8 Taxonomy of Industrially Important White-Rot Fungi

HAROLD H. BURDSALL JR.

INTRODUCTION

The industrially important white-rot fungi are still limited in number despite their obvious potential in biotechnological applications. Scientists involved in biotechnology research and those pursuing biotechnological ventures are well aware of the importance of using the best organisms for their particular applications. Identifying and choosing the best species constitute a critical problem. However, taxonomy and its utility in choosing the most appropriate organisms are little appreciated by those who use the fungi for biotechnological purposes. The emphasis in biotechnology is on optimizing the isolates already in hand or in general screening for more desirable isolates. It is in the latter endeavor that taxonomy can have a major impact. Knowledge of taxonomy allows the short-cutting of screening processes and aids in the selection of industrially useful biological organisms.

The goal of taxonomy is not merely to place names on organisms. Rather, it is to place meaningful names on organisms, that is, names that indicate relationship to other organisms. Related organisms have similarities, including morphology, genetics, and biology in general. As such, related organisms-for the purposes of this chapter, white-rot fungi-can be expected to have similar abilities to produce secondary metabolites that may be used in pharmaceuticals or to produce enzymes that may be of use in other biotechnologies, such as bioremediation or biologically enhanced pulping. Using the term *white-rot fungi* is, in fact, a form of taxonomy, that is, attributing a meaningful name to a group of objects. This particular group of objects has characteristics desired by a particular group of scientists and technologists. Realizing that white-rot fungi have these desirable qualities allows screening of only those organisms that possess these traits.

Using broad spectrum screening of fungi is certainly a viable method of obtaining fungi with desirable characteristics (Rills and Poolishook, 1994). However, such activities are less productive in cases in which a specific characteristic is de-

Environmentally Friendly Technologies for the Pulp and Paper Industry, edited by Raymond A. Young and Masood Akhtar ISBN 0-471-15770-8 © 1998 John Wiley & Sons, Inc.

sired and fungi possessing such a characteristic are able to be recognized and identified. Knowing that a species of a particular genus demonstrates particular characteristics, for example, produces particular secondary metabolites or enzymes, allows extrapolation of that knowledge to other members of the genus or to closely related genera. Thus, the screening can be more effectively targeted.

The kingdom Fungi is divided into many subunits, each more restrictive than the next higher level. The white-rot fungi are in the division Eumycota (true fungi), subdivision Basidiomycotina, class Hymenomycetes, subclass Holobasidiomycetidae (Hawksworth et al., 1995). This subclass contains nearly all of the wood-decay fungi, as well as the mycorrhizal, litter, and decomposer fungi. It contains the mushrooms, puffballs, conks, and crustlike fungi. At the ordinal level (one step below the subclass) the biological variation among representatives is more reduced, especially as to function, and at the family level there are only rare cases of functional diversity (mycorrhizal vs. wood-decay, brown-rot vs. white-rot). Within a genus there is no diversity in broad biological function, although species in the genus differ in their capability to perform particular functions. Thus, when a desirable characteristic is found in a particular species, the obvious place to find species with similar characteristics is in other members of the same genus or family.

INCOMPATIBILITY SYSTEMS

The genetic incompatibility systems found operating in the white-rot fungi are just as variable as those in the rest of the Basidiomycotina. There are homothallic species in which the life cycle of the organism can be completed by growth of a spore or other propagule containing a single haploid nucleus; that is, no anastomosis with elements from an individual with a compatible nucleus is needed. These species are uncommon, and no species known to be industrially important white-rotters have been unqualifiedly demonstrated to be homothallic.

Heterothallic species are more prevalent in the fungus kingdom. These species require that two compatible nuclei be associated through hyphal anastomosis in order for the life cycle to continue to completion, resulting in the formation of basidia and haploid basidiospores. A variation on this theme, secondary homothallism, places two compatible nuclei in a single basidiospore after meiosis, thus obviating the need for anastomosis to combine compatible nuclei. This type of incompatibility system mimics homothallism in that the life cycle can be completed by germination of a single spore.

Most of the white-rot fungi possess a heterothallic incompatibility system, which may be one of two types. The bipolar (unifactorial) system possesses a single incompatibility locus, which must differ in the associated nuclei, in order for completion of the 1ife cycle. However, other fungi possess two incompatibility loci, both of which must differ in associated nuclei in order for a completed cycle to occur. This is called a tetrapolar (bifactorial) incompatibility system. Unfortunately, the incompatibility system of one of the most important white-rot fungi used in industry, *Phanerochaete chrysosporium* Burds., is still in question. Alic and Gold (1985) re-

ported that their evidence indicates that *P. chrysosporium* possesses primary homothallism. Their conclusions are based on their obtaining fruiting in cultures derived from single uninucleate basidiospores. Conversely, Thompson and Broda (1987) found that the pairing of single spore isolates in all possible combinations gave results supporting the presence of a heterothallic incompatibility system. The fact that 12 of the isolates used in Thompson and Broda's (1987) work were demonstrated to be homokaryons, using restriction fragment length polymorphisms (RFLPs) (Raeder and Broda, 1986), lends significant support to the likelihood that *P. chrysosporium* is heterothallic and most likely bipolar (Thompson and Broda, 1987).

Blaha et al. (unpublished manuscript) observed the nuclear sequence of events in basidium and basidiospore formation using several types of staining. This data demonstrates that the fusion nucleus in the basidium frequently undergoes an extra mitotic division, producing eight nuclei before the nuclei migrate into the basidiospores. Normally, two nuclei migrate into each basidiospore. Thus, any combination of two daughter nuclei may migrate into the basidiospores. This process may have led to some of the present discrepancies in interpretation of the incompatibility system.

NOMENCLATURE AND TAXONOMIC CONCEPTS

A situation that frustrates users of taxonomy, which is anyone dealing with biological organisms, is the changing of names of the genera or species. It is a frustration for everyone, including taxonomists. But what is in a name, and why do names change? Many fungal species that are used in processes today were described and originally named 50 to 200 years ago. At that time the methods used to identify fungi were entirely morphological, that is, based entirely on visible characteristics. Most descriptions in earlier times were based only on characteristics observable with the naked eye. Genera were determined according to whether their species were annual or perennial, whether the spore-bearing surface had pores, teeth or gills, how these were attached to the stem (if a stem was present), the color of the basidiome, as well as other criteria. As the science developed and microscopes were more readily available and of higher quality, the microscopic characters, such as the type of hyphae of which the various parts of a fungus was composed, the shape, size, ornamentation, and wall thickness of the basidiospores, the type of basidium, the presence or absence and morphology of sterile structures, became important in determining relationships and both generic and specific limits.

More recently, the biology of a species has been included in determining relationship, with the use of functional characters such as mycorrhizal capability, ability to decay wood, the type of decay caused (white- or brown-rot), production of particular enzymes, or other reactions. These considerations extended to the cultural characteristics. Growth on media containing gallic acid, tannic acid, or tyrosine was used to determine whether a fungus produced extracellular oxidases (Davidson et al., 1938; Davidson et al., 1942). Later, Nobles (1958, 1965) began using gum guaiac for the

same purpose. These chemical tests have continued to develop, with a number of different chemicals being used to increase their reliability (Harkin and Obst, 1973; Harkin et al., 1974; Boidin, 1958; Nakasone et al., 1994). In addition to the tests to determine the production of extracellular oxidases, growth rates on standard media were used, as well as both macro- and micromorphological characteristics. Because of this type of more in-depth study we know today that similarity of morphological characteristics does not always indicate close relationship or a congeneric status. These characteristics are usually indicative of relationship, but not always. As a result, some species described according to only morphological characteristics have been placed in the wrong genus or family. With additional information regarding the total biology of a fungus, their misplacement in the wrong genus is discovered and the generic name must be changed.

With the availability of molecular characters based on differences in the makeup of the nuclear and mitochondrial DNA molecules, taxonomic mycologists have a too1 to make even more critical and accurate distinctions between taxa, at the species level and even below. These techniques are effective at suggesting relationships that have not been obvious or have been hidden by morphological similarities derived from parallel or convergent evolution. The techniques are also useful in resolving species complexes that were previously unresolvable or very difficult to resolve with the use of other techniques. Moreover, reexamining and reevaluating morphological characteristics in light of molecular data often leads to the discovery of morphological characteristics that are useful in delimitations, which were previously ignored or not observed (Nakasone and Sytsma, 1993).

The concepts of genera used in many discussions in the past have changed, and, in fact, some of the genera have been dissolved because of the taxonomic situations previously indicated. In addition, among mycologists the importance of particular characteristics may be considered differently, so that one mycologist places a species in one genus and a second places it in another. Finally, a species may have been described a second time (or more) by a mycologist who was unaware of the original publication. In these cases the earliest name must be used, resulting in a name change if the earliest name is not being used.

AUTHORITY CITATIONS

The citation of authorities after the name of a species need not be a concern for those using or reporting on a species when publishing on biotechnological aspects of fungi, except in a case in which the species epithet in two names is the same but the cited authority is different. The name immediately following the species epithet (the second of the two names in the fungus name) refers to the person who originally described the species. If the name is not in parentheses, the name is just as the person described it. For example, *Poria subvermispora* Pilat was described by Pilat, and there have been no changes in this status. However, if the citation read *Ceriporiopsis subvermispora* (Pilat) Gilbn. et Ryv., it means that Pilat described the species with the epithet *"subvermispora"* in the genus *Poria* and that Gilbertson and Ryvar-

den believed that the species belonged in the genus *Ceriporiopsis* and made that transfer. Using either of these names is technically correct, but the generic placement in one may be preferable to the other because it places the species in the genus that contains the species that are perceived to be biologically most closely related.

The biotechnologist has little use for authority citations except when seeing species epithets that are the same but the first authority name following the species epithet is different, for example, *Hebeloma arenosa* MacFall versus *Sepultaria arenosa* Berk. This means that they are different species described by different mycologists, whether the name is in parentheses or not. Usually, authority citations are of use only to the mycologist, as a guide to who described the species. This leads the mycologist to the literature that addresses the species.

BROWN ROTTERS

In a discussion of white-rot fungi one must mention the usually recognized alternative, the brown-rotters. Brown-rot fungi are in the extreme minority of wood-decay species, with fewer than 125 known species in North America (Gilbertson, 1981), and even fewer have been considered for industrial application. One exception is *Gloeophyllum trabeum* (Fr.)Murr., which was inoculated into wood blocks that were then treated with termiticides (Esenther et al., 1961). The fungus in the treated blocks acted as an attractant to the termites. Unfortunately, the termiticides used were not ecologically acceptable and the technology is no longer in use. Soft-rotters can also be mentioned, but they have neither the demonstrated industrial importance nor the destructive capability of the other two types. The biological differences have been discussed by many authors over the years (Cowling, 1961; Highley, 1973; Kirk and Highley, 1973) but in most cases the older names were used for the fungi discussed.

PHANEROCHAETE CHRYSOSPORIUM

The white-rot species *Phanerochaete chrysosporium* (Figure 8.1) demonstrates several of the previously mentioned situations because of its somewhat unusual life cycle (Figure 8.2). It is in the minority of white-rot fungi in that it produces an anamorphic state. When the fungus was originally isolated from wood chips, the anamorphic (conidium forming) state was obtained. Lindgren and Eslyn (1961) and Eslyn (1967) identified the isolates as belonging lo the genus *Sporotrichum* Link. However, Carmichael's (1962) concept of the genus with these particular characteristics was called *Chrysosporium* Corda. But, in either case, no species determination was made. These genera are both anamorphic; that is, they are names for asexual states of fungi. In some cases the anamorph is the only state of the fungus known and its name is the only name for the fungus. However, in other cases the sexual state, the teliomorph, is also sometimes formed. It did form in cultures of isolates of this fungus. When the teliomorph formed in culture, it produced sterile structures,

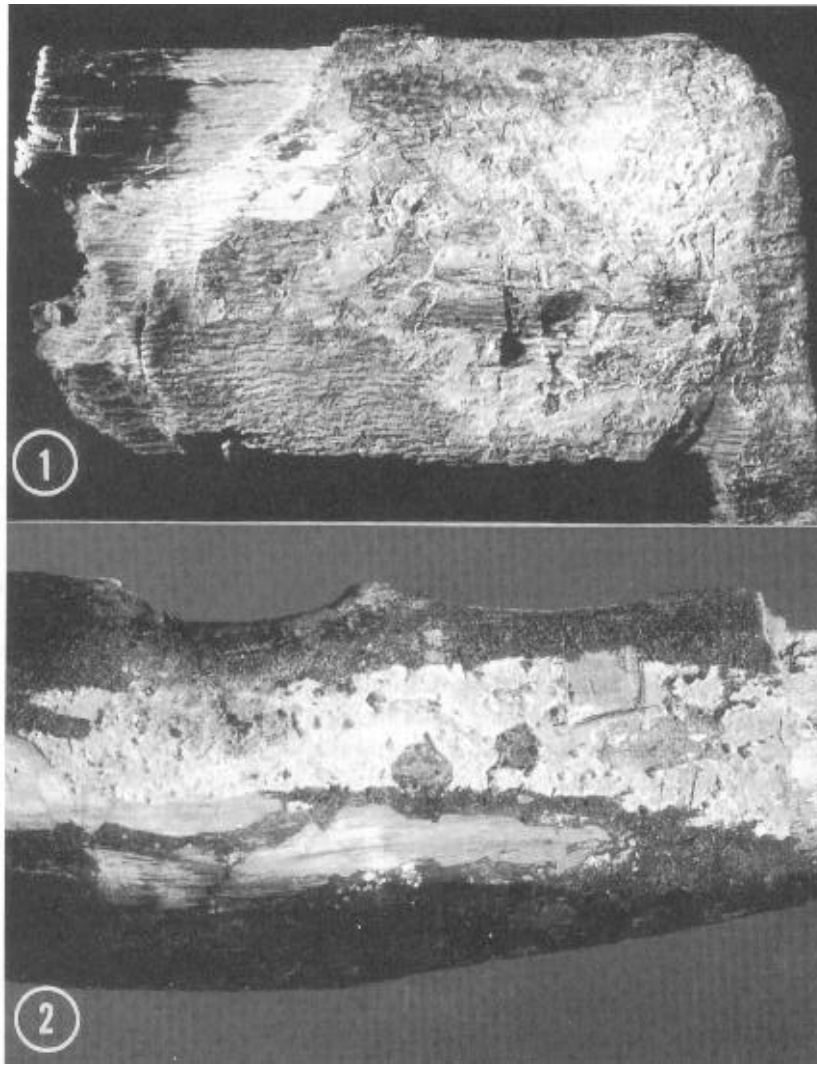

Figure 8.1 Photographs of basidiomes of white-rot fungi: (1) *Phanerochaete chrysosporium,* magnification = 2 ×; (2) *Phlebia subserialis,* magnification = 1.5 ×.

called cystidia, in the spore-bearing layer. Such fungi at that time were placed in the genus *Peniophora* Cooke by many mycologists. When data was reported for this fruiting isolate (Eslyn, 1967), no species epithet was used. It was merely reported as *Peniophora* "G". An examination of this species by Carmichael resulted in his applying the name the name *Chrysosporium pruinosum* (Gilman and Abbott) Carmichael to the anamorphic isolates. Nilsson (1965) isolated this same fungus and reported on it under the name *C. pruinosum.* He later decided that the species was

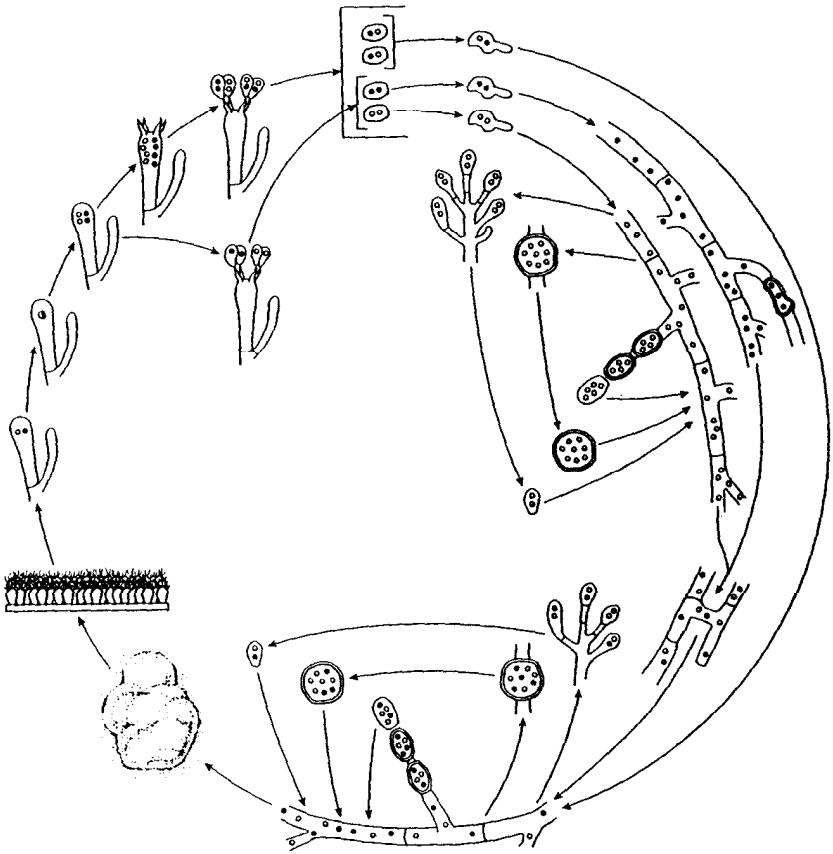

Figure 8.2 Life cycle of *Phanerochaete chrysosporium* showing the nuclear status of each state, assuming a heterothallic incompatability system.

different and described it as a new species, *Chrysosporium lignorum* (Bergman and Nilsson, 1966). Unfortunately, he did not publish the name validly. Thus, it has no status according to the International Rules of Botanical Nomenclature (1994) and cannot be used. Still later, the species was isolated but not recognized as *C. pruinosum* when Novobranova described it as a new species, *Sporotrichum pulverulentum* Novobranova (1972). This is a later name for *Sporotrichum pruinosum* Gilman and Abbott and, thus, merely a synonym (a later name for the same species).

With the exception of *Peniophora* "G", mentioned in the preceding discussion, all of the published names refer to the anamorph. However, when the teliomorph of a species is known, the correct name for the species is that of the teliomorphic state. Thus, with the publication of the name *Phanerochaete chrysosporium* Burds. (Burdsall and Eslyn, 1974), for the teliomorph, all of the names of the anamorph

become secondary. *Chrysosporium pruinosum* may still be used to refer to the anamorphic state, but the name of the fungus is that of the teliomorph, *P. chrysosporium.*

This concept is important because, just as the macroscopic characteristics are not effective in all cases to delimit related taxa (genera and species) of teliomorphs, the morphology of anamorphic states are not entirety dependable for associations to the teliomorphs. For example, the morphology of a particular anamorphic genus may be found in species with different teliomorphs.

OTHER IMPORTANT WHITE-ROT FUNGI

A number of species of white-rot fungi have found their way into industry or are being studied for their potential industrial application. Of these, the two best known and most intensively studied, *Lentinula edodes* (Berk.)Earle and *P. chrysosporium* are of vastly different applications. The former is of value for its edibility, and the latter because of numerous potential uses, ranging from biologically enhanced pulping of wood and bioremediation of contaminated soils to possible use in converting lignocellulosics into animal feeds (Akin et al., 1993). Several other fungi that have been well studied in regard to industrial application are *Ceriporiopsis subvermispora* (Pilat)Gilbn. et Ryv., *Phanerochaete sordida* (Karst.)Erikss. et Ryv., and *Trametes versicolor* (L:Fr.)Pilat.

Lentinula edodes illustrates a situation in which the morphological characteristics are suggestive of a genus that is biologically different. The basidiome possesses gills that are serrate on the edges, as found in the genus *Lentinus* Fr. However, the biology of *Lentinus* is significantly different. All of the species cause a brown-rot of wood, not a white-rot as with *Lentinula* Earle. A more critical examination demonstrates that the two genera differ in the types of hyphal systems and arrangement of the hyphae in the gill trama. They are similar in the same way that a panda is similar to a black bear, that is, similar at a superficial level but vastly different in other characteristics.

Because of the promising results of the studies of *P. chrysosporium* in the area of biopulping and soil bioremediation, related species are being investigated. This is possible because of the availability of current taxonomic studies (Burdsall, 1985; Nakasone et al., 1994). However, studying previously recognized species with cultural, isozyme, and molecular techniques reveals that there are a number of taxa that appear to be "complexes" of very closely related and difficult to distinguish species. This was discovered in the case of *P. filamentosa* (Berk. et Curt.) Burds. (Nakasone, et al., 1994) and is certainly the case with *P. sordida,* which is still under study. Present data from cultural and molecular studies of cultures named *P. sordida* suggests that several species are being addressed by the one name. Species in these complexes are so similar morphologically, and even microscopically, that other means are needed to distinguish them. Good examples of such complexes are the species *Sevtinostroma galactinum* (Fr.)Donk, which was found to be three morphologically nearly identical taxa, two species and a subspecies (Nakasone and Micales,

1988), and the brown-rotter, *Veluticeps abietina* (Pers.:Fr.)Hjort. et Telleria (Nakasone, 1990b), which was confused with the nearly identical *V. funbriata* (Ellis et Everh.)Nakas.

Another species with potential industrial importance is *Ceriporiopsis subvermispora* (Pilat)Gilbn. (Figure 8.3). It has been studied in respect to its potential as a biopulping agent and has been found to have excellent characteristics for this purpose. Because of the desirable results in energy savings observed in biomechanical pulping trials using *C. subvermispora* in early studies, Akhtar and co-workers examined two other species for the same effect. Although neither *C. rivulosa* (Berk. et Curt.) Gilbn. et Ryv. nor *C. pannocincta* (Rom.)Gilbn. et Ryv. were as effective at energy reduction, they did accomplish such reductions at a lower level. Such similarity in effect is expected because of their congeneric status, and there is the possibility (probability?) that other isolates of these species will be better at energy savings just as some isolates of *C. subvermispora* are better than others.

The genus *Ceriporiopsis* Dom. is a poroid genus of white-rot fungus (Figure 8.3). It is classified in the family polyporaceae along with other genera that possess a paired spore-bearing layer. This is unfortunate, because members of this genus are more similar to members of the corticiaceae than to other polypores. Thus, the taxonomic classification, because it is not well worked out in this group, does not serve the user effectively and requires a taxonomist knowledgeable in the taxonomic group to understand the relationships. Interestingly, the true relationship of *Ceriporiopsis* appears to be to *Phlebia* Fr. and somewhat less *so* to the genus *Phanerochaete* P. Karst. There is still some "hangover" in the modern classifications from the Friesian (the old system), such that the macromorphology still has significant impact on the taxonomic classification. Other evidence of this conservative attitude is the fact that the genus *Merulius* Fr. was recognized until Nakasone and Burdsall (1984) demonstrated its similarity to the genus *Phlebia* and placed it in synonymy and transferred the remaining two species into the genus *Phlebia* because of the nearly identical basiome micromorphology, similarity of cultural characters, identical mating system, and ability to cause the same type of wood decay, a white-rot. More recent molecular data has indicated that the species formerly placed in *Merulius* are "mainstream" *Phlebia* species (Nakasone et al., 1994). Interestingly, the former *Merulius tremellosus* Schrad.:Fr., now *Phlebia tremellosa* (Schrad.:Fr.) Nakas. et Burds., is a species with potential as a biological pulping agent (Reid and Seifert, 1982; Reid, 1989; Reid and Deschamps, 1991). *Phlebia incarnata* (Schw.)Nakas. et Burds. (= *Merulius incarnatus* Schw.) might also have that potential because of its close relationship. *Phlebia subserialis* (Bourd. et Galz.)Donk (Figure 8.1(2)) is another species that has demonstrated excellent potential as a biological pulping agent. In pulping tests, isolates of *P. subserialis* have performed very well and. in fact, may prove to be the best fungus for use in biologically assisted pulping (Akhtar et al., 1996). More work is needed to fully evaluate this species. However, it is interesting to note in this instance that another *Phlebia* species is proving to possess the desirable characteristics of use to biotechnologists, as would be expected. Consider also that there are many other *Phlebia* species that have not been studied with regard to this ability. Eventually, when the work of studying these

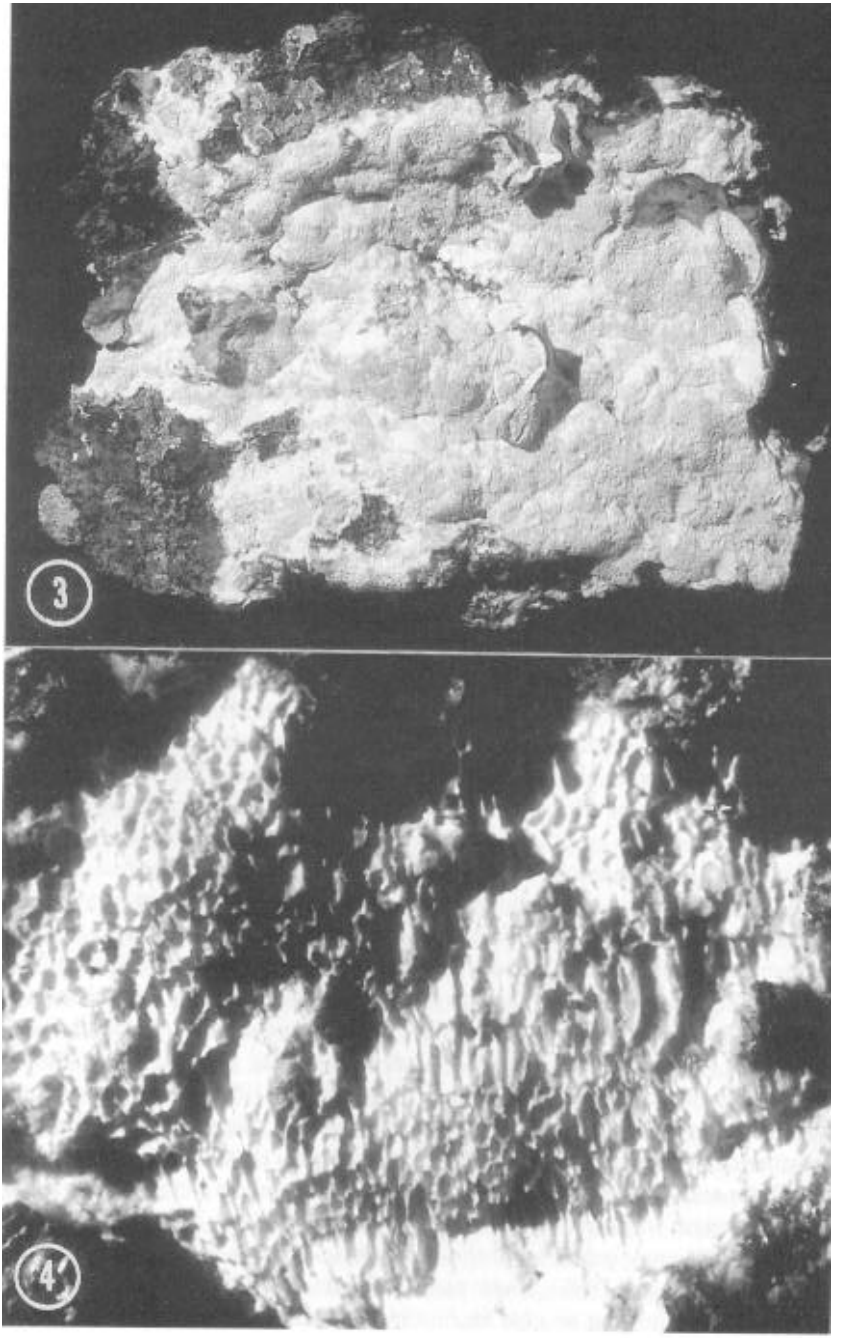

Figure 8.3 Photographs of basidiomes of *Ceriporiopsis subvermispora:* (3) magnification 1.25 × ; (4) magnification = 10 ×

species with the modern technology is complete, there is a likelihood that many of the genera in the polyporaceae and the corticiaceae will be moved to more correctly reflect their true relationships and the screening of these species for desirable characteristics will be more easily targeted.

Another group of industrially important white-rotters is the genus *Ganoderma* P. Karst. *Ganoderma* species may cause decay of living trees and roots, having an economic impact, though small, in that respect. Species of this genus are difficult to

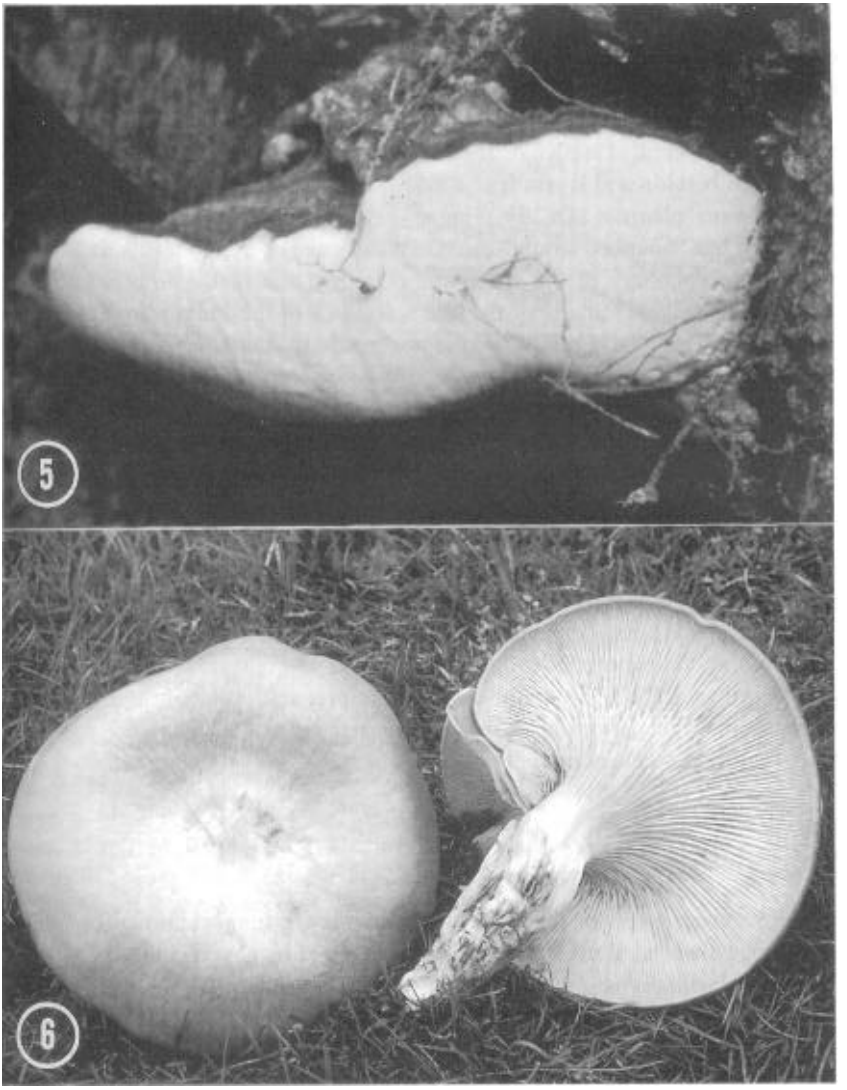

Figure 8.4 Photographs of basidiomes of white-rot fungi: *(5) Ganoderma australis,* magnification = 1 × ; (6) *Omplalotus olearius,* magnification = 0.25 ×.

distinguish, although species concepts of the recent past have proved to be too narrow. Species are delimited mainly on distributional characters, host, or substrate type, and on characteristics of the basidiospores, their size, shape, ornamentation, and color. *Ganoderma lucidum* (W.Curt.:Fr.)P. Karst. is known by the common name "zizhi" (Ji-Ding and Xiao-Quing, 1995) or "ling chi" (Stamets, 1993) in China and "reishi" among other less known names (Stamets, 1993) in Japan, and is said in mushroom literature of these countries to have medicinal qualities. Its possible other industrial utility is unknown. The species of *Ganoderma* have not been welt investigated for these purposes. However, a Southern Hemisphere species, *G. australe* (Fr.)Pat. (Figure 8.4(5)), decays some species of trees causing "huempe," completely delignified wood with the conservation of the cellulose. The potential of this capability in industrial application is obvious, but the phenomenon appears to be restricted to the association of *G. australe* and one tree species, under specific conditions (Martinez et al., 1995). For the identification of *Ganoderma* species in North America, Gilbertson and Ryvarden (1986) should be consulted.

Omphalotus olearius (DC.:Fr.)Singer (Figure 8.4(6)) is another example of a species that has "bounced around" taxonomically as generic concepts have changed. The gross morphology of the species is certainly that of the Friesian concept of *Clitocybe* Fr. However, many of the characteristics of the fungus are not those of a true *Clitocybe.* They have different micromorphology, including spore shape, hyphal composition, and hymenial elements, and their biology is distinctly different, with *O. olearius* causing a white-rot of wood while species of *Clitocybe* are mycorrhizal. The species concept is still under debate. This is an important concern because of the ability of the species to produce the chemical illudin S, a potentially important anticancer drug. Presently, it is not resolved whether *O. olearius* is the same species as *O. subilludens* (Murr.)H.E. Bigelow and C. illudens (Schw.)Sacc. Research is in progress to resolve this problem (R. H. Petersen, University of Tennessee, personal communication). One of the species formerly considered distinct, *O. olivascens* (Bigelow et al., 1976), has been found to be merely an ecological variant, as demonstrated by the complete compatibilily of matings in confrontations of single-spore isolates (Miller, VPI&SU, unpublished data in preparation). This sort of study and the employment of molecular techniques are necessary to resolve the species concepts of this and other industrially important taxa.

CONCLUSIONS

There are some aspects of taxonomy of the white-rot fungi that may be confusing to the user. However, it must be considered that just as new technology is bringing additional information and advances to the sciences using the fungi, it is also providing the means to make better and more useful taxonomic decisions in regard to these fungi. Such taxonomic decisions are absolutely necessary for conducting the most efficient screening of the fungi for effective application in biotechnology. The cooperation of taxonomists with biotechnologists will provide the information that both need to further their particular interests.

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