RY, Singh GN (1969). A new species of Oidiodendron from Indian soil. Journal of the Indian Botanical Society 48: 159-160.
- Sigler L, Carmichael JW (1976). Taxonomy of Malbranchea

and some other hyphomycetes with arthroconidia. Mycotaxon 4: 349-488.

- Sigler L, Flis A (1998). Catalogue of the University of Alberta Microfungus Collection and Herbarium. 3rd edn. University of Alberta, Edmonton, AB, Canada. (available online at www.devonian.ualberta.ca/uamh).
- Sigler L, Gibas CFC (2005). Utility of a cultural method for identification of the ericoid mycobiont Oidiodendron maius. Studies in Mycology 53: 63-74.
- Sigler L, Lumley TC, Currah RS (2000). New species and records of saprophytic ascomycetes (Myxotrichaceae) from decaying logs in the boreal forest. Mycoscience 41: 495-502.
- Smith G (1946). Note on the occurrence of species of Oidiodendron Robak in Britain. British Mycological Society Transactions 29: 232–234.
- Smith RE (1977). Rapid tube test for detecting fungal Applied cellulase production. Environmental Microbiology 33: 980-981.
- Söderström BE, Bååth E (1978). Soil microfungi in three Swedish coniferous forests. Holarctic Ecology 1: 62-72
- Stalpers JA (1974). Revision of the genus Oedocephalum (Fungi Imperfecti). Koninklijk Nederlandse Akademie van Wetenschappen – Amsterdam. 77: 383–402.
- Sugivama S, Ohara A, Mikawa T (1999). Molecular phylogeny of onygenalean fungi based on small subunit ribosomal DNA (SSU rDNA) sequences. Mycoscience 40: 251-258.
- Tewari RP, MacPherson CR (1968). Pathogenicity and neurologic effects of Oidiodendron kalrai for mice. Journal of Bacteriology 95: 1130–1139.
- Tewari RP, MacPherson CR (1971). A new dimorphic fungus, Oidiodendron kalrai: morphological and biochemical characteristics. Mycologia 63: 602-611.
- Thormann MN, Currah RS, Bayley SE (2001). Microfungi isolated from Sphagnum fuscum from a southern boreal bog in Alberta. The Bryologist 104: 548-559.
- Thormann MN, Currah RS, Bayley SE (2002). The relative ability of fungi from Sphagnum fuscum to decompose selected carbon substrates. Canadian Journal of Microbiology 48: 204-211.
- Thormann MN, Currah RS, Bayley SE (2004). Patterns of distribution of microfungi in decomposing bog and fen plants. Canadian Journal of Botany 82: 710-720.
- Tokumasu S (1973). Notes on Japanese Oidiodendron. Transactions of the Mycological Society of Japan 14: 246-255.
- Tribe HT, Weber RWS (2002). A low-temperature fungus from cardboard, Myxotrichum chartarum. Mycologist 16: 3-5.
- Tsuneda A, Currah RS (2004). Ascomatal morphogenesis in Myxotrichum arcticum supports the derivation of the Myxotrichaceae from a discomycetous ancestor. Mycologia 96: 627-635.
- Tsuneda A, Thormann MN, Currah RS (2001). Modes of cell wall degradation of Sphagnum fuscum by Acremonium cf. curvulum and Oidiodendron maius. Canadian Journal of Botany 79: 93-100.
- Uchiyama S, Kamiya S, Udagawa S (1995). Five onygenalean fungi from Japan. Mycoscience 36: 211-220.
- Udagawa S, Toyazaki N (1987). A new species of

Oidiodendron. Mycotaxon 28: 233–240.

- Udagawa S, Uchiyama S (1998). Three hyphomycetes isolated from soil and feather debris. *Canadian Journal of Botany* **76**: 1637–1646.
- Udagawa S, Uchiyama S (1999). Taxonomic studies on new or critical fungi of non-pathogenic *Onygenales* 2. *Mycoscience* **40**: 291–305.
- Udagawa S, Uchiyama S (2000). Two onygenalean fungi from Russian Far East soil. *Mycoscience* **41**: 217–221.
- Udagawa S, Uchiyama S, Kamiya S (1993). *Gymnostellatospora*, a new genus of the *Myxotrichaceae*. *Mycotaxon* **48**: 157–164.
- Udagawa S, Uchiyama S, Kamiya S (1994). A new species of *Myxotrichum* with an *Oidiodendron* anamorph. *Mycotaxon* **52**: 197–205.

Usuki F, Abe JP, Kakishima M (2003). Diversity of

ericoid mycorrhizal fungi isolated from hair roots of *Rhododendron obtusum* var. *kaempferi* in a Japanese red pine forest. *Mycoscience* **44**: 97–102.

- Von Szilvinyi A (1941). Mikrobiologische Boden untersuchungen im Lunzer Bebiet. Zentralblatt für Bakteriologie Abteilung II. 103: 133–189.
- Xiao G, Berch S (1999). Organic nitrogen use by salal ericoid mycorrhizal fungi from northern Vancouver Island and impacts on growth *in vitro* of *Gaultheria shallon*. *Mycorrhiza* **9**: 145–149.
- ZhdanovaNN (1963). Redki ta novi vydy temnozabarvlenykh hifomitsetiv v hruntakh Ukrayiny. [Rare and new species of dark-coloured hyphomycetes in the soils of the Ukraine]. *Mikrobiologiecheskiy Zhurnal Akademiya Nauk Ukrainskiy RSR.* **25**: 13–19.