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FUNGICOLOUS FUNGI

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The term *fungicolous fungi* refers to species of fungi that consistently are associated with other fungi, including the lichenicolous fungi that consistently grow on lichens. The term is used even when the biological nature of the association and its trophic relationship are obscure (Jeffries 1995). Hawksworth (1981b) and others have spoken, for example, of "fungi growing on other fungi as parasites ('mycoparasites'), commensals, or saprobes. . . . The fungi may be 'necrotrophic' (destructive), or 'biotrophic' (forming balanced relationships)" (Hawksworth et al. 1995:172). Gilman and Tiffany (1952), Barnett (1963, 1964), and many others used the term for the totality of fungi associated with other fungi. However, fungicolous fungi (or mycophilic fungi) also have been restricted to those growing on sporocarps of other fungi or slime molds. Here we use the term sporocarp-inhabiting fungi (SCIF) to refer to the latter group.

Fungicolous fungi have been known for centuries (Ainsworth 1976). Various aspects of fungicolous associations and mycoparasitism have been reviewed many times in both the older and more recent literature (e.g., Buller 1924; Weindling 1938; Barnett 1963, 1964; Boosalis 1964; Madelin 1968; Barnett and Binder 1973;

Cooke 1977; Lumsden 1981; Baker 1987; Jeffries and Young 1994; Jeffries 1995). Jeffries and Young (1994) provided a highly readable survey of the general basis of mycoparasitism, including numerous examples of fungicolous associations categorized mainly according to the type of host–parasite interface, its physiological and ecological characteristics, and its applications in biocontrol. Since the 1980s, the taxonomy of fungicolous fungi has progressed considerably, particularly with many discoveries of anamorph–teleomorph connections in the Hypocreales, as well as discoveries of new mycoparasitic heterobasidiomycetes. Regional inventories mostly have been confined to taxa of SCIF (e.g., Helfer 1991). Besides published information, this chapter also refers to unpublished data available in the files of the Centraalbureau voor Schimmelcultures in Utrecht, The Netherlands (Anonymous 2001) with the designation "CBS, unpublished data."

Fungicolous and lichenicolous fungi are widespread in nature. Rudakov (1978), in his survey of fungicolous fungi, counted about 1700 (nonlichenicolous) species. He also inventoried fungicolous fungi (Rudakov 1981) occurring in the former Soviet Union, but many of his identifications need to be revised. In an exhaustive revision of the conidial fungicolous fungi, Hawksworth (1979a, 1981a) reported 1100 species on approximately 2500 species of host fungi (including lichens). Some 550 species of lichenicolous fungi were recognized in 1979, and their number now probably is more than 1500.

In this chapter, we do not cover the mere decomposers of fungi, and we ignore most of the unspecific colonizers of decaying substrata. Therefore, our admittedly incomplete estimates of numbers of fungicolous species are in some instances lower than those reported by Hawksworth (1981a) and Rudakov (1978). However, we incorporate new data that have become available only during the last two decades.

Wherever fungi are found, fungicolous fungi also are found. Fungicolous fungi are represented in many ecological categories, and the fungicolous mode of life has numerous variations. Those fungi play an important role in ecosystems through their detoxification of substrata not otherwise accessible to decomposition. In addition, many fungicolous fungi are economically important as biocontrol agents of plant-pathogenic fungi or as parasites that damage crops of edible fungi.

TYPES OF FUNGICOLOUS ASSOCIATIONS

Interspecific relationships between fungicolous fungi and their hosts can be characterized broadly as neutralistic, mutualistic, or antagonistic/competitive (Cooke and Rayner 1984). Different kinds of fungicolous associations are difficult to distinguish in the field, but mycoparasitism can be inferred when a colonized fungus shows signs of deformation. The term *mycoparasite* (Butler 1957) applies strictly to relationships in which one living fungus serves as a nutrient source for another, although this kind of nutrient flow rarely has been demonstrated (Jeffries 1995). Within that group, necrotrophic and biotrophic mycoparasites generally are distinguished from each other (Barnett 1963; Boosalis 1964; Barnett and Binder 1973; and many others). Biotrophs live in a balanced relationship with a living host, without causing it immediate, overt harm (reviewed by Manocha 1987, 1991), whereas necrotrophs kill the cells of the host. Some biotrophic parasites become necrotrophic in the later stages of a relationship and may cause at least some degeneration of the host when they begin to sporulate. Necrotrophic mycoparasites are relatively unspecialized and tend to have a broader range of fungal hosts than biotrophic mycoparasites, which also often form specialized infection structures (Jeffries 1995).

Biotrophic and necrotrophic mycoparasites are not sharply delimited, and many intermediate forms exist. Rudakov (1978) assigned fungicolous species to six groups: biotrophs, facultative biotrophs, necrotrophs, facultative necrotrophs, "semisaprophytic" mycophiles, and "saprophytic associates" (associated with mycophilic fungi without having antibiotic activity). Some mycoparasitic species change their behavior toward a host during the course of their development (Rudakov 1978, 1981), and other species (e.g., *Pythium oligandrum*) develop different types of contact structures on different hosts. Trophic relationships also may be host-dependent; many species grow as biotrophs on certain hosts but as necrotrophs on others. Species causing polypore and mushroom rot develop biotrophically in the hyphae of certain other filamentous fungi. *Hypomyces chrysospermus* (generally its anamorph, *Sepedonium chrysospermum*), for example, always causes necrosis of the cells of its mushroom hosts. It, however, can grow biotrophically inside the cells of fungi such as *Botrytis cinerea* and *Trichothecium roseum*, when the latter two species colonize a mushroom that it has already parasitized, or when it is grown with one of those fungi *in vitro* (Rudakov 1981).

A phenomenon termed *hyphal interference* (Ikediugwu and Webster 1970a; Dennis and Webster 1971c) occurs when the mycelium of one fungus, growing either close to (within 50 μm) or in contact with that of another species, reduces the growth rate and causes cytoplasmic disruption of the second fungus. Electron-microscopy studies have revealed vacuolation, or an abundance of

lipid droplets and invaginations of the host plasmalemma at the point of contact with the parasite—for example, when *Coprinus heptemerus* touches *Ascobolus crenulatus* (Ikediugwu 1976a), or *Phlebiopsis* (*Peniophora*) *gigantea* encounters *Heterobasidion annosum* (Ikediugwu 1976b). Similar vacuolation induced by *Fusarium oxysporum*, *Trichoderma viride*, and *Penicillium expansum* in hyphae of *Aspergillus niger* has been described (Park and Robinson 1964; Robinson and Park 1965). This very localized phenomenon usually has been observed only in dual culture *in vitro*.

The regular association between a fungicolous fungus and its host that has little visible effect on the host is termed commensalism (e.g., Jeffries and Young 1994; for lichenicolous fungi, Hawksworth 1988b). Mycoparasites growing on other fungi that are parasitic on either plants or animals have been called hyperparasites, but we confine this term to those fungi that parasitize fungicolous fungi.

Many arguments support the view that a semibiotrophic mode of parasitism (biotrophic organisms later becoming necrotrophic or saprotrophic) is more primitive in plant parasites than are holobiotrophy and saprotrophy (Cooke and Whipps 1980); that view may also be true of mycoparasitic fungi. Obligate parasitism may not be a belated evolutionary development, but a fundamental attribute of the primitive groups, from which saprotrophic subgroups have arisen repeatedly. Necrotrophic parasites that are facultatively saprotrophic, however, may in some cases have been derived from saprotrophs (Jeffries and Young 1994). It is evident that the specific associations between parasites and hosts are the products of a long coevolutionary process that is likely to be as old as the fungi involved (Hass et al. 1994).

Mycoparasite–Host Interface

The hyphae of a mycoparasite generally contact a host by hyphal apposition, by coiling around the hyphae, or by growth of short hyphal pegs. Appressoria and haustoria may or may not form, and the host hypha may or may not be penetrated. Coiling, which does not occur in all host–antagonist interactions, is not necessarily evidence for mycoparasitism. Penetration may occur immediately after hyphal contact in the absence of any coiling. Coiling occurs particularly in those cases in which some resistance to entry is encountered (Deacon 1976; Jeffries and Young 1994). Depending on the circumstances and the condition of the host, different structures may be produced by the same parasitic fungus (e.g., van den Boogert et al. 1989). Swart (1975) described a defense reaction, in which callosities, or wall thickenings, form around penetrating haustorial branches of *Verticillium dahliae* or *Fusarium solani* in the walls of sporangiophores of Mucorales and conidiophores of *Aspergillus*. The term *callosity* originally was applied to similar structures, also called lignitubers, that are produced by plants as a defense reaction against fungi (Young 1926). In a few cases, transmission-electron-microscopy studies have shown a micropore connecting the haustorium of the parasite and the host cell. A specific organelle of the parasite that facilitates nutrient exchange between the host and certain parasites is the colacosome or lenticular body (see "Urediniomycetes, Platygloeomycetidae" in the section on "Taxonomic Groups of Fungicolous Fungi and Fungus-like Microorganisms," later in this chapter).

Jeffries and Young (1994) and Jeffries (1995) distinguished five principal types of mycoparasite–host interfaces. The first two types are necrotrophic interfaces, and the other three types are biotrophic interfaces.

With *necrotrophic interfaces* the cytoplasm of the host degenerates, and hyphal lysis often occurs:

1. Contact necrotrophic. Neither hyphae nor haustoria of the parasite penetrate the host mycelium; it is damaged by hyphal interference. Examples include *Arthrobotrys superba* and *A. oligospora*, predaceous, nematophagous fungi that can also function as contact mycoparasites; *Tilletiopsis* species, which contact and kill cells of the powdery mildew *Sphaerotheca fuliginea*.
2. Invasive necrotrophic. Hyphae of the parasite penetrate the cell wall and enter the host cell; they show considerable growth within the host hyphae (Jeffries and Young 1994). Examples include *Talaromyces flavus*, *Schizophyllum commune*, *Trichoderma* species, and many others.

With *biotrophic interfaces* the host cytoplasm remains healthy (at least initially).

3. Haustorial. A short haustorial branch from the hypha of the parasite penetrates the hypha of a host. Examples include Mycoparasites among the Zygomycota and the Tremellales; *Sporidesmium sclerotivorum* parasitizing *Sclerotinia sclerotiorum*.
4. Fusion. Micropores develop in the walls of the host and parasite hyphae that are in contact or in the walls of a short penetrating hyphal branch of the parasite, allowing cytoplasmatic contact. This is an unusual type of interface. Examples include *Gonatobotrys simplex*, *Hansfordia parasitica*, *Melanospora zamiae*, and related fungi. *Tetragoniomyces uliginosus* on *Rhizoctonia solani* and *Syzygospora pallida* on *Phanerochaete* produce micropores in their haustoria.

Anchoring cells of *Parasitella parasitica* have a wide cytoplasmic connection with the host *Absidia glauca*.

5. Intracellular. The complete thallus of the mycoparasite enters a hypha of the host. Examples include many species of Chytrids and some Oomycetes growing inside other fungi.

Additional categories may be needed to accommodate commensal and gall-forming fungicolous associations. Lichenicolous fungi growing on a lichenized fungus exploit and often kill the associated alga, generally penetrating it with haustoria.

Determining the Mode of Interaction

The significance of mycoparasitism in nature has been underrated, although interfungal parasitic relationships likely play an important role in the development of fungal community structure. Mycoparasitism is difficult to observe in the field but can be assumed to occur in nature when growth abnormalities are seen in a host. In contrast, many examples of mycoparasitism have been described from laboratory cultures. Even the unequivocal demonstration of a parasitic association under laboratory conditions, however, does not prove that such a relationship occurs in nature (Jeffries 1995).

Infection structures can be observed in various ways. Preparations in water, lactic acid (better and safer than lactophenol) with cotton blue, or other standard mountants are appropriate for microscopic observation of fungi. Other stains, however, may do a better job of differentiating living from dead cells. For example, when agar blocks taken from paired slide cultures are stained with a drop of dilute phloxine, dead cells absorb the dye immediately, whereas living cells remain unstained for several minutes (Griffith and Barnett 1967). Specific organisms have been located by means of immunolabeled dyes (Mendgen and Casper 1980). Fluorescence methods also have been used to locate areas of great enzymatic activity or the locations of lectins (see "Mycoparasites of Mycelia, Ectomycorrhizae, Sclerotia, and Spores in Soil," later in this chapter). Infrared photomicrography also has been used to detect sites of strong enzymatic activity in the interaction between *Trichoderma harzianum* and *Rhizoctonia solani*; bright regions were visible in the coiling cells of the parasite in slide cultures (Elad et al. 1983b). Electron-microscopic investigations of infected host structures are also numerous.

In a few cases, the flow of nutrients from host to parasite has been proved definitively by means of radiolabeled compounds. ^{32}P was translocated from *Rhizoctonia solani* to the parasite *Arthrobotrys oligospora* (Olsson and Persson 1994). Foley and Deacon (1986) demonstrated that mycoparasitic *Pythium* species probably obtain carbon and nitrogen, as well as thiamine and sterols, from their host, with detrimental consequences for the host. Many mycoparasites can grow in culture without a host, but a number of contact biotrophs require at least host extracts for growth in culture. If axenic growth is possible, nutritional requirements for mycelial development of the parasite can be determined. Requirements for *in vitro* growth, however, are likely to differ from those of the fungus growing on a host. Dual cultures may represent a more natural system for physiological studies, but then the nutrient requirements of the host also must be determined, and the parasitized host may modify the nutrients in the growth medium before they are absorbed by the parasite. Moreover, the parasitized host may have nutrient requirements different from those of the unparasitized host (Jeffries and Young 1994).

The ability of some fungicolous fungi to reduce the growth rate of some test-host fungi before making contact has been interpreted as evidence of production of antibiotic metabolites, an effect that is strongly medium-dependent (e.g., Lerner and Sidorova 1978; Whipps 1987). Some efficient mycoparasites, such as *Acremonium strictum, Clonostachys rosea*, *Trichothecium roseum*, and *Sistotrema brinkmannii*, are able to overgrow other fungi without being inhibited themselves. After such an infection, the parasitized fungus usually cannot be recovered.

The effects of antibiotics and volatile substances on antagonist–pathogen interactions in dual cultures should be distinguished from the effects of temperature, water potential, and individual isolates (Whipps 1987; Jeffries and Young 1994). *Trichoderma* species exhibit various modes of interspecific interaction that are mediated by volatile and nonvolatile metabolites (Dennis and Webster 1971a, 1971b; Whipps 1987). Besides studying interactions in dual culture, those investigators grew potential antagonists of a particular fungus on cellophane disks placed on potato-dextrose agar and other media for a few days. After removal of the cellophane, the medium was inoculated with test fungus in the same spot, and the degree to which it was inhibited (if at all) was assessed. The action of volatile metabolites was assessed in Petri dishes inoculated with a host organism and then fastened opposite plates inoculated with the antagonist. Jackson and colleagues (1991) used this methodology to screen for potential biocontrol capacities of numerous soil isolates against *Sclerotium cepivorum*.

Lutchmeah and Cooke (1984) adopted a slide-culture technique to observe the parasitic action of *Pythium*

oligandrum microscopically. They coated large cover slips with water agar and inoculated opposite sides with blocks of potato-dextrose agar—cultures of the fungi to be tested. Interactions were observed usually for 1–1.5 hours at the margins of the sparse developing colonies by bright-field microscopy, using a 70 × oil-immersion objective. Laing and Deacon (1991), Berry and Deacon (1992), and Berry and associates (1993) thus beautifully illustrated the aggressiveness of *P. oligandrum* and *P. nunn* toward a range of hosts using electronically enhanced video-micrography.

The physiological bases of mycoparasitism are diverse. Necrotrophic mycoparasites often release toxins and lytic enzymes (particularly chitinase) into the environment, whereas no biotrophic types have been demonstrated to do so (Jeffries 1995). Rudakov (1978) grew each of nearly 200 species of fungicolous fungi in paired culture with a test host, looking for production of antibiotics (*in vitro* antagonism). He found that production of inhibitory metabolites was most pronounced in necrotrophs but also common in many fungicolous fungi that grow on macromycetes (e.g., Turner and Aldridge 1983; Bastos et al. 1986; Hoßfeld 1990). The production of inhibitory metabolites and wall-degrading hydrolytic enzymes is probably less important for fungi that can make physical contact with a host than it is for fungi whose hyphae do not directly infect a host (Jloba et al. 1980). Production of inhibitors may be positively correlated with intensity of pigmentation in *Hypomyces aurantius*, *H. odoratus*, and *H. rosellus* because strains with only weak pigmentation or none had no inhibitory effect (Lerner and Sidorova 1978). When a typically pigmented strain of *H. odoratus* was transferred to a medium that caused it to lose color, inhibitor production also decreased and interactions with test fungi were modified. Hypodoratoxide, a sesquiterpene eremophilane ether with phytotoxic properties, is a major component of the volatile metabolites of that species (Kühne et al. 1991). Toxins occurring in *Hypomyces aurantius*, *H. orthosporus* (anamorph *Cladobotryum orthosporum*), *H. semitranslucens* (*C. fungicola*), *Eudarluca caricis*, and *Sesquicillium microsporum* are also effective against various test fungi (Hoßfeld 1990).

Lawrey and associates (1994) examined selected hypocrealean fungi for their sensitivity to lichen metabolites. Subsequently, he (Lawrey 1995) reviewed data on the tolerance of lichenicolous fungi to secondary metabolites of lichens. Tolerance is a prerequisite for that mode of life. Some nonlichenized host fungi that contain acrid metabolites also are colonized by specific mycoparasites; it is likely that those metabolites are the selective agent determining which mycoparasites are present (see "On Fleshy Sporocarps of Boletales and Agaricales" under "Major Groups of Fungicolous Fungi, Arranged by Host Group," later in this chapter). Diverse mycoparasites can tolerate cyanide to levels of 0.01% in a synthetic medium, although this compound is not generally present in their natural substrata (Singh and Plunkett 1967).

Most mycoparasites are unspecialized and can infect a wide range of host fungi across diverse systematic groups. Not only can certain fungi parasitize other fungi belonging to diverse orders, but some are also entomogenous or nematophagous (see Chapters 18 and 19). More specific associations, however, also exist (see "Factors Determining Host Specificity," later in this chapter). Lichenicolous fungi, for example, generally are specialized and rarely have been observed to grow on nonlichenized host fungi. Several fungicolous fungi are hyperparasites of other fungicolous (see "Fungi on Sporocarps of Fungi or Myxogastrea," "Lichenicolous Fungi," and Aquatic Fungi and Fungus-like Organisms," later in this chapter).

The tremelloid *Aporpium caryae* has features of both Tremellales (cruciate basidia) and polypores (consistency of sporocarp). Setliff (1984) speculated that such an unusual morphology may have resulted from the horizontal transfer of genetic material from a host fungus to its mycoparasite. A similar hypothesis could be applied to many other tremelloid fungi. Bandoni (1984) argued, however, that Auriculariales–Aporpiaceae are closer to the Aphyllophorales than to the Tremellales, which may account for the morphological similarities among the groups. However, gene transfer from parasite to host has been demonstrated experimentally in the mucoralean association between *Absidia glauca* and its parasite *Parasitella parasitica* (Kellner et al. 1993; Wöstemeyer et al. 1995). In those species a plasmatic connection is established between a sikyotic ("sucker" or "anchor") cell of the parasite and the host (Burgeff 1924). The prototrophic parasite was found to compensate for artificially induced deficiencies in the host, compensation that became established in 0.4% of the uninucleate sporangiospores of the offspring. Transfer of a neomycin-resistance–conferring plasmid also was observed. Although the "pararecombinants" were unstable, such a natural gene transfer mechanism could have important evolutionary implications (Jeffries 1995).

TAXONOMIC GROUPS OF FUNGICOLOUS FUNGI AND FUNGUS-LIKE MICROORGANISMS

Although the fungicolous habit is widespread throughout the fungi, it is particularly common in certain taxonomic groups. We characterize those groups here. We

provide more detailed treatments of the fungicolous fungi in the section dealing with "Major Groups of Fungicolous Fungi, Arranged by Host," later. Table 17.1 gives estimates of numbers of species in these taxonomic groups, distributed over the five major ecological groups.

For some fungi, we include often-used generic names in parentheses after the presently correct genus, but we do not mean to imply that the previous genus as a whole is a synonym of the correct name given. We do not capitalize names suggesting class or ordinal rank, but consisting of very heterogeneous elements, such as heterobasidiomycetes and aphyllophorales. We also adopt the convention from Seifert and colleagues (2000) in regarding generic names of hyphomycetes in connection with "-like" as morphological terms rather than as formal generic designations and, therefore, neither italicize nor capitalize them.

Oomycota

One-celled members of the Olpidiopsidales (*Olpidiopsis*) and Rozellopsidales (*Rozellopsis* and *Dictyomorpha*) can form biotrophic associations with a diversity of other Oomycota (particularly Saprolegniales and Pythiales), some Chytridiomycetes, and many algae. Sparrow (1960) and Karling (1981) listed 18 and 22 fungicolous species, respectively, of *Olpidiopsis*, four of *Rozellopsis*, one of *Skirgiellopsis*, two of *Pythiella*, two and three of *Lagenidium*, one of *Myzocytium*, and one and three of *Petersenia*. With the exception of the endobionts of *Rozellopsis,* the endobiotic thalli of the taxa are surrounded by walls. The walled endoparasites usually form several zoosporangia in one compartment of the host, which is hypertrophied considerably. Only a single thallus of the wall-less endoparasites forms in a host compartment, which then is delimited by a septum induced in the host. The species of *Rozellopsis* known to have naked thalli fall into several groups analogous to the subgroups composing the genus *Rozella* (Held 1981).

In the soil several specialized species of *Pythium* parasitize some congeneric plant pathogens, as well as other fungi. In particular, the four *Pythium* species with spiny oogonia (i.e., *P. oligandrum*, *P. acanthicum*, *P. periplocum*, and *P. acanthophoron*) are mycoparasitic, as are two species with smooth oogonia (*P. nunn* and *P. mycoparasiticum*). Those species differ from the plant-pathogenic *Pythium* species in that they require organic nitrogen and thiamine for growth; they are noncellulolytic and thus can play the role of "secondary sugar fungi,"—that is, they profit from a surplus of reducing sugars liberated by cellulolytic fungi from cellulose (Foley and Deacon 1986; Jones and Deacon 1995; Ribeiro and Butler 1995). In addition, zoospores of the mycoparasitic species tend to encyst on chitinous substrata, whereas those of plant-pathogenic species preferentially encyst on cellulose; the form of cyst attachment is a particularly sensitive indicator of taxonomic affinity and determines host–parasite specificity (Deacon 1988a; Jeffries and Young 1994)

Hyphochytridiomycota

Two genera of Hyphochytridiales, *Hyphochytridium* and *Rhizidiomyces*, include one and two species, respectively, that parasitize oospores of *Phytophthora* species.

Plasmodiophoromycota

A few species of *Woronina*, *Octomyxa*, and *Sorodiscus*, in the Plasmodiophorales parasitize species of the Oomycota (genera of the Saprolegniales and *Pythium*). They form intracellular naked plasmodia and later transform into cystosori and sporangiosori (Batko 1975; Held 1981).

Chytridiomycota

One-celled members of the Chytridiomycota live in either intracellular or epibiotic parasitic associations, mostly with algae, occasionally with other Chytridiomycota and Oomycota, and rarely with Zygomycota. They cause some host fungi to hypertrophy. Epibiotic taxa of *Caulochytrium* and *Sparrowia* grow on a diversity of hosts (Karling 1977). Endobiotic taxa form an intracellular thallus that either is surrounded by a wall ensheathed in the endoplasmatic reticulum of the host (e.g., *Catenaria allomycis* in *Allomyces*, Sykes and Porter 1980; Powell 1982), or is naked (e.g., *Rozella allomycis* in *Allomyces*, Karling 1942; Held 1981; and *Rozella polyphagi* in *Polyphagus euglenae*, an ectoparasite on flagellates, Powell 1984). The naked endobionts consume part of the host cytoplasm by phagocytosis. Their thallus is surrounded only by the plasmalemma, which disintegrates when sporogenesis of the parasite begins, leaving the mature endoparasitic thallus in direct contact with the host cytoplasm. The developing thallus induces a septum to form in its vicinity so that each compartment of the host contains only one zoosporangium. The segmented host of *R. allomycis* then appears to have multiple infections (Held 1980). When *R. allomycis* first invades an *Allomyces* hypha, it elicits a host reaction at the site of penetration. The host forms lomasomes to which wall material is apposed giving rise to an internal papilla. The parasite enters through the center of the

TABLE 17.1
Approximate Numbers of Species Known from Orders Containing Fungicolous Fungi*

Taxon	Sporocarp-inhabiting	Lichenicolous	Biotrophic plant parasites	Hyphal parasites	Aquatic	Total†
Oomycota				11	37	43
Hyphochytriomycota				2	3	3
Plasmodiophoromycota					3	3
Labyrinthulomycota				1		1
Chytridiomycota				3	50	50
Zygomycota						
Mucorales	10					10
Zoopagales				50		50
Dimargaritales				13		13
Ascomycota (and associated anamorphs)						
Saccharomycetales	12					12
Leotiales	40	67				107
Ostropales		22				22
Patellariales		3				3
Pezizales	2	1				2
Eurotiales	5			1		6
Chaetothyriales	5	10				15
Pyxidiophorales	15			2		17
Arthoniales		150				150
Caliciales‡		44				44
Verrucariales		191				191
Dothideales	10	224	30			264
Lecanorales		112				112
Pyrenulales		1				1
Ophiostomatales	6					6
Trichosphaeriales		1				1
Xylariales		1				1
Sordariales	58	37				95
Hypocreales (excl. Clavicipitaceae)	185	59	3			247
Clavicipitaceae	18	4	4	5		22
Phyllachorales		26				26
Ascomycetes incertae sedis		84				84
Ascomycetous conidial fungi	30	198	27		1	256
Basidiomycota						
Urediniomycetes	92				1	93
Ustilaginomycetes		4	8			12
Tremellales	120	50				170
Aphyllophorales	15	2		3		19
Boletales	3	1				4
Agaricales	15	3				18
Basidiomycetous condial fungi	2					2
TOTAL	643	1295	72	91	95	2175

* Numbers of species/genus taken from Hawksworth et al. (1995) and Lawrey and Diederich (2003), plus some additional observations; lichenicolous fungi do not include lichenized species.
† Because some fungi occur on multiple substrata, totals may be less than the sum of the columns in a particular row.
‡ The Caliciales are no longer accepted, but are considered to be a synonym of the Lecanorales; some species previously included in the Caliciales are now placed in the Mycocaliciales or in the Microcaliciaceae family incertae sedis.

papilla with minimal cell disruption. The reaction does not occur in hyphae that already are infected, so renewed penetration by the parasite cannot occur (Held 1972). Held (1981) assigned the 25 known mycoparasitic species of *Rozella* to five groups according to morphology and host affinities. The groups consisted of fungi parasitic on (1) monocentric Chytrids, (2) *Blastocladia* and Leptomitales, (3) *Monoblepharis* and Pythiaceae, (4) *Allomyces* and Saprolegniaceae, and (5) miscellaneous hosts. Sparrow (1960), Karling (1960, 1977), and Batko

(1975) described and illustrated about 45 potentially mycoparasitic taxa (Table 17.2).

ZYGOMYCOTA

Obligate, biotrophic, contact parasites are found in the orders Zoopagales and Dimargaritales. These haustorial mycoparasites grow on other members of the Mucorales or, exceptionally, on nonmucoralean fungi (Benjamin 1979). The mycoparasites and some unrelated saprotrophic groups sometimes are combined in an unnatural group of "merosporangiferous Mucorales." The biotrophic zygomycete associations have been reviewed by Jeffries (1985) and Jeffries and Young (1994).

On contact, the mycoparasite forms an haustorium that induces gall formation in the host. Burgeff (1924) noted that mating type factors often determine the compatibility of a host and its parasite. He also observed plasmatic continuity between a sikyotic cell (contact cell) of the parasites *Parasitella parasitica* and *Chaetocladium brefeldianum* and their hosts.

The order Zoopagales includes numerous endoparasites, as well as predators of amoebae, nematodes, and other small animals. Members of the family Piptocephalidaceae are obligate haustorial mycoparasites (Fig. 17.1A,B). *Piptocephalis* and *Kuzuhaea* species are purely biotrophic, forming small haustoria in the host cell. *Piptocephalis xenophila* can grow on *Penicillium* species and *Chaetomium* species (Dobbs and English 1954; Shigo 1960b), but all other species in the family grow only on Mucorales *sensu lato*. When inoculated on suitable host fungi (e.g., *Umbelopsis* [*Mortierella*] *isabellina*), they develop best on media containing sources of organic nitrogen and a low concentration of sugar (Berry 1959). The haustoria are enucleate and delimited from the host cytoplasm by a very thin layer of electron-transparent wall material (Jeffries and Young 1976).

Host morphology hardly is affected by species of *Piptocephalis,* apart from an increase in branching and a decrease in marginal density of the hyphae (Evans and Cooke 1981), but overall growth of the host can be inhibited. Other parasitic species stimulate growth of certain host species (Curtis et al. 1978); such cases are assumed to be mutualistic. Axenic growth of *P. virginiana* on a malt extract-yeast extract medium was very limited, and the culture could not be maintained (Manocha and Deven 1975). Apparently *P. virginiana* can only parasitize fungi in which the concentration of linolenic acid exceeds a certain threshold, although other nutrients also are required (Manocha and Deven 1975). Trehalase activity in sporelings of the parasite increases during the interaction, indicating that trehalose reserves of the host may be exploited by the parasite (Evans et al. 1981).

Syncephalis species are more necrotrophic than *Piptocephalis* species (Hunter et al. 1977). They form a highly branched haustorial system in the hypha of the host and impair its growth and sporulation (Fig. 17.1B). Axenic cultivation of *S. californica* succeeded after transfer from a monoxenic culture onto a liver medium (Emerson 1958; Ellis 1966).

The order Dimargaritales comprises the mycoparasitic genera *Dimargaris* (Fig. 17.1C), *Dispira,* and *Tieghemiomyces. Dispira cornuta* (Ayers 1935; Brunk and Barnett 1966) is a biotrophic parasite that forms nucleate haustoria from gall-like swellings and is found on rat dung. It grows on *Mucor* species and other Mucorales but not on *Mortierella*. It can be grown axenically on media rich in proteins, with the addition of growth factors (Kurtzman 1968; Barnett 1970; Barker and Barnett 1973; Singh 1975). *Dispira simplex* and *D. parvispora* grow on *Chaetomium;* the latter also grows on *Monascus* species. As far as is known, the Dimargaritales cannot utilize glucose; axenic growth requires glycerol, organic nitrogen, and some vitamins (Brunk and Barnett 1966; Kurtzman 1968; Barnett 1970). Singh (1975) found an exceptional strain of *D. cornuta* for which starch was the best carbon source.

TABLE 17.2
Numbers of Mycoparasitic Chytridiomycota Taxa*

Chytridiales
Chytridiaceae
Chytridium—3, 1, 3†
Chytriomyces—1, 4, 5
Rhizophydium (incl. *Phlyctidium*)—9, 3, 2
Phlyctochytrium—3, 1, 0 (parasites in Glomales recognized later, see Sylvia and Schenck 1983)
Blyttiomyces—2, 2, 1
Rhizidium—0, 2, 1
Septosperma—2, 2, 2
Solutoparies—1, 1, 1
Sparrowia—0, 1, 1
Spizellomycetales
Olpidiaceae
Olpidium (incl. *Pleotrachelus*?)—5, 5, 4
Spizellomycetaceae
Rhizophlyctis—1, 1, 0
Caulochytriaceae
Caulochytrium—1, 1, 1
Blastocladiales
Catenariaceae
Catenaria—1, 2, 1
Rozella‡—19, 3, 16

* Classification modified according to Barr (1980) and Hawksworth et al. (1995).
† The three numbers given represent taxon estimates from Sparrow (1977), Karling (1977), and Batko (1975), respectively.
‡ The placement of *Rozella* in this order is debated; three additional species of *Skirgiellia* are close to this genus (Batko 1975).

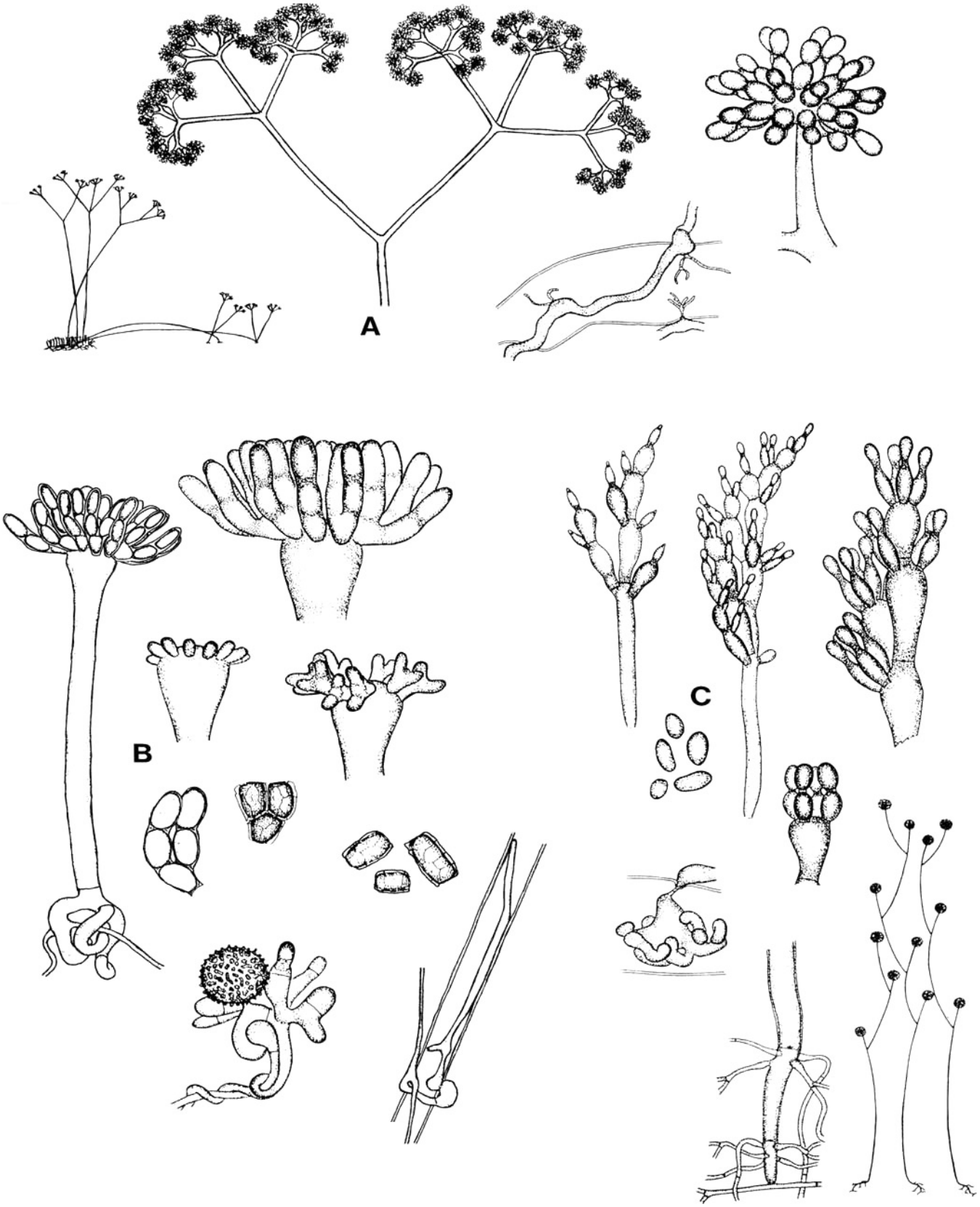

FIGURE 17.1 Biotrophic mycoparasites from the Piptocephalidaceae and Dimargaritaceae. **A.** *Piptocephalis lepidula*, habit sketch of colony, sporangiophore with merosporangia; hypha of the parasite overgrowing the host hypha forming minute branched haustoria. **B.** *Syncephalis nodosa*, sporangiophores with merosporangia, a zygospore, and hypha in contact with a *Mucor* host, showing appressorium and extended haustorium. **C.** *Dimargaris cristalligena*, habit sketch of sporangiophores, details of sporangiophore head with sporiferous branchlets, complex haustorium inside host hypha. (All reprinted with permission, from Benjamin 1959.)

Nonspecific mycoparasites growing on other Mucorales also are found among the Mucoraceae (*Parasitella parasitica* and *Absidia parricida*), Thamnidiaceae (*Chaetocladium*), and Mortierellaceae. Species of *Spinellus, Syzygites,* and *Dicranophora* (all Mucoraceae) parasitize agarics. Axenic cultivation of *Spinellus* requires organic nitrogen and temperatures near or below 20°C; its spores require chemical stimulants from host extracts or ascorbic or gluconic acid to germinate (Watson 1962, 1965; Jeffries 1985; Jeffries and Young 1994). *Syzygites*, however, grows easily on any culture medium (Hesseltine 1957), as does the weakly parasitic *Chaetocladium* (Benny and Benjamin 1976). *Parasitella parasitica* is a weak parasite of various Mucoraceae, Thamnidiaceae, and Choanephoraceae, which it contacts by means of a kind of capturing hypha (Burgeff 1924; Zycha et al. 1969). The genus *Mortierella* comprises highly chitinolytic fungi that often appear indiscriminately on old fungal sporocarps; exceptions are the more specific *M. bainieri,* which commonly is found on *Amanita* species, and *M. armillariicola,* which is known only from *Armillaria* species.

ASCOMYCOTA

Orders Rich in Fungicolous Fungi

Laboulbeniales. Pyxidiophoraceae. In contrast to the majority of Laboulbeniales, which is associated with insects, the genus *Pyxidiophora* (anamorphs in *Gabarnaudia* or *Chalara*) is heteroxenous, which means that some of its species are able to change hosts during their life cycles (Malloch 1995). Most species are biotrophic mycoparasites that parasitize their hosts by means of noninvasive contact cells. Their ascospores generally are translocated by mites, and the fungus can penetrate its vector with haustoria (Lundqvist 1980; Malloch and Blackwell 1993a; Blackwell 1994; see "Spore-Dispersal Interactions" in Chapter 18). *Gabarnaudia tholispora* is a common fungicolous anamorph species, the teleomorph of which has not yet been established. *Pleurocatena acicularis*, which can be found in association with *Hypocreopsis,* probably also belongs to this family (G. Arnold, personal communication). An unnamed *Pyxidiophora* (CBS 665.93 and 626.94) can be grown on *Cylindrocarpon destructans* but usually not axenically (G. Fischer and W. Gams, unpublished data).

Leotiales. Species of *Orbilia,* in the family Orbiliaceae (mainly *O. inflatula*), are found on stromata of ascomycetes and even more frequently on decaying basidiomata of aphyllophorales. *Orbilia* species have anamorphs in the genera *Arthrobotrys*, *Dactylella*, *Dicranidion*, and others. The *Arthrobotrys* anamorphs are mainly nematophagous but also mycoparasitic, whereas *Dactylella* includes only nonnematophagous species, some of which have been described as parasites of fungal oospores (Rubner 1996). The genus *Helicogonium,* originally erected for two mycoparasites of Stereales, has been expanded to cover 15 species growing on inoperculate discomycetes, a situation in which their asci easily are mistaken for a deviating form of the host asci (Baral 1999). The genus is classified in the Leotiales, although the species lack discrete ascomata. The genus *Unguiculariopsis,* in the family Helotiaceae, includes at least 24 species, all of which grow on fungi; 10 of those species also grow on lichenized ascomycetes. The species of *Llimoniella* (six species), *Rhymbocarpus* (nine species) and *Skyttea* (17 species) are all lichenicolous (Diederich and Etayo 2000).

Chaetothyriales. Herpotrichiellaceae. *Capronia* (Untereiner et al. 1995) comprises four fungicolous species commonly found on pyrenomycetes, plus at least five lichenicolous species (Aptroot et al. 1997). Anamorphs of these fungi mainly belong in the genus *Exophiala*.

Sordariales. The Ceratostomataceae (Melanosporaceae), as revised by Cannon and Hawksworth (1982), includes many mycoparasites (Table 17.3). Anamorphs of this family comprise *Harzia* (synonym *Acremoniella*),

TABLE 17.3
Mycoparasitic Teleomorphic Ceratostomataceae and Their Hosts

Parasites	Hosts
Melanospora species	Various discomycetes, *Fusarium*, *Botrytis*, *Paecilomyces*, *Beauveria*, *Tuberculariа* species, and several aphyllophorales
Persiciospora species	*Fusarium* species
Sphaerodes species*	*Labyrinthomyces* and *Sphaerozone* species (truffle genera) *Hypomyces armeniacus* *Sclerotinia sclerotiorum* and *Trametes* species
Syspastospora parasitica (= *Melanospora parasitica*)	*Paecilomyces*, *Beauveria*, *Hirsutella*, and *Verticillium* species
Sphaeronaemella helvellae	*Gyromitra* species
Viennotide fimicola†	*Ascobolus* species

* *Microthecium* in part, see also Hawksworth and Udagawa (1977).
† Other species of *Viennotidea* (formerly merged with *Sphaeronaemella*, anamorph *Gabarnaudia*) apparently are not fungicolous.

Gonatobotrys, Nematogonum, Gonatobotryum, Olpitrichum, and *Papulaspora,* which are mainly mycoparasitic and commonly associated with an aspergillus-like hyaline, phialidic synanamorph (*Proteophiala*). The best-studied anamorphic biotrophic contact mycoparasites are in that group: *Gonatobotrys simplex* (teleomorph *Melanospora damnosa*), heterothallic and fruiting *in vitro* (Vakili 1989); *Nematogonum ferrugineum* (synonym *Gonatorrhodiella highlei*); and *Gonatobotryum fuscum*. Species of *Gonatobotrys, Gonatobotryum,* and *Nematogonum* were revised by Walker and Minter (1981). Another well-studied species, *Hansfordia* (*Calcarisporium*) *parasitica,* may be related to the Xylariales; it is unusual in that it develops 0.2–1.0-µm-wide pores at the point of contact with its host fungi (Hoch 1977a). Some of the ecologically obligate mycoparasites can be grown axenically on media with thiamine, biotin, and fungal extracts that contain mycotrophein (Gain and Barnett 1970; Calderone and Barnett 1972; Barnett and Binder 1973; Hwang et al. 1985). Mycotrophein, found in extracts of various fungal cultures, is a mixture of tetraethyleneglycol and pentaethyleneglycol mono-(nonylphenyl) ethers. It may act as carrier of a biologically active factor (Hwang et al. 1985).

Gonatobotrys simplex normally grows on *Alternaria* and *Cladosporium* species (Whaley and Barnett 1963; Hoch 1977b). It contacts a host by means of fingerlike branches (Hoch 1977b). Its nutritional requirements have been analyzed by Whaley and Barnett (1963). *Gonatobotryum fuscum* can grow on *Polyporus, Poria, Ganoderma, Tremella, Leptographium, Hypocrea,* and *Hypomyces* species (Shigo 1960a, 1960b; Calderone and Barnett 1972; Walker and Minter 1981). Jordan and Barnett (1978) found similar biotrophic relationships in *Melanospora zamiae* and also showed that the parasite can withdraw all required nutrients from washed host mycelium; mycotrophein is not required. The biotrophic contact parasite *Hansfordia parasitica* has similar requirements. It shows a unique mutualistic relationship with *Graphium fuscum*. Under certain circumstances, the parasitic relationship of *H. parasitica* with its hosts can be reversed, and old aerial mycelium and conidiophores are overgrown and attacked by the *Graphium*. The parasite produces pyridoxine and the host biotin; each partner requires the compound produced by the other (Shigo 1960a; Barnett 1968). *Stephanoma phaeosporum* is a biotrophic contact mycoparasite of *Fusarium* species and 14 other fungi (Butler and McCain 1968; Rakvidhyasastra and Butler 1973; Hoch 1978; Hawksworth 1981a). It also can be grown axenically with fungal extract, but its dependence on mycotrophein is uncertain. *Olpitrichum tenellum* is a contact mycoparasite of *Fusarium* species and various dematiaceous hyphomycetes. It first was discovered on *Fusarium moniliforme* on maize ears in Illinois (Kuykendall et al. 1983); it requires thiamine and biotin, but not mycotrophein, for axenic growth.

In several genera of Sordariales, including *Globosphaeria, Lasiosphaeriopsis, Reconditella, Rhagadostoma, Roselliniella, Roselliniomyces,* and *Roselliniopsis,* all species are lichenicolous.

Hypocreales. The order Hypocreales consists of the families Hypocreaceae, Nectriaceae, Bionectriaceae, Clavicipitaceae, and Niessliaceae. The former three families were partly revised by Rossman and colleagues (1999). The positions of the Clavicipitaceae and Niessliaceae relative to the other families are not yet settled. A large portion of hypocrealean fungi is mycoparasitic or mycosaprotrophic, a fact that often is unrecognized (Rossman et al. 1999). They are extremely versatile in their abilities to exploit fungal substrata (Rossman 1996). A key to 24 genera of the Hypocreales known to contain one or more fungicolous, lichenicolous, or myxomyceticolous species can be found in Samuels (1988), although some of the poorly known genera may not actually belong to the order.

Hypocreaceae. Within the family Hypocreaceae, *Hypocrea* is reported less frequently as a mycoparasite than are its anamorphs in *Trichoderma*. However, the genus includes fungicolous species that are either host-specific or occur on a variety of aphyllophorales in addition to woody substrata. Several *Trichoderma* species are polyphagous mycoparasites. The species are difficult to distinguish from each other on morphological grounds, even using the most refined criteria (Bissett 1991b; Gams and Bissett 1999). Strains of *T. harzianum* that are beneficial biocontrol agents of plant pathogens can hardly be distinguished microscopically from genetically distinct strains that are aggressive competitors of the cultivated mushroom (Muthumeenakshi et al. 1994). A related species, *T. virens,* was distinguished clearly from other *Trichoderma* species by Webster and Lomas (1964) and redescribed as a member of *Gliocladium,* but it is unrelated to other species of that genus and is best classified in *Trichoderma* (Bissett 1991b; Rehner and Samuels 1994) as *T. aggressivum*. In view of the poor differentiation of these anamorphs, accurate reference to the strain used in experiments with *Trichoderma* is crucial.

Generally, *Trichoderma* species produce a great diversity of secondary metabolites (Ghisalberti and Sivasithamparam 1991) that, in addition to their enzymatic actions, antagonize host fungi over some distance, causing cell vacuolization, collapse, and disintegration of the cytoplasm. A volatile fungal inhibitor from *T. harzianum* has been identified as an alkyl pyrone

(Claydon et al. 1987). Peptaibols are a class of potent polypeptide antibiotics, commonly found in species of *Trichoderma, Gliocladium,* and *Clonostachys,* and the often-observed bursting of hyphal tips induced by *Trichoderma* has been ascribed to such compounds (Brückner and Przybylski 1984; Brückner et al. 1989). The mycoparasitic interaction between *T. harzianum* and *Lentinula edodes* on agar has been characterized as (1) parasitic contact, (2) direct penetration of host cells, and (3) production of diffusible toxic agents prior to physical contact (Hashioka et al. 1961; Hashioka and Komatsu 1964; Komatsu and Hashioka 1964; Hashioka and Fukita 1969; Komatsu 1976; Tsuneda and Thorn 1995). In contrast with other species of the genus, *T. virens* produces gliotoxin, which has a very specific fungitoxic effect (Weindling 1941; Webster and Lomas 1964).

Several species of *Hypocreopsis* are known to be fungicolous, including *H. lichenoides,* which occurs with species of *Hymenochaete* on tree bark (Cauchon and Ouellette 1964), and *H. xylariicola,* found on old perithecia of *Xylaria* species (Samuels 1988). The *Hypocreopsis* species cannot be cultured, and their physiology is unknown.

The genus *Hypomyces* comprises the most characteristic mycoparasites on macromycetes (Fig. 17.2). The genus is heterogeneous (Rogerson and Samuels 1994; Põldmaa 2000). Some species colonize host sporocarps systemically, are not known to have an anamorph, and produce ascospores that do not germinate *in vitro* (Fig. 17.3). Other species cause decay of sporocarps in various stages of development, form copious anamorphs, and grow easily in culture (Fig. 17.4). Ecological and morphological differences may justify the recognition of several genera (Põldmaa 2000). Species of *Hypomyces* can be grouped according to host type (viz., discomycetes, boletes, aphyllophorales, or agarics) but members of the last two groups overlap. The largest number of *Hypomyces* (23 species) parasitizes aphyllophorales and are not usually host-specific (Rogerson and Samuels 1993, 1994; Põldmaa 1999, 2000). Anamorphs, which originally were distributed among 12 genera, are confirmed for most of these species. *Hypomyces* species that parasitize boletes or agarics tend to be specific to a host family or genus (Rogerson and Samuels 1989; Sahr et al. 1999).

Rogerson and Samuels (1993) combined most anamorphs of agaricicolous and aphyllophoricolous *Hypomyces* species, including species of *Arnoldiomyces, Eurasina, Helminthophora, Pseudohansfordia, Sibirina, Sympodiophora,* and part of *Trichothecium,* in the expanded anamorph genus *Cladobotryum* (Figs. 17.2 to 17.4). The phialidic anamorphs of other species are mostly verticillium-like. Chlamydosporic or aleurial or bulbillar synanamorphs often are formed and classified in the genera *Sepedonium, Mycogone, Blastotrichum, Stephanoma*, or *Papulaspora*. The dormant aleurioconidia can be activated by basidiome tissue or extracts from several basidiomycete species (Holland and Cooke 1990).

Several smaller genera that share characters with species of *Hypocrea* and/or *Hypomyces* also contain fungicolous species. Most of the members of *Sphaerostilbella* (anamorphs *Gliocladium* sensu stricto) grow mainly on *Stereum* species (Seifert 1985). *Sporophagomyces* (anamorph acremonium-like) (Fig. 17.5) is characterized by a subiculum that traps hosts basidiospores, which obviously serve as source of nutrients. The hosts are mostly members of the Ganodermataceae (Põldmaa et al. 1999). *Arachnocrea*, *Protocrea,* and *Podostroma* also include fungicolous species, but whether these genera are distinct from *Hypocrea* is dubious, and their taxonomy currently is being revised.

Nectriaceae. *Nectria* was, until recently, a vast and heterogeneous aggregate that now is subdivided into several distinct genera (Rossman et al. 1999). Most of the approximately 60 species of *Cosmospora* (formerly *Nectria* subgenus *Dialonectria* = *N. episphaeria*-group) generally are fungicolous (Rossman et al. 1999). The most conspicuous species occur on carbonized perithecia of pyrenomycetes, most notably members of the Xylariales and Diatrypales, and less frequently on loculoascomycetes; one species is found on a discomycete. A few species that have been collected repeatedly are known to be restricted to certain host fungi. Cosmospora leptosphaeriae, for example, occurs mainly on *Leptosphaeria* and *C. coccinea* (synonym *Nectria cosmariospora*) on polypores (Samuels et al. 1991).

Bionectriaceae. The family is centered around *Bionectria,* the former *Nectria ochroleuca* group (Booth 1959; Schroers et al. 1999; Schroers 2000, 2001). The genus is comprised of a series of destructive fungicolous species with anamorphs in *Clonostachys* (*Gliocladium* sensu lato, particularly *C. rosea* and related species). The *Nectria* species with *Sesquicillium* anamorphs now also are classified in *Bionectria* (Schroers 2001). Some of them are fungicolous (Samuels 1989). A group of morphologically similar mycoparasitic pyrenomycetes with yellow perithecia (five fungicolous and seven lichenicolous species, from the genera *Hypocreopsis, Nectriopsis, "Nectria", Ijuhya* [synonym *Peristomialis*]), and *Trichonectria*) was revised by Samuels (1988); the *Nectria* species of that study are now classified in *Hydropisphaera* and *Bionectria*. *Pronectria* (14 species) is mostly lichenicolous (one algicolous species known). The three species of *Paranectria* are all lichenicolous.

Nectriopsis includes 39 species, although they are somewhat heterogeneous. Most of them grow on

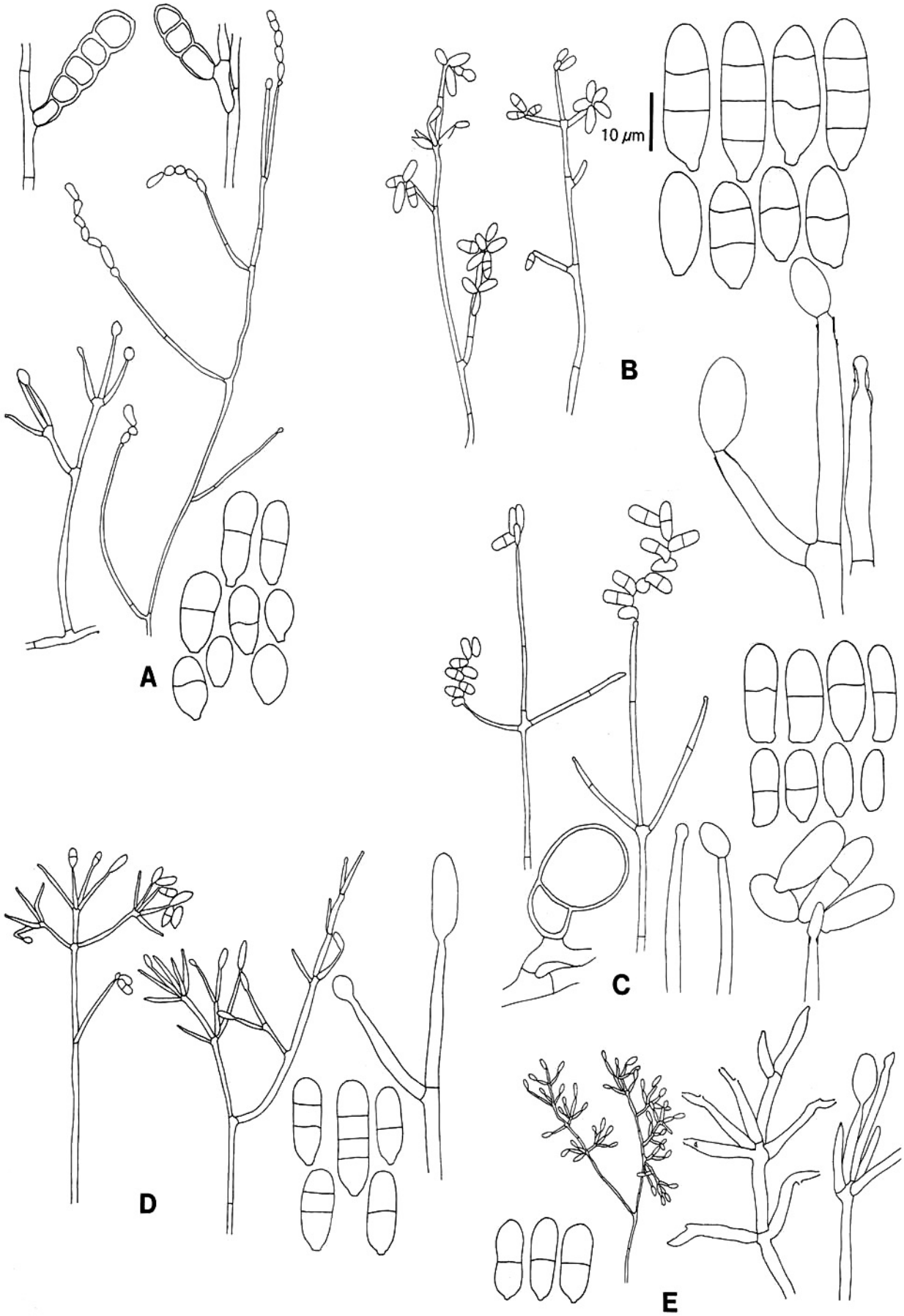

FIGURE 17.2 Morphologic variation in *Cladobotryum* anamorphs of *Hypomyces*. **A.** *H. aurantius*. **B.** *H. rosellus*. **C.** *H. subiculosus*. **D.** *H. semitranslucens*. **E.** *H. sympodiophorus*. Scale bar applies to detailed drawings of conidiophores and conidia. (Reprinted with permission, from Rogerson and Samuels 1993.)

FIGURE 17.3 Mummified fruitbody of an agaric (probably *Lactarius* species) parasitized by *Hypomyces lactifluorum*. (Photo by K. Põldmaa)

FIGURE 17.5 Fanlike colony of *Sporophagomyces chrysostomus* hanging under a basidioma of *Ganoderma applanatum*. The brownish color of the subiculum is due to the basidiospores of the host trapped in the subiculum. (Photo by K. Põldmaa)

FIGURE 17.4 Subiculum and perithecia of *Hypomyces rosellus* on *Basidioradulum radula*. (Photo by U. Kõljalg)

myxomycetes, pyrenomycetes, loculoascomycetes, or discomycetes, and at least six grow on lichens. Three species of *Trichonectria* are known from nonlichenized ascomycetes, and six, *T. hirta* and *T. rubefaciens,* are from lichens (Samuels 1988; Sérusiaux et al. 1999). White to yellow perithecia commonly are observed in fungicolous taxa (Samuels 1988). That feature also is found in the superficially similar Tubeufiaceae (Dothideales), which contains several fungicolous taxa (Rossman 1987).

Clavicipitaceae. Whereas numerous species of the genus *Cordyceps* are entomogenous, three species commonly grow on *Elaphomyces* species. Among numerous anamorph genera associated with *Cordyceps, Verticillium* sect. *Prostrata,* now *Lecanicillium* (Gams 1971; Zare et al. 2000; Zare and Gams 2001), is comprised of species, some of which exhibit high levels of chitinase activity and have great potential as entomogenous, nematophagous (mainly parasitizing eggs), and fungicolous biocontrol agents.

Niessliaceae. Although the majority of species in this family are saprotrophic, some appear to be fungicolous, particularly the *Monocillium* anamorphs of *Niesslia*. Whereas species of *Circinoniesslia* and *Valetoniella* have been found only on perithecia of various *Nectria* species, *Trichosphaeriella decipiens* mostly is reported on sporocarps of aphyllophorales (Samuels and Barr 1997). Three species of *Niesslia* are lichenicolous.

Dothideales (Pleosporales). The Tubeufiaceae comprise a large number of fungicolous taxa found on meliolaceous (18 species) or phyllachoraceous (nine species) leaf-inhabiting ascomycetes, as well as rusts (three species). Other taxa grow on decaying wood (20 species) (Rossman 1987). Associated anamorphs often have helicoid conidia. The Dacampiaceae include several genera with exclusively lichenicolous species: *Clypeococcum* (six species), *Dacampia* (three species), *Kalaallia* (one species), *Polycoccum* (30 species), *Pyrenidium* (15 species, mostly undescribed), and *Weddellomyces* (eight species). Most of the species are specialized on a single host genus or species. The genus *Lichenopeltella* (Microthyriaceae) comprises a large number of lichenicolous species, most of which parasitize macrolichens (Aptroot et al. 1997). Other genera of the Dothideales that include only lichenicolous species are *Buelliella, Cercidospora, Didymellopsis, Endococcus, Lichenostigma, Sagediopsis, Sphaerellothecium,* and *Zwackhiomyces.*

Orders Relatively Rich in Lichenicolous Fungi

Arthoniales. Most species of the genera *Arthonia, Lecanographa,* and *Opegrapha* are lichenized. Approximately 45 of the species of *Arthonia* are lichenicolous (Fig. 17.6) (Clauzade et al. 1989; Grube et al. 1995), however, as are three of the *Lecanographa* species (Egea and Torrente 1994), and 35 of the *Opegrapha* species (Fig. 17.7) (Clauzade et al. 1989; Hafellner 1994). In addition, at least 23 species of *Plectocarpon* are lichenicolous (Diederich and Etayo 1994).

Caliciales. Species of the Caliciales order can be lichenized, lichenicolous, fungicolous, or saprotrophic on bark or wood. Several genera (e.g., *Chaenothecopsis, Microcalicium, Sphinctrina*) comprise a high percentage of lichenicolous species, many of which grow on other lichenized species of Caliciales. *Microcalicium arenarium* develops either on the saxicolous lichens *Psilolechia lucida* and *P. clavulifera* (lichens with a *Stichococcus* photobiont) or on saxicolous *Stichococcus* species.

FIGURE 17.6 *Arthonia molendoi*, an ascomycete growing on *Xanthoria elegans.* (Photo by P. Diederich, width of picture 2.2 mm)

FIGURE 17.7 *Opegrapha cladoniae*, an ascomycete confined to *Cladonia* species. (Photo by P. Diederich, width of picture 1.7 mm)

Lecanorales. *Toninia* comprises numerous lichens, including several species parasitic on other lichens, and some nonlichenized, lichenicolous fungi. The genera *Buellia, Carbonea, Catillaria, Rhizocarpon, Tephromela,* and *Thelocarpon* include mostly lichenized species as well, some of which develop on other lichens; a few species are nonlichenized but lichenicolous. *Phacopsis* (14 species) is exclusively lichenicolous; most species grow on members of the Parmeliaceae.

Ostropales. In the Odontotremataceae, *Odontotrema* (including *Lethariicola*) comprises 15 lichenicolous and some nonlichenicolous species (Lumbsch and Hawksworth 1990; J. Etayo and P. Diederich, personal

communication) and *Nanostictis* (3 + 2 undescribed; J. Etayo and P. Diederich, personal communication).

Verrucariales. Although most species of the Verrucariales are lichenized, a number of species of *Verrucaria* are parasitic lichens. Several related genera include only nonlichenized, lichenicolous species: *Adelococcus* (three species; Matzer and Hafellner 1990), *Merismatium* (nine species; Triebel 1989), *Norrlinia* (two species; Santesson 1989), and *Stigmidium* (approximately 70 species; Clauzade et al. 1989; Roux and Triebel 1994). Species of *Muellerella* (12 species; Triebel 1989) are lichenicolous or hepaticolous.

Genera Incertae Sedis. The genus *Abrothallus* includes at least 20 species that grow on macrolichens (mainly belonging to the Parmeliaceae). At least 30 species of *Dactylospora* are lichenicolous, whereas other members of the genus are muscicolous or saprotrophic on wood.

Anamorphic Conidial Ascomycota

Species of the heterogeneous genera *Acremonium* (mostly anamorphs of Hypocreales), *Verticillium* and *Lecanicillium* (anamorphs of Hypocreales and Clavicipitaceae), and *Chalara* (anamorphs of Leotiales) commonly are found in fungicolous associations. In particular, the species *A. strictum, A. berkeleyanum* (synonym *A. butyri*), *A. domschii, A. crotocinigenum, A. psammosporum, V. luteo-album* (synonym *V. tenerum*, often cited erroneously as anamorph of "*Nectria*" *inventa*), *V. fungicola, Lecanicillium lecanii, L. psalliotae, Simplicillium lamellicola,* and *V. leptobactrum* grow on a great diversity of substrata. A new section, *Lichenoidea* of *Acremonium,* was described for nine mostly common lichenicolous species with unbranched conidiophores, some of which are anamorphs of *Pronectria* (a segregate of *Nectria*) (Lowen 1995). More than 100 lichenicolous conidial fungi are known currently (see Hawksworth 1979a, 1981b). In addition, the genera *Acrodontium, Calcarisporium, Gabarnaudia,* and *Rhinotrichella,* related to various other ascomycete orders, contain common fungicolous species that will be dealt with in the following sections.

BASIDIOMYCOTA

Mycoparasitism is particularly widespread in various groups of Heterobasidiomycetes (Urediniomycetes, Ustilaginomycetes, and phragmobasidial Hymenomycetes).

Urediniomycetes, Platygloeomycetidae

Two major lineages are distinguished within the class Urediniomycetes (Swann and Taylor 1995a, 1995b, 1995c), the Urediniomycetidae and Platygloeomycetidae. The subclass Platygloeomycetidae (or Sporidiales clade) comprises the majority of the species formerly included in the Auriculariales sensu lato, for the most part parasites of fungi, mosses, ferns, and flowering plants (Bandoni 1984). Besides a series of saprotrophic yeastlike genera and the dicot-inhabiting smuts (*Microbotryum*), this subclass includes four orders with mycoparasitic genera.

The parasite and host are generally in contact through haustoria. In a few cases, the parasites have large numbers of a specialized organelle in the periplasmic region. These organelles first were described by Kreger-van Rij and Veenhuis (1971) for *Sporidiobolus* species and called lenticular bodies. When described from *Cryptomycocolax* species, and later from *Colacogloea*, the structures were referred to as colacosomes (Oberwinkler and Bauer 1990; Bauer and Oberwinkler 1991). The organelles are vesicular structures with an electron-opaque core and an electron-transparent sheath (Bauer and Oberwinkler 1991); the vesicular content projects through the cell wall of the parasite and makes contact with the plasmalemma of the host. Lenticular bodies also have been found in *Bensingtonia* and *Rhodosporidium,* which suggests that those yeasts also may have mycoparasitic capabilities (Boekhout et al. 1992).

Atractiellales. Although not originally described as such, species of *Chionosphaera* and *Stilbum,* in the Atractiellaceae, may be mycoparasites (Bandoni 1995; Roberts 1997). Two species of *Chionosphaera* grow on lichens (Diederich 1996).

Platygloeales. Cystobasidiaceae. The genera *Platygloea, Cystobasidium, Mycogloea,* and *Colacogloea* contain mycoparasitic species. *Platygloea fimetaria* and *Colacogloea* (*Platygloea*) *peniophorae* parasitize corticiaceous hosts, but also *Dacrymyces* and *Poria* (Bauer and Oberwinkler 1991; Bandoni 1995). *Cystobasidium lasioboli* is found on *Lasiobolus*; two other species in the genus elicit formation of conspicuous galls on lichens (Diederich 1996). *Naohidea* forms pustular basidiomes on old pyrenomycetes, and the intrahymenial mycoparasites *Occultifur* and *Kryptastrina* are found in basidiomata of *Dacrymyces* and on corticioid fungi, respectively (Oberwinkler 1990).

Cryptomycocolacales. Cryptomycocolacaceae. *Cryptomycocolax*, possibly one of the most primitive basidiomycetes, is unusual in having simple septal pores and apparently some ascomycete features. It was found par-

asitizing an unidentified ascomycete in *Cirsium* culms in Costa Rica. The host fungus produces botryose outgrowths that are engulfed by the parasite (Oberwinkler and Bauer 1990).

Heterogastridiales. Heterogastridiaceae. *Heterogastridium pycnidioideum* (Oberwinkler et al. 1990a, b), with the anamorph *Hyalopycnis blepharistoma,* parasitizes various fungi on rotting plant material, including decaying walnuts (*Juglans ailanthifolia*) in Japan (CBS, unpublished data), and various fungal sporocarps (Bandoni and Oberwinkler 1981). It can be grown axenically, but some strains require a host, such as *Plectosphaerella cucumerina,* for pycnidium formation *in vitro* (G. Fischer and W. Gams, unpublished data). T. Boekhout (unpublished data) noted the presence of lenticular bodies in *Heterogastridium*.

Ustilaginomycetes

Tilletiopsis (revised by Boekhout 1991) is an anamorph genus that contains mycoparasites of powdery mildews. The redefined genus *Pseudozyma* (Boekhout 1995), which is characterized by dimorphic growth, variously shaped blastoconidia borne on sympodially proliferating conidiophores, and the absence of ballistoconidia, comprises anamorphs of *Ustilago* and also includes the mycoparasites of powdery mildews formerly described as *Stephanoascus* species (Traquair et al. 1988).

Hymenomycetes, Tremellomycetidae

The order Tremellales includes species with a dimorphic life cycle, a septal pore apparatus with sacculate caps, and a tremelloid basidium. That most or all species of the Tremellales are mycoparasites has been reported repeatedly. The dikaryotic, somatic phase shows restricted growth, which may reflect the mycoparasitic nature of many, if not all, of the species. Many species have monokaryotic "haustorial branches" subtended by a clamp that consists of a bulbous base and a tubular appendage. The tubular appendage has been shown to attach to and/or penetrate the hyphal wall of a host fungus (Bauer and Oberwinkler 1990a, 1990b; Oberwinkler and Bandoni 1981, 1982; Oberwinkler et al. 1984). The haustorium may have an absorptive role, leading eventually to the degeneration of the host cytoplasm (Oberwinkler et al. 1984). Micropore openings have been demonstrated in the haustoria of some species (*Syzygospora*, *Phragmoxenidium*; Bauer and Oberwinkler 1990b; Oberwinkler et al. 1990b). The pore membrane appears to be continuous with the plasmalemma of both cells (Zugmaier et al. 1994). Somewhat larger pores are present in *Tetragoniomyces uliginosus* (Oberwinkler and Bandoni 1981; Bauer and Oberwinkler 1990a). Haustoriumlike cells also can be observed in pure cultures without a host fungus.

Explicit information on fungicolous relationships is available for six of the 10 families included in the order (Kirk et al. 2001).

Tremellaceae. *Tremella* (more than 170 species known), *Holtermannia, Sirotrema, Trimorphomyces, Xenolachne, Bulleromyces*, and probably *Itersonilia* (anamorphic) contain numerous mycoparasites. *Tremella* is the largest and most heterogeneous genus in the Tremellaceae. It includes mycoparasitic species growing on hymenia of aphyllophorales, in basidiomes of Dacrymycetales, on ascomata and/or stromata of pyrenomycetes, and on hymenomycetes and lichens (Bandoni 1995; Diederich 1996). *Trimorphomyces* and *Sirotrema* species have been found on conidial masses of *Arthrinium* or on hymenia of Hypodermataceae, respectively (Oberwinkler and Bandoni 1983), and *Holtermannia* has been found on a polypore (Bandoni 1995). *Tremella*-type haustoria also have been found in the yeastlike *Bulleromyces albus*, suggesting that it has mycoparasitic capacities (Boekhout et al. 1991). *Itersonilia* species have been found as mycoparasites on powdery mildews. *Xenolachne* is found on inoperculate discomycetes. The lichenicolous *Biatoropsis usnearum* may also belong here.

Syzygosporaceae. (synonym Carcinomycetaceae). *Syzygospora* (fide Ginns 1986; originally *Syzygospora*, *Christiansenia*, and *Carcinomyces*; see Oberwinkler and Bandoni 1982). The Syzygosporaceae comprise parasites on *Phanerochaete* species, *Gymnopus* species, and *Marasmius* species, often causing gall-like deformations. They have holobasidia of various shapes, and in some species, "zygoconidia" arise from the fusion of blastoconidia thrust forward by adjacent cells; their septa lack parenthesomes (Oberwinkler and Bandoni 1982). Ginns (1986) synonymized *Syzygospora*, *Christiansenia*, *Carcinomyces* in *Syzygospora*, recognizing nine species in three subgenera, distinguished according to basidial and conidial shape. A key for the species found in Norway is given in Torkelsen (1996). The species *C. mycetophila*, *C. effibulata*, and *C. tumefaciens* grow on *Gymnopus dryophilus*, inducing gall-like fructifications (Fig. 17.14) (Ginns and Sunhede 1978; Oberwinkler and Bandoni 1982; Oberwinkler et al. 1984; Ginns 1986). *Syzygospora alba* produces tremelloid sporocarps on an unknown host (Oberwinkler and Lowy 1981). The common and widespread lichenicolous species *Syzygospora bachmannii* (Fig. 17.8) and *S. physciacearum* grow on *Cladonia* species and on Physciaceae (Diederich 1996).

Filobasidiaceae (raised by some authors to Filobasidiales). *Filobasidium, Filobasidiella,* and *Cystofilobasidium* are more or less mycoparasitic. The otherwise

FIGURE 17.8 *Syzygospora bachmannii*, a heterobasidiomycete inducing the formation of galls on *Cladonia* species. (Photo by P. Diederich, width of picture 10 mm)

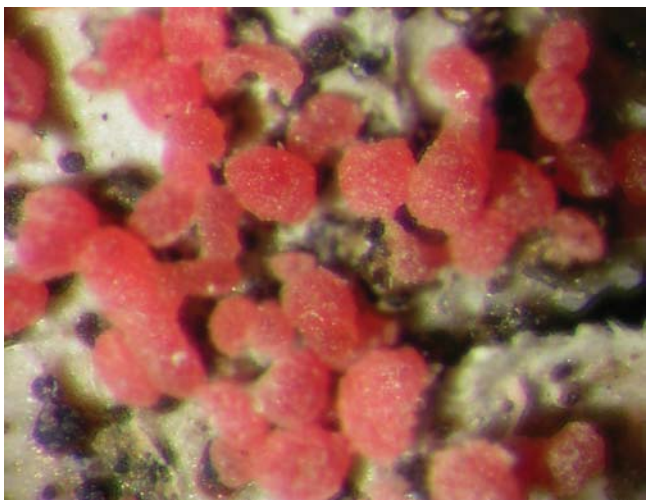

FIGURE 17.9 *Marchandiomyces corallinus*, a sclerotial basidiomycete anamorph (Corticiaceae?) parasitizing thalli of *Parmelia*. (Photo by P. Diederich, width of picture 1.4 mm)

yeastlike genera *Filobasidium* (Olive 1968) and *Cystofilobasidium* have hyphal structures with haustoria only in the dikaryotic phase; species of *Filobasidium* and the vertebrate parasites in *Filobasidiella* (best known as the *Cryptococcus neoformans* anamorph) also have haustoria, suggesting mycoparasitic capacities (Bandoni 1995). *Cystofilobasidium capitatum* was found in the gleba of Phallaceae (Oberwinkler et al. 1983).

Rhynchogastremaceae. Mycoparasitic species of *Rhynchogastrema* contact their various hosts in the soil with haustoria, but axenic growth is possible (Metzler et al. 1989).

Phragmoxenidiaceae (doubtful classification). *Phragmoxenidium mycophilum* (Oberwinkler et al. 1990b) grows on *Uthatobasidium fusisporum*, contacting its host through micropores; its septa lack a parenthesome.

Tetragoniomycetaceae. *Tetragoniomyces uliginosus* (Oberwinkler and Bandoni 1981) grows on *Ceratobasidium*.

Hymenomycetes, Hymenomycetidae

Aphyllophorales. The aphyllophorales is an artificial assemblage of divergent elements of homobasidiomycetes. Destructive necrotrophic mycoparasites of some ascomycetes (e.g., *Ceratocystis*) have been found *in vitro* among diverse genera such as *Bjerkandera*, *Lenzites*, *Trichaptum*, *Trametes*, *Schizophyllum*, and *Pleurotus* (Griffith and Barnett 1967; Traquair and McKeen 1978). The conidia and hyphae of the hosts are affected by hyphal interference. Mutual displacement of several aphyllophorales seems to be an important phenomenon in wood decay (see "On Polypores" under "Fungi on Basidiomycota," later in this chapter). Tzean and Estey (1978b) discovered that the wood-decaying *Schizophyllum commune* is a potent mycoparasite of many plant-pathogenic fungi. It coils around and penetrates the host hyphae, which it then destroys. A suitable host is the nematophagous and fungicolous *Arthrobotrys oligospora*.

Tzean and Estey (1991, 1992) also described an arthroconidial basidiomycete, *Geotrichopsis mycoparasitica*, with characteristic spindle-shaped chlamydospores. The parasite attacks *Arthrobotrys oligospora*, *Monacrosporium cionopagum*, and other nematophagous fungi; some Mucoraceae; *Mortierella* species; *Pythium* species; *Chalara elegans*; and *Rhizoctonia solani* but not species of *Aspergillus*, *Penicillium*, *Geotrichum*, *Drechslera*, and *Nematoctonus*. *Athelia* (*Corticium*) *rolfsii* and *Heterobasidion annosum* are resistant. However, *Athelia arachnoidea* is mainly lichenicolous. The lichenicolous sclerotial genus *Marchandiomyces* (Fig. 17.9) (teleomorph *Marchandiobasidium*) probably belongs to the family Corticiaceae.

Boletales and Agaricales. A few fungicolous boletes and agarics from diverse groups are known. Host-specific associations are found in the genera *Asterophora* and *Squamanita*.

MAJOR GROUPS OF FUNGICOLOUS FUNGI, ARRANGED BY HOST GROUP

For the present survey, we divide the fungicolous fungi into five major groups according to the substrata on

which they grow and their biotopes: (1) fungal sporocarps; (2) lichens; (3) biotrophic plant parasites; (4) mycelia, sclerotia, and spores in soil; and (5) aquatic fungi and fungus-like microorganisms. The five groups are not sharply delimited, however, and they also merge with saprotrophs that grow incidentally on other fungi. For example, certain fungi normally obtained as soil isolates also commonly are associated with macromycetes or lichens in decay. Similarly, the presence of microscopic endoparasitic *Tremella*-related species in *Asterophora* chlamydospores (Laaser et al. 1988; Prillinger et al. 1993) is consistent with the definitions of both groups 1 and 4; and zoosporic fungi can parasitize oomycete hosts both in water (group 5) and in soil (group 3).

Different methods are used to study each of these major groups. We discuss those methods and identification sources, as well as the species richness and geographic distribution of each group. The numbers of fungicolous species in various fungal orders that pertain to each major group are summarized in Table 17.1.

Fungi on Sporocarps of Fungi or Myxogastrea

It is easy to single out a group of fungi that live on fresh or decaying sporocarps of other, nonlichenized fungi. The substrata of such SCIF usually consist of dry or soft macromycete sporocarps (which may show more or less conspicuous deformations as a result), but the SCIF often colonize their anamorphs, conidiomata, conidiophores, and conidia as well. We also include under this heading fungi growing on myxomycete sporangia and a few that grow on above-ground conidiophores or conidiomata of anamorphic fungi. The SCIF are mainly ascomycetes or their anamorphs, but they also include some Zygomycota and many Basidiomycota; most of the latter are Tremellales, but a few others are Agaricales (Buller 1924; Redhead et al. 1994). The species of SCIF are relatively well-known.

The SCIF on a decaying sporocarp gradually are replaced by a wide array of saprotrophic fungi (many species of *Penicillium* and *Cladosporium*) that are in no way specialized to the substratum; we do not consider them here. Certain species of *Penicillium*, however, specifically are associated with the decay of sporocarps of particular fungi, as in *Chroogomphus* (*Gomphidius*) *rutilus* and *Boletus parasiticus*. *Hygrocybe virginea* (synonym *Camarophyllus niveus*) is colonized regularly by the common soil fungus *Paecilomyces marquandii* (Ellis and Ellis 1988; CBS, unpublished data).

The fungal substrata available to SCIF are by no means homogeneous. Here we group the SCIF into a polyphagous group and major-host groups.

Polyphagous Fungicolous Fungi

Many kinds of fungal substrata can function as hosts of polyphagous fungicolous fungi, including *Clonostachys* (*Gliocladium*) *rosea*, *Trichothecium roseum*, *Calcarisporium arbuscula*, *Trichoderma* species, *Acremonium strictum*, *Lecanicillium* [*Verticillium*] *lecanii*, and *V. luteo-album* (Domsch et al. 1980).

Clonostachys rosea is a ubiquitous mycoparasite whose hyphae penetrate and destroy those of many host fungi, including some Mucorales, *Ceratocystis fimbriata*, and even the potent toxin producer *Trichothecium roseum* (Barnett and Lilly 1962; Barnett and Binder 1973; Berry and Deacon 1992; Jeffries and Young 1994). In natural infections of *Botrytis aclada* on onions, *C. rosea* hyphae grow along the host hyphae, which they contact with appressorial branches, and then penetrate the hyphal wall (Walker and Maude 1975). Hyphae of *C. rosea* also can attack the sclerotia of *Botrytis* species.

Calcarisporium arbuscula grows equally well on many kinds of Ascomycota and Basidiomycota (Barnett and Lilly 1958; Nicot 1968), which usually do not survive the infection. *Acremonium strictum* has been found on many saprotrophic fungi, several plant-pathogenic fungi (Gams 1971), and on the mycoparasite *Mycogone perniciosa* (Gandy 1979), whose growth it inhibited.

Verticillium luteo-album has a wide range of hosts, but host susceptibility seems to vary among taxa, according to the type and age of the host structure attacked, and with the culture medium used. *In vitro*, the species has been observed to overgrow and destroy colonies of *Alternaria brassicae*, *A. raphani*, *Phoma lingam*, *Trichothecium roseum*, *Ulocladium atrum*, and *Rhizoctonia solani*. *Trichoderma harzianum*, in turn, destroys *V. luteo-album* (Tsuneda et al. 1976; Tsuneda and Skoropad 1980).

Sistotrema brinkmannii, found mainly on decaying sporocarps of aphyllophorales, is a common air-borne contaminant that can overgrow and destroy any *in vitro* fungal culture. *Athelia arachnoidea* is a common corticiaceous species that overgrows and kills epiphytic lichens (and algae) and can destroy whole lichen communities, especially in areas with significant air pollution (Arvidsson 1976, 1978; Parmasto 1998). The anamorph of this species, *Fibulorhizoctonia carotae*, is a cold-storage pathogen of carrot in Europe, North America, and India. *Athelia arachnoidea* is the only known lichenicolous fungus whose anamorph is nonlichenicolous (Adams and Kropp 1996).

Fungi on Slime Molds

Sporocarps (but not the plasmodia) of slime molds (Myxogastrea) often are colonized by more or less

specialized fungi. Most obligate myxomyceticolous conidial fungi smother the sporangia, usually turning them white. Whether most of those should be viewed as parasites is doubtful because they colonize an already terminal phase of the sporocarp and flourish after a great many spores already have been liberated (Hawksworth 1981b). However, the relationship between myxomyceticolous fungi and their hosts could be regarded as parasitic because the mycelium usually grows over the entire surface of the host fructification (Rogerson and Stephenson 1993). Hyphae penetrate the spore mass of the host, killing the spores and preventing their release. In the vast majority of the collections examined, only a single colonizing species was present, and usually most of the fructifications of the host were colonized.

Rogerson and Stephenson (1993) distinguished two groups of parasites: those that parasitize the calcium-rich fructifications of the Physarales (*Gliocladium album*, *Nectriopsis violacea*, *Sesquicillium microsporum*) and those that attack only noncalcareous myxomycetes (*Aphanocladium album* sensu stricto; *Byssostilbe stilbigera*, usually observed as the anamorph, *Blistum tomentosum*). More specifically, *N. violacea* has been found only on *Fuligo* species, and *B. tomentosum* had been found only on members of the Trichiales. Other myxomyceticolous ascomycetes occur on different host species or are too poorly collected to allow for conclusions about their host specificity. Most myxomyceticolous conidial fungi occur on various host species. *Nectriopsis exigua* (anamorph *Verticillium rexianum*), one of the most ubiquitous species, has been recorded from all major groups of myxomycetes and so is *Stilbella byssiseda* (Fig. 17.10). All the species mentioned here are found exclusively on sporocarps of myxomycetes.

Some less specific colonizers are also known. The hemiascomycete *Dipodascus macrosporus* can live in the slime trail of *Badhamia utricularis* cultured on cornmeal agar. If ingested by the plasmodium, the fungus resists digestion and seems to play the role of a facultative parasite (Madelin and Feest 1982). The yeast cells of *D. macrosporus* multiply within the plasmodium as well as on the supporting medium. Also, various fungi other than ascomycetes and their conidial relatives (e.g., the Zygomycetes *Umbelopsis* [*Mortierella*] *ramanniana* and *Mucor hiemalis;* Helfer 1991) have been encountered on sporocarps of myxomycetes. The occasional presence of hyphae of unidentified saprotrophic or wood-decaying basidiomycetes on myxomycete fructifications is considered to be coincidental co-occurrence (Rogerson and Stephenson 1993).

FIGURE 17.10 Synnemata of *Stilbella byssiseda* growing on a slime mold. (Photo by U. Kõljalg)

TABLE 17.4
Characteristic Ascomycetes and Their Anamorphic Relatives Parasitic on Nonlichenized Discomycete Sporocarps

Fungicolous species	Host
Hypomyces cervinigenus (anamorph *Mycogone cervina*)	*Mycolachnea* (*Humaria*) *hemisphaerica*
Hypomyces stephanomatis (anamorph *Stephanoma strigosum*)	*Helvella* species
Stephanoma tetracoccum	Geoglossaceae
Hypomyces papulasporae (anamorph *Papulaspora candida*)	Geoglossaceae
Hypomyces mycogones	Geoglossaceae
Sphaeronaemella helvellae	*Gyromitra* species
Hormiactis species	*Morchella* and *Peziza* species
Hypomyces leotiicola (anamorph *Sepedonium leotiarum*)	*Leotia lubrica*
Nectriopsis discophila	*Lachnum* species
Nectria sepultariae	Inoperculate discomycetes
Nectria discicola	Inoperculate discomycetes
Trichonectria albidopilosa	Inoperculate discomycetes
Exochalara longissima	*Bulgaria inquinans* (CBS)

Data from Rogerson and Samuels (1985), Helfer (1991), and CBS (unpublished data). Additional species that grow on discomycetes are listed by Hawksworth (1981a).

Fungi on Ascomycota

On Sporocarps of Discomycetes (Cup Fungi) and on Fleshy Epigeous Sporocarps of Discomycetes (Pezizales, Leotiales).

The most characteristic colonizers of ascomata of discomycetes are listed in Table 17.4. Most of them occur only on sporocarps of this group of hosts.

The heterobasidiomycete *Xenolachne longicornis* can grow on ascomata of *Cudoniella* species and *Disciniella*

species where the parasite replaces the hymenium (Hauerslev 1977; Jülich 1983). A stronger displacement of ascal hymenia by a parasite occurs in *Helicogonium* (Baral 1999; see "Leotiales" under "Ascomycota," in the section "Taxonomic Groups of Fungicolous Fungi and Fungus-like Microorganisms," earlier). *Cystobasidium lasioboli* was found in Europe growing on *Lasiobolus pilosus*, and *Exidiopsis fungicola* was found on *Mollisia cinerea* (Jülich 1983). *Clitocybe sclerotoidea* can parasitize and deform *Helvella lacunosa* in the western United States (Trappe 1972). Many fungal interactions can be observed on dung; the growth of *Ascobolus* species, *Pilobolus crystallinus*, and other coprophilous fungi, for example, is strongly inhibited by *Coprinus heptemerus*, a case of lethal hyphal interference (Ikediugwu and Webster 1970a, 1970b; Ikediugwu 1976a).

Penicillium glabrum has been found on twigs affected by *Monilinia laxa* peach twig blight. Its antifungal substances seem to render it suitable as a biocontrol agent (de Cal et al. 1988, 1990).

On Sequestrate Ascomycetes. Species of *Tuber* and other tuberoid hypogeous Pezizales often are colonized by species of *Acremonium*, *Verticillium* sect. *Prostrata*, and *Mortierella* (CBS, unpublished data). *Nodulisporium* (*Sporothrix*) *tuberum* was described from *Tuber maculatum* (Fontana and Bonfante 1971). A few species of *Sphaerodes* (synonym *Microthecium*) are specialized on hypogeous fungal substrata (Hawksworth and Udagawa 1977). *Battarrina inclusa* (Bionectriaceae) also is found inside ascomata of *Tuber puberulum* (Jeffries and Young 1994). The subterranean sporocarps of *Elaphomyces* often can be detected when the conspicuous epigeous ascomata of their parasites, *Cordyceps ophioglossoides*, *C. capitata*, and *C. canadensis*, appear. What impact they have on their hosts has not been investigated. The ascomata of *Elaphomyces* species also often are colonized by *Gabarnaudia tholispora* and other conidial fungi (CBS, unpublished data).

On Coriaceous Discomycetes (Phacidiales, Rhytismatales). Hawksworth (1981b) listed a few rather unspecific species of mycoparasites occurring on members of these orders. Species of *Sirotrema* (*Pseudostipella*) have been found growing on apothecia of *Lophodermium*, *Hypoderma*, and *Hypodermella* species (Ellis and Ellis 1988). A rather specific competitive mycoparasitic relationship seems to exist between *Hendersonia pinicola* or *H. acicola* and *Lophodermium concolor* or *Lophodermella sulcigena*. *Hendersonia pinicola* causes needle cast in *Pinus contorta* (Stahl et al. 1988); as secondary invaders, it and *H. acicola* can prevent ascoma formation in *L. sulcigena* and thus naturally control epidemics (Funk 1985; Jalkanen and Laakso 1986). Also *Hemiphacidium* species regularly follow *Bifusella* or *Lophodermella* species and other fungi on *Pinus* species, preventing them from fruiting (Funk 1985). *Cosmospora* (*Nectria*) *ganymede* has been reported from the rhytismataceous *Zeus olympius* (Minter et al. 1987).

Species of *Platygloea* (*Achroomyces*), *Mycogloea*, and *Sirobasidium* occur on species of *Colpoma* and *Lophodermium*. *Tremella juniperina* is found on sporocarps of *Colpoma juniperi*, and *T. translucens* is found on *Lophodermium* (Jülich 1983).

On Stromata and Ascomata of Pyrenomycetes and on Dry, Carbonized, Mostly Stromatic Fructifications (Especially Xylariaceae and Diatrypaceae). Common colonizers of old carbonized stromata include *Polydesmia pruinosa* and species of *Cosmospora*—for example, *C.* (*Nectria*) *episphaeria* and more rarely *C. purtonii* (e.g., on *Diatrype stigma*, *Hypoxylon fragiforme*, and other stromatic ascomycetes; Samuels 1976; Domsch et al. 1980; Samuels et al. 1991; Helfer 1991). The associated anamorphs, classified as varieties of *Fusarium aquaeductuum*, are equally common on these substrata. Old stromata of *Hypoxylon* species, as well as polypores, are commonly colonized by *Cosmospora vilior* (synonym *Nectria viridescens*) and its *Acremonium berkeleyanum* (synonym *A. butyri*) anamorph and by *Monocillium tenue* (Gams 1971). A unique fungus growing on carbonized perithecia of ascomycetes was described as *Hypomyces triseptatus* (Rossman and Rogerson 1981). Many Xylariaceae and *Physalospora obtusa* are among the hosts of *Calcarisporium arbuscula* (Hoch 1977b). *Capronia parasitica* grows frequently on old stromata of *Diatrype* and *Hypoxylon* but is easily overlooked because it is small and the same color as its substratum (Helfer 1991). The ascomata of *Capronia* (*Berlesiella*) *nigerrima* are found on *Eutypa* (Jeffries and Young 1994). Less common discomycetes found on such stromata are species of *Phaeohelotium*, *Bisporella*, and *Cistella* (Ellis and Ellis 1988). *Orbilia inflatula* (*O. auricolor*) is rather common on *Hypoxylon fragiforme* (Baral and Krieglsteiner 1985; Helfer 1991).

Tubeufia cerea (often with its *Helicosporium* anamorph), the most common north-temperate representative of the genus, occurs on old stromata of *Diatrype stigma*; *Graphostoma platystoma*; and species of *Eutypa*, *Eutypella*, and *Hypoxylon*, as well on other fungi (Barr 1980). Hawksworth (1981b) listed numerous potential colonizers of pyrenomycetes. Many more hypocrealean species growing on this and other groups of fungi were revised by Samuels (1988).

Certain perithecial Ascomycota, such as species of *Didymosphaeria* and *Phaeodothis* (*Didymosphaeria*) *winteri*, live inside the ascomata of other pyrenomycetes (see Munk 1957 and a revision by Aptroot 1995).

Ascodichaena rugosa is parasitized in southern Germany by *Keissleriella bavarica* (Lophiostomataceae), whereas *Tripospermum myrti* and *Eriomyces* species grow on both fungi (Butin 1981). *Neobarya* and some undescribed *Acremonium* species are obligate parasites on *Bertia moriformis* and some other pyrenomycetes; their physiology is not yet understood (Munk 1954, 1957; Helfer 1991). *Chaetosphaerella fusca* and *C. phaeostroma* (with *Oedemium* anamorphs) frequently are found on stromata of diatrypaceous fungi (Ellis and Ellis 1988). *Epicoccum nigrum* and *Coniothyrium olivaceum*, which can suppress canker development, have been considered as promising control agents of the anamorphic *Cytospora cincta*, the causal agent of canker in peach twigs (Royse and Ries 1978).

Catulus aquilonius (Mycosphaerellaceae) has been found on *Seuratia millardetii* (Myriangiales) growing on needles of *Abies balsamica* (Malloch and Rogerson 1978).

On Soft Perithecia (Particularly Hypocrealean Fungi). *Nectria cinnabarina* and its *Tubercularia vulgaris* anamorph are commonly overgrown by the hyphomycete *Tympanosporium parasiticum*, which can be grown in axenic culture (Gams 1974), as well as by many nonspecific colonizers. *Gabarnaudia tholispora* and an obligate parasitic species of *Acremonium* also have been observed on *N. cinnabarina* (W. Gams, personal observation). *Nitschkia parasitans* grows only on *Nectria cinnabarina* (Ellis and Ellis 1988). *Circinoniesslia nectriae*, *Valetoniella crucipila*, and *V. pauciornata* have been reported on *Nectria* species. *Nematogonum ferrugineum* (synonym *Gonatorhodiella highlei*) commonly colonizes *Neonectria* (*Nectria*) *coccinea* and related species; *in vitro*, it also grows on *Cladosporium*, *Penicillium*, and *Sporobolomyces* species (Walker et al. 1982). *Sphaerodes episphaeria* (synonym *Microthecium epimyces*) also has been found on *Hypomyces armeniacus* (Cannon and Hawksworth 1982).

On Anamorphic Ascomycota. A number of condial Ascomycota are hosts to biotrophic parasites. The entomogenous *Hirsutella citriformis*, a destructive parasite of brown planthoppers on the Solomon Islands, was colonized by *Calcarisporium* (*Cladobotryum*) *ovalisporum*; because this fungus requires sterilized host hyphae to grow on agar media, it also may be dependent on the fungal metabolite mycotrophein (Rombach and Roberts 1987). The biotrophic *Debaryomyces hansenii* can control penetration of citrus fruit by *Penicillium digitatum* (Droby et al. 1989); in high concentrations, the parasite inhibits the conidial germination and hyphal growth of its host, apparently through competition for nutrients. This yeast also acts similarly against *Rhizopus stolonifer*, *Botrytis cinerea*, and *Alternaria alternata* on tomatoes and grapes.

Anamorphic Ascomycota also host necrotrophic parasites. *Hansfordia* (*Dicyma*) *pulvinata* is a destructive parasite on many dematiaceous conidial fungi (Hepperly 1986), particularly *Cercospora* (Hawksworth 1981b), but also *Passalora* (*Mycovellosiella*, *Cladosporium*, *Fulvia*) *fulva* on tomato (Peresse and Le Picard 1980; Le Picard and Trique 1987), and *P.* (*Cercosporidium*, *Phaeoisariopsis*) *personata* on peanut leaves (Mitchell et al. 1986, 1987). The fungus coils over hyphae and conidia of its host and kills them (Peresse and Le Picard 1980) with a fungistatic sesquiterpene metabolite, deoxyphomenone (Tirilly et al. 1991). A conidial suspension of this fungus with carboxymethyl cellulose sprayed on *P. personata* prevented secondary spread of the pathogen under moist conditions (Mitchell et al. 1986, 1987). *Passalora personata* also can be parasitized by *Cladosporiella cercosporicola* (Esquivel-R. 1984).

Biocontrol of the plant-pathogenic *Verticillium dahliae* has been attempted repeatedly, as reviewed under "Mycoparasites of Mycelia, Ectomycorrhizae, Sclerotia, and Spores in Soil." *Alternaria brassicae*, *Pleospora* species, and *Trichothecium roseum* are highly susceptible to hyphal interference by *Verticillium luteo-album* (Tsuneda et al. 1976; Tsuneda and Skoropad 1978, 1980), which forms coils and appressoria and sometimes penetrates the host hyphae. Turhan (1993) found a number of additional, interesting antagonists of *Alternaria alternata*, particularly *Dicyma olivacea*, *Stachybotrys elegans*, a species of *Sesquicillium*, five species of *Myrothecium*, and *Coniothyrium sporulosum*.

Penicillium funiculosum can smother various fungi in culture and thus prevent pineapple fruit diseases (Lim and Rohrbach 1980). *Aspergillus luchuensis* and a diversity of other fungi are parasitized in India by *Fusarium udum* (Upadhyay et al. 1981), which produces a diffusible toxin and induces vesicular deformations in its host.

The ascomycete *Letendraea helminthicola* parasitizes the hyphomycete *Helminthosporium velutinum* (Ellis and Ellis 1988). The discomycete *Bisporella pallescens* (synonym *Calycella monilifera*) fruits densely on the conspicuous black conidial patches of *Bispora antennata* on tree stumps (Jahn 1968).

In a search for parasites of *Macrophomina phaseolina* (synonym *Rhizoctonia bataticola*), *Arachniotus* species and *Aspergillus aculeatus* were found to be promising control agents (Dhingra and Khare 1973). In Varanasi, India, *Colletotrichum dematium* is parasitized by *Acremonium sordidulum*, which smothers the host and reduces its sporulation on the plant (Singh et al. 1978). Hawksworth (1981a) gives a long list of additional mycoparasites growing on conidial fungi.

Sphaeronaemella helvellae, *Trichoderma viride*, *Exobasidiellum* species, and others (Vakili 1985) are efficient antagonists of pathogens, such as *Fusarium verticillioides* (synonym *F. moniliforme* sensu stricto), *Cochliobolus* (*Helminthosporium*) *carbonum*, and *Colletotrichum graminicola* involved in stalk rot of corn.

Fungi on Basidiomycota

On Aphyllophorales. Most fungicolous colonizers of sporocarps of aphyllophorales are Ascomycota or related anamorphic fungi. Usually, they colonize the less protected hymenophore.

On Crustose, Mainly Resupinate, Aphyllophorales. *Sphaerostilbella aureonitens* (anamorph *Gliocladium penicillioides*), *S. lutea* (anamorph *G. aurifilum*), and *S. novaezelandiae* grow on basidiomata of several wood-decaying aphyllophorales. The first species and *Gliocladium polyporicola* (Fig. 17.11) are particularly common on *Stereum* species (Samuels 1976; Seifert 1985). *Sphaerostilbella berkeleyana* also grows on polypores (Samuels 1976; Helfer 1991; Candoussau and Magni 1995). Some species of *Hypomyces* (*H. sympodiophorus*, *H. albidus*, *H. corticiicola*) are found most frequently on the hymenophore of resupinate apyllophorales. *Cladobotryum stereicola* grows preferentially on *Chondrostereum purpureum* (K. Põldmaa, personal observation).

Hypocreopsis lichenoides has been found in central and northern Europe on species of *Hymenochaete*, especially *H. tabacina* (Cauchon and Ouellette 1964; Niemelä and Nordin 1985; Læssøe 1989; Kristiansen and Torkelsen 1994). In addition to species in the Hypocreales, several ascomycetes with dark perithecia grow on the hymenium of species in the aphyllophorales; *Helminthosphaeria odontiae* and *H. hyphodermatis* are found on *Hyphoderma tenue* and *Odontia cristulata*, and *Helminthosphaeria corticiorum* is found on *Peniophora* species (Doll 1973; Samuels et al. 1997).

Only a few ascomycetes have been found in the basidiocarps of corticioid fungi. *Helicogonium* (*Myriogonium*) *odontiae* occurs on *Dacryobolus sudans* (Cain 1948) and *H. jacksonii* occurs on *Ceraceomyces* (*Athelia*) *sublaevis* (White 1942; Parmasto 1974). Vegetative mycelium of *H. jacksonii* grows in the subiculum and subhymenium of the host, and scattered asci emerge among the basidia of the normally developed carpophore. It apparently does little harm to its host. The other species of the genus parasitize members of the Leotiales (see "Leotiales" under "Ascomycota," in the section "Taxonomic Groups of Fungicolous Fungi and Fungus-like Microorganisms," earlier).

Phaeospora corae and several undescribed species have been recorded from the lichenized corticiaceous *Cora glabrata* (Santesson 1989). *Phaeocalicium polyporaeum* (Caliciales) grows on basidiocarps of *Trametes versicolor* and *Trichaptum biforme* (Tibell 1984).

Acremonium psammosporum and other species of the genus commonly are found on *Peniophora* species (Helfer 1991; W. Gams, personal observation). *Denticularia limoniformis* is a host-specific parasite of *Hyphodontia* (*Grandinia*) *breviseta* (de Hoog 1978). Mycoparasitism of nematophagous species of *Arthrobotrys* that form mats on corticiaceous fungi is described in the section "On Sclerotia" under "Mycoparasites of Mycelia, Ectomycorrhizae, Sclerotia, and Spores in Soil."

Stilbella flavipes, *S. sebacea*, and *S. stereicola* grow on sporocarps of aphyllophorales (Seifert 1985). *Zakatoshia hirschiopori* is so far known from decayed basidiomes of the polypore *Trichaptum* (synonym *Hirschioporus*) species in Canada, whereas *Z. erikssonii* is known from *Sistotrema brinkmannii* in Europe (Sutton 1973a; Gams 1986).

In Denmark, galls on *Coniophora puteana* are caused specifically by a biotrophic parasite, *Nodulisporium cecidiogenes* (Koch 1994), a fungus that cannot be grown axenically.

Several intrahymenial heterobasidiomycetes occur also on the sporocarps of aphyllophorales. *Peniophora* species can host *Colacogloea* (*Platygloea*) *peniophorae* (Burdsall and Gilbertson 1974; Bauer and Oberwinkler 1991). The firm nucleus that regularly is seen in the basidiomes of the common *Tremella encephala* is nothing other than its host fungus, *Stereum sanguinolentum* (Bandoni 1984; Helfer 1991). One species of *Tulasnella* and three of

FIGURE 17.11 Synnemata of *Gliocladium polyporicola* growing on *Stereum* species. (Photo by K. Põldmaa)

Exidiopsis have been found growing inside corticioid fungi, whereas two species of *Platygloea* (*Achroomyces*) and *Syzygospora* and four of *Tremella* have been found growing on their hymenia (Jülich 1983). Gelatinous and hyaline basidiocarps of *Syzygospora* species grow on basidiocarps of *Leucogyrophana* and *Phanerochaete* species (Hauerslev 1969; Ginns and Sunhede 1978). *Tremella mycophaga* and *T. simplex* parasitize *Aleurodiscus amorphus* (Ginns and Sunhede 1978).

Clavariaceous fungi often are colonized by *Mycogone calospora* (Gams 1983) and *Helminthosphaeria clavariarum* (anamorph *Spadicoides clavariarum*; Samuels et al. 1997).

On Jelly Fungi. While jelly fungi (mainly Tremellales) are often mycoparasitic, few reports are available about their function as hosts for other parasites. *Acremonium psammosporum*, *Verticillium*, and *Chalara* species; *Hypomyces aurantius*; and *Ophiostoma epigloeum* have been found as parasites on *Tremella* species, and *Dactylaria lanosa* has been isolated from *Pseudohydnum gelatinosum* (CBS, unpublished data). *Tremella danica* can grow on or in *Myxarium nucleatum* (Hauerslev 1979). Fungi parasitizing *Auricularia* species include *Acremonium* and *Verticillium* species, *Hypomyces semitranslucens*, and three species of *Cladobotryum* (CBS, unpublished data). *Hypomyces mycophilus* (anamorph *Cladobotryum polypori*, synonym *Pseudohansfordia* [*Dactylaria*] *mycophila*) also was reported from *Hirneola* (*Auricularia*) *polytricha* (Tubaki 1955). *Hypocrea sulphurea* is always found on remnants of *Exidia* species (B. Overton, personal communication).

An epibiotic chytrid, *Rhizophlyctis* species, was found on *Dacrymyces stillatus* (Canter and Ingold 1984). *Tremella obscura* (Reid 1970), *Sebacina penetrans* (Hauerslev 1979; Oberwinkler and Bandoni 1982), and *Itersonilia perplexans* (CBS, unpublished data) also can attack *Dacrymyces* species. Two species of *Platygloea* (*Achroomyces*) and two of *Tremella* were found on or in the hymenium of Dacrymycetaceae (mainly *Dacrymyces* species). While *Achroomyces peniophorae* has a thin, gelatinous, pustulate basidiocarp, which later turns confluent and resupinate; the other species of *Platygloea* and *Tremella* lack basidiocarps (Jülich 1983).

Several ascomycetes and mitosporic fungi that are normally lichenicolous grow preferentially on basidiomata of lichenicolous heterobasidiomycetes (Diederich and Christiansen 1994; Diederich 1996).

On Polypores (Bracket Fungi). A considerable range of fungicolous species can grow on sporocarps of polypores; the most commonly recorded species are listed in Table 17.5. Those fungicolous fungi often cover the surface of the perennial carpophores without harming the host (Rudakov 1981). *Hypomyces aurantius* disrupts the cytoplasm and causes irreversible changes in the host cells (Kellock and Dix 1984). Besides *H. aurantius* and several other *Hypomyces* species (Table 17.5), a number of closely related anamorphic species (*Cladobotryum* species) also inhabit the sporocarps of aphyllophorales. Several anamorph–teleomorph connections have been established in this complex (Helfer 1991; Rogerson and Samuels 1993; Põldmaa 1996; Põldmaa et al. 1997; Põldmaa and Samuels 1999).

Fungi occupying decaying wood, particularly polypores, are frequently strong antagonists of a wide range of other fungi, at least in laboratory culture (Cooke 1977). Antagonism may facilitate colonization of freshly cut stumps or logs (i.e., primary resource capture); it also may suppress predecessors from older, precolonized substrata (secondary resource capture) (Griffith and Barnett 1967; Rayner et al. 1987). Antagonistic activities of any kind are influenced by the available carbon and nitrogen sources (Griffith and Barnett 1967; Barron 1992). Displacement reactions between several wood-decaying aphyllophorales, such as *Trametes versicolor* by *Lenzites betulina*, *Bjerkandera adusta* by *Pseudotrametes gibbosa*, various fungi by *Schizophyllum commune*, and *Datronia mollis* by *Phanerochaete magnoliae*, have been examined in experiments using agar cultures or wood blocks and interpreted as cases of hyphal interference (Ainsworth and Rayner 1991; Jeffries and Young 1994). It is not clear whether laboratory-based observations of the replacement reactions will be supported by field observations because a succession need not be followed by sporocarp formation in nature (Niemelä et al. 1995).

Polypores commonly are colonized by some *Cosmospora* species. *Hydropisphaera* (*Nectria*) *peziza* is also frequent on *Polyporus*, mostly *P. squamosus*. *Pseudonectria tilachlidii* and the synnemata of its anamorph, *Tilachlidium brachiatum*, common on agarics, also can be found on the hymenium of polypores, especially of *Tyromyces* species (Helfer 1991; K. Põldmaa, personal observation).

The ascomata of *Ophiostoma polyporicola*, often hidden inside pores of bracket fungi, have been discovered only recently (Constantinescu and Ryman 1989; Helfer 1991). The species frequently is found on sporocarps of *Fomitopsis pinicola* and *Piptoporus betulinus* and almost always occurs together with *Hypocrea pulvinata*, sometimes growing out from its stromata (K. Põldmaa, personal observation). It has been recorded from sporocarps of other aphyllophorales (*Antrodia*, *Tyromyces*) as well (Helfer 1991). *Melanospora lagenaria* (Fig. 17.12) also grows on *F. pinicola*, often together with *O. polyporicola* and *H. pulvinata* (Fig. 17.13). It also has been recorded on species of *Bjerkandera*, *Trametes*, *Polyporus*, *Pipto-*

TABLE 17.5
Common Fungi That Grow on Polypores

Species (anamorph)	Host	Reference
Hypomyces aurantius (anamorph *Cladobotryum varium*), *H. rosellus (C. dendroides)*, *H. semitranslucens (C. fungicola)*, *H. orthosporus (C. orthosporum)*, *H. odoratus (C. mycophilum)*	Various aphyllophorales	Kellock and Dix 1984; Rogerson and Samuels 1993; Pöldmaa and Samuels 1999
H. polyporinus (*C. clavisporum*)	Mostly *Trametes versicolor*, occasionally other aphyllophorales	Kellock and Dix 1984
H. subiculosus (*Cladobotryum* species)	Various aphyllophorales, often *Trametes* species	Kellock and Dix 1984
H. mycophilus (C. polypori)	Various aphyllophorales, often *Polyporus* species	Kellock and Dix 1984
Cosmospora vilior (Acremonium berkeleyanum)	Various polypores	Gams 1971
C. coccinea (syn. *Nectria cosmariospora;* anamorph *Verticillium olivaceum*)	*Inonotus*	Gams 1971; Helfer 1991; Samuels et al. 1991
Cosmospora purtonii (Fusarium aquaeductum var. *aquaeductuum)*	Polypores	Wollenweber and Reinking 1935; Domsch et al. 1980
Hydropisphaera (Nectria) peziza (*Acremonium* species)	*Polyporus* species, mostly *P. squamosus*	Samuels 1976
Pseudonectria tilachlidii (Tilachlidium brachiatum)	Agarics, polypores, especially *Tyromyces*	Helfer 1991
Sphaerostilbella (Hypomyces) broomeana (Gliocladium microspermum)	*Heterobasidion annosum*	Põldmaa 1999; Pöldmaa et al. 1999; Gams and van Zaayen 1982
Hypocrea pulvinata (syn. *H. fungicola*)	*Fomitopsis pinicola, Piptoporus betulinus*	Doi 1972; Helfer 1991
Hypocrea pallida	Various aphyllophorales, often *Tyromyces* species	Doi 1972; Helfer 1991
Trichoderma polysporum	Polypores	Helfer 1991
Sporophagomyces chrysostomus	Ganodermataceae	Rogerson and Samuels 1993; Põldmaa et al. 1999
Ophiostoma polyporicola	*Fomitopsis pinicola, Tyromyces* species, *Piptoporus betulinus*	Constantinescu and Ryman 1989; Helfer 1991
Melanospora lagenaria	*Fomitopsis, Bjerkandera, Trametes, Polyporus, Piptoporus, Stereum* species	Cannon and Hawksworth 1982
Albertiniella polyporicola (syn. *Cephalotheca splendens*)	*Ganoderma* species	Helfer 1991
Orbilia inflatula	*Fomes fomentarius*	Helfer 1991
Cistella hymeniophila (Phialophora rhodogena)	*Antrodia, Piptoporus* species	Helfer 1991
Bisporella citrina	*Daedaleopsis confragosa*	Helfer 1991
Eleutheromyces subulatus	*Trametes* species	Helfer 1991
Endomyces polyporicola	*Piptoporus betulinus*	Schumacher and Ryvarden 1981; de Hoog et al. 1986
Rhinotrichella globulifera	Polypores	Helfer 1991

porus, and *Stereum* (Cannon and Hawksworth 1982), whereas the related *M. caprina* is found primarily on *Tomentella* species and other tomentelloid fungi.

Some discomycetes occur on carpophores of polypores and other aphyllophorales (Helfer 1991). The apothecia of *Hyphodiscas hymenophilus* rarely are found on sporocarps of *Antrodia* and *Piptoporus*, whereas its anamorph, *Catenulifera rhodogena*, commonly stains the hymenium of many aphyllophorales red (Helfer 1991). *Hyaloscypha epiporia* has been found only on polypores growing on softwood, usually covering the pore surface of old, partly decayed sporocarps of *Amylocystis lapponica* (Huhtinen 1989). It is one of the few *Hyaloscypha* species that fruits in culture. A few other discomycetes (e.g., *Bisporella citrina*) have been reported on sporocarps of polypores. However, the apothecia usually also are found on the wood nearby.

Coelomycetes are not frequent on sporocarps of aphyllophorales. A characteristic and common representative is *Eleutheromyces subulatus* with an almost yeastlike synanamorph; it is not easily found because it may be hidden among the pores of the host. The tiny black pycnidia of the rare *Eleutheromyces* (*Eleutheromycella*) *mycophilus*, which only occur on *Trametes* species, are even harder to find.

Endomyces (*Dipodascus*) *polyporicola* is a parasitic hemiascomycete found on *Piptoporus betulinus* (Schumacher and Ryvarden 1981; de Hoog et al. 1986).

FIGURE 17.12 Perithecia of *Melanospora lagenaria* growing on the hymenophore of *Ganoderma* species. (Photo by K. Põldmaa)

FIGURE 17.13 Stromata of *Hypocrea pulvinata* on a decaying basidioma of *Piptoporus betulinus*. (Photo by U. Kõljalg)

Mycelia of different mycoparasites, particularly species of *Acremonium*, *Monocillium*, *Fusarium*, *Gliocladium*, *Scopulariopsis*, *Sporotrichum*, and *Rhinotrichella* often are found growing inside perennial carpophores. *Calcarisporium arbuscula*, *Rhinotrichella globulifera*, *Clonostachys rosea*, *C. catenulata*, *Gliocladium polyporicola*, and *G. viride* are found on decaying polypore sporocarps.

Antagonists of the mycelium of the root rot fungus, *Heterobasidion annosum*, have been studied intensively. *Phlebiopsis* (*Peniophora*) *gigantea* is its most successful competitor (Rishbeth 1963). Among the antibiotically most active antagonists are species of *Scytalidium*; polyphenol oxidases that induce brown discoloration also seem to be involved in their competitive activity (Klingström and Johansson 1973).

Two species of heterobasidiomycetes associated with poroid fungi are known. *Tremella polyporina* can replace the hymenium on the basidiocarps of *Postia* (*Tyromyces*) *caesia* and *P. lactea* (Reid 1970), and *Exidiopsis opalea* is found on other old polypores (Jülich 1983). A yeast isolated from a sporocarp of *Ganoderma applanatum* was identified as *Ustilago maydis* when examined with molecular methods (Prillinger et al. 1989). Hawksworth (1981a) lists many additional, often rather nonspecific, colonizers of polypores.

Sporocarps of wood-rotting aphyllophorales often appear on those of other polypores. A special group of wood-rotting fungi (called successors) inhabits woody material that previously has been decayed by certain other species (predecessors) (Niemelä et al. 1995). *Fomes fomentarius*; *Fomitopsis pinicola*; and species of *Inonotus*, *Trichaptum*, and *Phellinus* are common predecessors. The great majority of successors are white-rot fungi, with *Antrodiella* species being the best known. The sporocarps of the successors often develop on those of the predecessors. For example, *Antrodiella citrinella* grows on sporocarps of *Fomitopsis pinicola*, and *A.* (*Trametes*) *hoehnelii* grows mainly on those of *Inonotus radiatus* (Jahn 1963). Possibly the repeatedly observed association of the rare *Boletus* (*Buchwaldoboletus*, *Pulveroboletus*) *lignicola* and *Phaeolus schweinitzii* on the same conifer stump is such a phenomenon (Szczepka and Sokól 1984; Lipka 1985). Sporocarps of successors also can develop away from those of predecessors on the same trunk. Because an interaction between the mycelia may take place within the decaying wood, the fruiting of one fungus on another could signal a competitive, parasitic, or dominance relationship (Niemelä et al. 1995). However, channels left inside the wood by mycelial strands of dead fungi may act as canals for hyphae of succeeding fungi, which may result in their fruiting on the dead basidiocarps of the first colonizer. Thus, an observed succession in fruiting does not indicate whether a successor is behaving as a selective parasite or whether it is just profiting from the way opened by its predecessor (Niemelä et al. 1995). Many observations of this kind

simply may represent the accidental co-occurrence of different wood-rotting fungi. Tomasi (1977), building on the work of Bourdot and Galzin (1928), and Besl et al. (1989) presented overviews of aphyllophorales growing on different polypores. The common occurrence of *Sistotrema brinkmannii* on old basidiomes is obviously a case of succession of a rapid and competitive colonizer onto a suitable substratum (Eriksson et al. 1984).

On Fleshy Sporocarps of Boletales and Agaricales. Zygomycetes that grow on agarics and boletes include species from common genera such as *Mortierella* and *Umbelopsis* (*M. bainieri*, particularly on *Amanita* species, and the less specific *U. ramanniana*) and nonspecific species of *Mucor* and *Rhizopus* found in soil and other substrata. The genera *Spinellus*, *Syzygites*, and *Dicranophora* comprise only mycoparasitic species. *Spinellus fusiger* and four congeners occur mainly on *Mycena* species but also have been recorded from other agarics (*Amanita*, *Gymnopus* [*Collybia*], *Hygrophorus*). *Syzygites megalocarpus* grows on decaying agarics and boletes (Hesseltine 1957). *Dicranophora fulva* is a rare species found on *Paxillus*, *Gomphidius*, and *Leccinum* species (Jeffries and Young 1994; Voglmayr and Krisai-Greilhuber 1996).

The most common and representative fungicolous ascomycete genus is *Hypomyces*. Many species of the genus and their anamorphs attack fleshy sporocarps (Rogerson and Samuels 1989, 1994). Boleticolous species of *Hypomyces* more or less malform host basidiocarps, although the tube layer usually is still recognizable. Such partially altered hosts still may be identifiable to genus and species (Rogerson and Samuels 1989). Most boleticolous *Hypomyces* species can use a wide range of hosts, and only a few appear to be specialized to a host genus or species (Sahr et al. 1999). *Hypomyces chrysospermus* (anamorph *Sepedonium chrysospermum*) attacks all kinds of Boletales with tubular and lamellar hymenophores, including the gasteroid *Scleroderma* and *Melanogaster*. The species also has been reported as a mycoparasite of *Sclerotinia sclerotiorum* (F. Marziano, personal communication; CBS, unpublished data) and powdery mildews (Hijwegen 1992a). *Hypomyces completus* (anamorph *S. brunneum*) and *H. transformans* colonize species of *Suillus* (Rogerson and Samuels 1989; Sahr et al. 1999). *Sepedonium chalcipori* specifically parasitizes the acrid *Chalciporus piperatus* (Helfer 1991), and *H. melanocarpus* is found only on the bitter *Tylopilus* species (Rogerson and Samuels 1989).

Eight of the agaricicolous species of *Hypomyces* occur only on members of the Russulaceae. *Hypomyces luteovirens* is restricted to *Russula* species; *H. lithuanicus* (*H. torminosus*) is restricted to the *Lactarius torminosus* group; and *H. lateritius*, *H. lactifluorum*, *H. macrosporus*, and *H. banningiae* also are restricted to species of *Lactarius*. *Hypomyces hyalinus* grows only on *Amanita* species, Three other species are found on brown- (or pink-) spored agarics: *H. succineus* on *Pholiota* species, *H. porphyreus* on *Entoloma* (*Leptonia*) *strigosissimum*, and *H. tremellicola* on *Crepidotus* species (Rogerson and Samuels 1994). In addition, *Nectriopsis tubariicola* (probably also a member of *Hypomyces*) is found on *Tubaria* species (Gams and van Zaayen 1982).

Some *Hypomyces* species transform the gill surface of the host's pileus into an ascomycetous hymenium. In fact, *H. lactifluorum* and *H. hyalinus* render their hosts unrecognizable so that only healthy basidiocarps in the neighborhood allow identification of the host (Fig. 17.3). One of the most ubiquitous parasites on species of *Russula* and *Lactarius* is *H. armeniacus* (synonym *H. ochraceus*, anamorph *Cladobotryum verticillatum*, synonym *Monosporium agaricinum*), which occurs mainly as an anamorph and completely destroys its host. After the host basidiome has decayed, *H. armeniacus* grows away from it onto soil, mosses, or other nearby substrata, where the perithecia are formed. The anamorphs of the common aphyllophoricolous *H. aurantius*, *H. odoratus*, and *H. rosellus* also often are found on various agarics but form perithecia only on aphyllophorales, wood, or bark (Põldmaa 1999). Some anamorphic species related to *Hypomyces* also colonize the sporocarps of agarics (de Hoog 1978; Helfer 1991). *Mycogone rosea*, for example, has been recorded on agarics belonging to nine genera, but particularly *Amanita* (Arnold 1976), whereas *Cladobotryum apiculatum* is known to grow mainly on sporocarps of *Lactarius* and *Russula* species (Gams and Hoozemans 1970; Helfer 1991). Other anamorphic species have so far been collected only once or twice on agarics. *Hypocrea avellanea* and its *Verticillium* anamorph have been found only on *Marasmius subnudus* (Carey and Rogerson 1976).

Melanosporopsis subulata and *Dendrostilbella mycophila* rarely are found on dark, discolored agarics. Their coexistence, identical nuclear DNA content, and other evidence indicate that the latter is the anamorph of the former (Helfer 1991).

The *Geotrichum* anamorph of *Dipodascus armillariae* (Gams 1983) is observed regularly and specifically on the gills of old sporocarps of *Armillaria* species, but its asci could not be obtained on agar media. The redefined genus *Endomyces*, which is characterized by hat-shaped ascospores and slimy blastoconidia (Redhead and Malloch 1977), comprises a group of SCIF found on agarics. Redhead and Malloch also found a related taxon, *Phialoascus borealis*, on a decaying *Cortinarius*. An additional species of *Endomyces* occurs on *Tricholoma* species (Helfer 1991).

Putrefying agarics and boletes provide suitable substrata for a number of yeasts. Ramírez Gómez (1957) obtained more than a hundred yeast species from about the same number of macromycetes. Several anamorphic yeasts, including *Candida anomala* (*Debaryomyces hansenii*), *C.* (*Rhodotorula*) *buffonii* (on *Boletus edulis*), *C. obtusa* var. *arabinosa* (*Pichia mississipiensis*; on *Clitopilus prunulus*), and *C.* (*Torulopsis*) *kruisii* (on *Boletus purpureus*) are known only from agarics. The ubiquitous *Sporobolomyces roseus* has been isolated from *Leccinum aurantiacum* (Hawksworth 1981a).

Among the fungicolous hyphomycetes, one of the most common species is *Calcarisporium arbuscula*, found in the growing sporocarps of many agarics, including species of *Russula* and *Lactarius* (Watson 1955). It either sporulates quickly and profusely or develops as a symptomless "endophyte," revealing its presence only when it begins to sporulate on old host sporophores or when small pieces of the sporophores are placed on agar (Barnett and Lilly 1958; Nicot 1968). It generally colonizes the basidiomes of *Cantharellus cibarius* so that isolation of that species from tissue is impossible (Schouten and Waandrager 1979). Damaged hyphae of many Russulaceae produce isovelleral, a defense metabolite, which *C. arbuscula* detoxifies by reducing it to isovellerol; other SCIF tolerate isovelleral without transforming it (Anke and Sterner 1988).

Verticillium fungicola and its varieties occur frequently on agarics in nature (see also "On Fleshy Sporocarps and Mycelium of Cultivated Agaricales," later in this chapter). An undescribed species of *Verticillium* regularly occurs on *Gymnopus* (*Collybia*) *peronatus* in the Netherlands (W. Gams, personal observation). The synnemata of *Tilachlidium brachiatum* are rather common on the stipes of old agarics, particularly *Hypholoma* and *Mycena* species (Gams 1971); its rare teleomorph, *Pseudonectria tilachlidii*, also has been found on an old agaric (Gams 1975a). The species has not been recorded outside fungal sporocarps, but it is difficult to distinguish *in vitro* from *Acremonium berkeleyanum*.

Various other anamorphic fungi occur on sporocarps of agarics and boletes. *Gabarnaudia tholispora* has been found on *Russula nigricans* (Hawksworth 1983). Rarer mycoparasites include *Amblyosporium* on *Peziza*, *Paxillus*, and *Lactarius* species (Nicot and Durand 1965, citing a discomycete teleomorph; Pirozynski 1969; CBS, unpublished data) and *Harziella capitata* on *Lepista nuda* (Fontana 1960).

Only a few species of coelomycetes are known to grow on agarics, particularly *Eleutheromyces subulatus* (Seeler 1943; Helfer 1991) and the basidiomycete anamorph *Hyalopycnis blepharistoma* (Bandoni and Oberwinkler 1981).

Among the fungicolous basidiomycetes, species of *Syzygospora* are causal agents of gall formation. This is a rare phenomenon confined to particular agaric hosts and a few associated parasites (Fig. 17.14) (Hauerslev 1969; Ginns and Sunhede 1978; Oberwinkler et al. 1984; Ginns 1986). Their hymenia cover galls, which appear on the lamellae, the surface of the pilei, and the stipes of *Gymnopus* and *Marasmius* species, sometimes almost enveloping the mushroom. The inner part of the gall is formed of the hyphae of the host.

Only in two agaric genera are all species fungicolous. Two species of *Asterophora* (= *Nyctalis*; Tricholomataceae) attack species of Russulaceae and rarely *Gymnopus* (*Collybia*) *fusipes* and form abundant chlamydospores in their basidiomes. Both *Asterophora lycoperdoides* (synonym *N. asterophora*) and *A. parasitica* complete their entire development on an agaric in about 3 weeks (Buller 1924). These species grow and sporulate well in pure culture when the substratum contains a high ratio of organic nitrogen to carbohydrate (Jeffries and Young 1994).

The irregular swellings always present at the base of *Squamanita* species (Tricholomataceae) have been described as protocarpic tubers. *Squamanita* is recognized as an obligately parasitic genus whose species grow on sporophores of other basidiomycetes. Systemic infection of host sporophore primordia causes gall formation (Redhead et al. 1994). The galls vary from pileate or stipitiform to amorphous, are composed of host basidiome tissue infused with *Squamanita* hyphae, and bear one to several *Squamanita* basidiomes. The 10 known species have hosts in the genera *Cystoderma*, *Phaeolepiota*, *Tubaria*, *Galerina*, and others.

Isolated fungicolous species occur in some larger genera. *Volvariella surrecta* (synonym *V. loveiana*) (Fig. 17.15), for example, specifically colonizes intact or deformed caps of *Lepista nebularis* and *Clitocybe*

FIGURE 17.14 Galls of *Syzygospora tumefaciens* on *Gymnopus* (*Collybia*) *dryophilus*. (Photo by W. Gams)

FIGURE 17.15 *Volvarialla surrecta* fruiting on old *Lepista nebularis*. (Photo by W. Gams)

clavipes. *Psathyrella* (*Stropharia*) *epimyces* fruits on deteriorated *Coprinus atramentarius* and *C. comatus* in North America. *Entoloma* (*Claudopus*) *parasiticum* has been reported from *Cantharellus cibarius*, *Craterellus cornucopioides*, and *Coltricia* (*Polyporus*) *perennis* (Noordeloos 1992; Helfer 1991; Jeffries and Young 1994); *Entoloma pseudoparasiticum*, with paler basidiocarps, also grows on *Cantharellus cibarius* and *Craterellus lutescens* (Noordeloos 1992), and the related *E. byssisedum* grows on hypogeous sporocarps of truffles and gasteromycetes (Malençon 1942). Conversely, the phenomenon of abortive basidiomes in *E. abortivum* (Fig. 17.16) is ascribed to mycoparasitism by *Armillaria mellea* (Watling 1974; Jeffries and Young 1994).

Four species of *Collybia* sect. *Collybia* have been found to attack a wide range of hosts from several orders of basidiomycetes. *Collybia cookei*, *C. racemosa*, and *C. tuberosa* form sclerotia in mummified host basidiomes and may develop their own basidiomes directly from their sclerotia in soil, often after all visible remains of the hosts have vanished; *C. cirrhata* is similar, but lacks sclerotia. Mycophagy (not necessarily mycoparasitism) by two species of *Lyophyllum* on rotting basidiocarps of *Russula* and *Lactarius* species and unidentified rotting basidiomycetes also has been documented (Redhead et al. 1994).

A phenomenon termed sporophagy was observed when the large pigmented basidiospores of *Leccinum aurantiacum* and other basidiomycetes (including *Paxillus*, *Suillus*, *Gomphidius*, *Pluteus*, and *Thelephora*) were offered as bait to other basidiomycetes. Hyphae of *Coprinus comatus*, *Pluteus cervinus*, and numerous aphyllophorales, but not ectomycorrhizal fungi, penetrated

FIGURE 17.16 Abortive basidiomata of *Entoloma abortivum* parasitized by *Armillaria mellea*. (Photo by K. Põldmaa)

the spores (Fries and Swedjemark 1985), but the hyphae of the same fungi were not attacked. The effect was influenced by the nutrient content of the supporting medium.

Examples of hyperparasitism on SCIF include species of *Asterophora* that can host *Pyxidiophora asterophorae* (Lundqvist 1980) and an intracellular *Tremella*-like yeast (Laaser et al. 1988). *Eleutheromyces subulatus*, which also grows on old sporocarps of *Russula* species, supports growth of *Nematogonum mycophilum* (Gams 1975b). *Boletus parasiticus*, growing on *Scleroderma citrinum*, is attacked by a particular species of *Penicillium* (W. Gams, personal observation).

On Thalli of Lichenized Agarics. *Norrlinia peltigericola*, *Lichenopeltella minuta*, and *Stigmidium joergensenii* parasitize the thallus of the lichenized *Lichenomphalia* (*Omphalina*) *foliacea* (Santesson 1989). An undescribed species of *Cercidospora* has been collected twice on the lichenized thallus of *Lichenomphalia umbellifera* (J. Hafellner, personal communication). *Merismatium nigritellum* parasitizes *Lichenomphalia hudsoniana* and various lichenized ascomycetes (Triebel 1989). The congeners of all of the parasitic species grow on lichenized ascomycetes.

On Fleshy Sporocarps and Mycelium of Cultivated Agaricales. Fungal infections may cause great losses in mushroom farms. Infections are of two types: weed molds that contaminate the mushroom compost and compete with the mycelium of the commercial mushrooms and parasites of the sporocarps. Weed molds include *Myceliophthora* (*Chrysosporium*) *lutea*, *Peziza ostracoderma* (anamorph *Chromelosporium fulvum*), and *Trichoderma* species (Jeffries and Young 1994; Samuels et al. 2002). Generally, the cobweb disease damaging the cultivated *Agaricus* has been ascribed to the anamorph of *Hypomyces rosellus* (*Cladobotryum dendroides*). McKay and colleagues (1999), however, showed by the analysis of molecular data that most of the isolates responsible

for the disease represent the anamorph of *H. odoratus* (*C. mycophilum*). The cobweb disease can be controlled relatively easily by hygienic measures. The false truffle, *Diehliomyces microsporus*, is mainly a competitor that prevents colonization of the substratum by the mushroom. It is found primarily in warmer countries and always is associated with cultivated mushrooms (van Zaayen and van der Pol-Luiten 1977).

Hypocrea and *Trichoderma* species adversely affect cultivated wood-decaying fungi (Hashioka et al. 1961; Hashioka and Komatsu 1964; Komatsu and Hashioka 1964; Komatsu 1976; Tsuneda and Thorn 1995). Tsuneda and Thorn (1995) found that frequency of occurrence and strength of mycoparasitic activity of *Trichoderma harzianum* on the wood decay fungi *Lentinula edodes* and *Pleurotus ostreatus* were influenced by the degree of wood decay. Tsuneda and associates (1997) found that the *Hyphozyma* synanamorph of *Eleutheromyces subulatus* is highly pathogenic to and causes black spot symptoms in the shiitake mushroom (*Lentinula edodes*) grown outdoors on *Quercus* bedlogs. Reper and Pennincky (1987) reported that a diffusible toxin from *T. hamatum* damaged *P. ostreatus*. The presence of cellulose and chitin microfibrils seemed to enhance the mycoparasitic activity. In the last decade, highly aggressive strains of a taxon initially identified as *T. harzianum* (genetically different from the biocontrol taxon and then named *T. aggressivum*) are causing heavy losses in cultivated mushrooms in the United Kingdom, Canada, the United States, and Australia (Seaby 1987; Muthumeenakshi et al. 1994; Samuels et al. 2002). Recently, aggressive strains of *Trichoderma virens* also have been found to attack cultures of *Pleurotus ostreatus* (CBS, unpublished data).

However, *Agaricus bisporus* benefits from a preceding colonization of the compost by *Scytalidium thermophilum*, which prepares the substratum during a thermophilic phase and then is inactivated by the *Agaricus* (Straatsma et al. 1989, 1994). The regular and intimate association of *Xylaria* and *Termitomyces* species in the fungus gardens of termites may be a comparable case, in which the *Xylaria* seems to prepare the substratum for colonization by the agaric, but the relationship is not fully understood (Batra and Batra 1977).

One of the best-known sporocarp diseases of *Agaricus bisporus* is the wet bubble caused by *Mycogone perniciosa*. Symptoms range from external infection of the normal sporophore to its total distortion into a spherical sclerodermoid form (Smith 1924). Up to 30% of apparently healthy sporophores from an affected crop may be infected at the base of the stipes (Fletcher and Ganney 1968). Other hosts of this species include wild species of *Agaricus* and the cultivated *Volvariella esculenta* (CBS, unpublished data). The top cell of the *Mycogone* aleurioconidia survives a long time but requires stimulation (e.g., mushroom extract or a period of low temperature) for germination (Holland et al. 1985). In paired cultures of some anamorphs of *Hypomyces* species or of *Verticillium* species with *A. bisporus*, the parasite usually overgrew the host and caused necrotization of its hyphae, an indication of intense mycoparasitism (Gray and Morgan-Jones 1981).

Verticillium fungicola var. *fungicola* (synonym *V. malthousei*), the common causal agent of dry bubble, also causes considerable damage to crops of *A. bisporus*. After *A. bitorquis*, which is immune to virus disease and cultivated at higher temperatures than *A. bisporus*, was introduced as a commercially grown mushroom, another parasitic form, *V. fungicola* var. *aleophilum*, appeared. It produces brown spots on the cap resulting in inferior quality mushrooms (van Zaayen 1981; van Zaayen and Gams 1982). *Lecanicillium psalliotae* is also pathogenic to *A. bitorquis* (van Zaayen and Gams 1982), whereas *Simplicillium lamellicola* leads to "gill mildew" at high cropping temperatures or development of dark brown spots in large, open mushrooms. The polyphagous *Lecanicillium aphlanocladii* (= *Aphanocladium album sensu lato*) also has been reported to infect mushroom sporocarps and to reduce yield in Australia (van Zaayen and Gams 1982). Apparently, *Verticillium fungicola* can be controlled by spraying with a mix of *Lecanicillium* species conidia (de Trogoff and Ricard 1976).

Lecanicillium psalliotae also has been found to parasitize conidiophores and spores of the nematophagous *Rhopalomyces elegans* and other Mucorales (Dayal and Barron 1970). *Mycogone perniciosa* has the same capacity, and the infected spores of a host may contribute to the spread of this parasite (Barron and Fletcher 1972). *Verticillium dahliae* and *V. albo-atrum* can parasitize the nematophagous *Rhopalomyces* (Barron and Fletcher 1970). The nonspecialized mycoparasite *Pythium oligandrum* causes a disorder in *Agaricus bisporus* that results in black patches on the cap (Fletcher et al. 1990). *Mortierella bainieri* occasionally attacks mushrooms causing "shaggy stipe" (Jeffries and Young 1994).

On Epigeous and Hypogeous Sporocarps of Gasteromycetes. Relatively few taxa have been studied for parasites, and few specific colonizers have been found. Most observations are of species of *Scleroderma*, which are colonized by many nonspecific fungicolous fungi, including *Verticillium luteo-album* and other *Verticillium* species, *Trichothecium roseum*, and *Sepedonium chrysospermum*. The latter species also has been found on *Melanogaster* and *Rhizopogon*, genera supposedly related to the Boletales. *Boletus parasiticus* (also classified in *Pseudoboletus* or *Xerocomus*) consistently fruits on sporocarps of *Scleroderma* species, particularly *S. citrinum*,

whereas *Xerocomus astraeicola* is found on *Astraeus hygrometricus* (Sclerodermataceae). *Xerocomus astraeicolopsis* has been reported from the same host in China (Redhead et al. 1994). The relationship between *B. parasiticus* and *Scleroderma* may not actually be parasitic but just coincidental fruiting stimulated by the host (Rayner et al. 1985). Agerer (1991) observed a probable association of *B. parasiticus* with the mycorrhiza of *Scleroderma* species in *Picea abies.*

A discomycete, *Gelatinipulvinella astraeicola* (yeastlike anamorph named *Aureohyphozyma astraeicola*), was found on the decaying peridium of *Astraeus hygrometricus;* the glebal portion of the host clearly was dead, suggesting that *G. astraeicola* does not need a living host for fruiting (Hosoya and Otani 1995). The stromata of *Hypocrea latizonata* form bands on the cuplike sporocarps of *Cyathus striatus* (Lohman 1938). *Podostroma solmsii* is another host-specialized fungus that grows on unexpanded sporocarps of *Phallus impudicus* (Doi 1978). *Hypomyces odoratus* also has been recorded from *Lycoperdon piriforme* (CBS, unpublished data). Additional colonizers are listed in Hawksworth (1981a). *Cystofilobasidium capitatum* is a rare case of a mycoparasite found in the gleba of Phallaceae (Oberwinkler et al. 1983), but this fungus also is found as a saprotroph on waxberries (*Symphoricarpus albus*; R.C. Summerbell, personal communication).

Methods of Study

Methods used to detect SCIF are similar to those used to collect macromycetes (Arnolds 1992; see Chapter 8). Parasites of slime molds usually are studied only by experts in the myxomycetes who have their own methods of collecting (see Chapter 25). Parasites of macromycetes also usually are studied by specialized investigators. Collection and quantification of SCIF are subjected to the same constraints as that of their hosts, with the additional difficulty that the occurrence of the parasites is often even more erratic than the fructification of the hosts (Arnolds 1992). The short-lived existence of macromycete sporocarps can be shortened even further by the attack of fungicolous fungi. Some of the latter outlive their hosts and fruit only on significantly decayed sporocarps; others sporulate abundantly with their anamorph on the basidiome, whereas perithecia appear only on the almost vanished host substratum or other substrata nearby.

SCIF usually are easy to detect in nature owing to macroscopically visible deformations and color changes of the host fungi. Still, mycelia with conidia and tiny perithecia (e.g., those of the species of Hypocreales) are scarce and easily overlooked on the sporocarps of Aphyllophorales. To study the fungi inside the hymenium of perennial polypores, the sporocarps must be cut open. Specimens are collected and stored separately in boxes or paper bags to keep them clean for culture work. We recommend that observations be made and fungi be isolated as soon as possible after collecting because soft sporocarps, especially those of agarics and boletes, always are inhabited by insects, which very quickly destroy the whole fungus under moist conditions. Also bacteria accumulate rapidly, reducing the chance of obtaining pure cultures. Alternatively, the specimens can be kept in a cool place to slow down their degradation. Preservation of voucher specimens following the procedures outlined in Chapter 2 is crucial (Agerer et al. 2000).

SCIF often sporulate abundantly on a host substratum and can be identified easily. Sometimes the invader can be named in the field, especially if found on a selective host. However, even species of agarics, in which host specificity seems to be the most pronounced, can be colonized by different fungicolous fungi with similar appearance, in which case microscopic examination is needed. In the case of *Hypomyces*, anamorphs often occupy large parts of the host sporocarp, whereas ascomata are scarce and appear only in a late stage of host decay. The anamorphs are often more strongly differentiated than the correlated teleomorphs, facilitating identification (Põldmaa and Samuels 1999). No general guidelines can be given for recognizing the extremely diverse fungicolous Sporidiales and Tremellales in the field (F. Oberwinkler, personal communication). When it is impossible to prepare pure cultures during field expeditions, parts of the infected fungi can be air-dried and used for isolations, even after several months. Conidial material should be kept in a cool place until isolation; dried conidia seem to lose their germination capability rapidly.

In many genera (mainly anamorphic ones), species determination is not possible unless different developmental stages of the fungus are examined in culture and growth rate, texture, pigmentation, and odor are observed. Small amounts of conidia or ascospores transferred with the tip of a fine (glass) needle to media containing antibiotics usually yield pure cultures directly or after a few transfers. However, old decaying sporocarps of polypores often host several fungicolous fungi so that mixed cultures are obtained on transfer. We recommend, therefore, that a dilute spore suspension (taken from the surface of the hymenium) be streaked on the agar medium to allow transfer of pure cultures. Fractions of a deformed host fungus not showing a visible parasite can be incubated in a moist chamber (Appendix I). Such incubation also may serve to promote ripening of ascomata and ascospore production. Transfer of intact remnants of a host onto agar as a whole, before purifying the cultures, also can activate some biotrophic mycoparasites (Rudakov 1981).

The majority of the SCIF (and fungicolous fungi in general), even true biotrophs and necrotrophs, are able to grow and produce their conidial apparatus and sometimes also the sexual fructifications on ordinary culture media. Some investigators prefer cornmeal agar (CMA; a nutritionally poor, transparent medium), sometimes with 2% dextrose or oatmeal agar; others use malt extract agar (MEA), MEA with peptone, or potato-dextrose agar (PDA). Rudakov (1981) used Czapek agar with yeast and malt extracts. A mixture of PDA and MEA, called *Hypomyces* fruiting agar, enhanced perithecial production of *Hypomyces polyporinus* (Carey and Rogerson 1981). The sporulation of *Cladobotryum* anamorphs of *Hypomyces* tends to deteriorate rapidly after maintenance of a culture on rich media; we recommend use of dilute media such as potato-carrot agar (Gams et al. 1998) or CMA, particularly for long-term preservation. Formulae for the media are available in Appendix II.

Improved sporulation can be obtained by using various mushroom agars containing either mushroom extract (Tubaki 1955, 1975) or homogenized and sterilized carpophores of various host fungi (e.g., *Russula* agar, de Hoog 1978). A polypore extract agar (200 g polypore flour infused with 1 liter of distilled water) or 1% glucose agar with gas-sterilized pieces of polypore blocks has been proposed for the same purpose (Udagawa and Horie 1971).

Reliable isolation from germinated ascospores (preferably single spores) is required to establish the connection of a particular anamorph with a presumed teleomorph. To induce teleomorph formation of heterothallic species in culture, compatible isolates have to be mated. This is often successful in species of *Hypomyces* (Gams and Hoozemans 1970; Rogerson and Samuels 1993, 1994), as well as in fresh ascosporic isolates of other ascomycetes (e.g., *Albertiniella polyporicola*, *Hypocrea pulvinata*, *Hydropisphaera [Nectria] peziza*, *Sphaerostilbella [Nectriopsis* or *Hypomyces] broomeana*, and *Ophiostoma polyporicola*).

Identification

The myxomyceticolous fungi are treated and keys are provided in Gams (1971) and Ing (1974) and in a major contribution by Rogerson and Stephenson (1993), who treated nine species of ascomycetes and 26 species of hyphomycetes.

Helfer (1991) prepared one of the most comprehensive treatments of fungi that grow on fungal sporocarps. Other keys for identifying common SCIF include Arnold (1969) and Ellis and Ellis (1988). Species of SCIF are among the best-studied fungicolous species; nevertheless, many teleomorph–anamorph connections as well as new species, particularly in tropical areas, still await discovery. Tubaki (1955, 1975) surveyed the SCIF in Japan. By far the most commonly observed mycophilic ascomycete genus is *Hypomyces* (Hypocreales) (approximately 55 species described) with (syn-)anamorphs in *Cladobotryum* and in several aleurioconidial genera. Comprehensive descriptions of species growing on discomycetes (five species), boletes (10 species), aphyllophorales (23 species), and agarics (13 species) are available (Gams and Hoozemans 1970; de Hoog 1978; Rogerson and Samuels 1985, 1989, 1993, 1994; Helfer 1991; Põldmaa and Samuels 1999). Several conidial species of *Cladobotryum* and related anamorphic genera have been described from Cuba (Arnold 1986, 1987, 1988; Castañeda 1986; Arnold and Castañeda 1987). The only key for identifying these as well as the other anamorphs associated with *Hypomyces* is provided by Helfer (1991). A review of the literature published on the *Hypomyces* complex was compiled by Arnold (1976).

Wells (1994) surveyed the modern classification of the Tremellales, but other than a key to 35 species of fungicolous heterobasidiomycetes known from Europe (Jülich 1983), no comprehensive literature for the identification of nonlichenicolous, fungicolous heterobasidiomycetes exists.

Major repositories (Appendix III) of authenticated specimens of SCIF include herbaria in Beltsville (BPI) and New York (NY) (collections from C. T. Rogerson and G. J. Samuels), CABI Bioscience in Egham (IMI, for species on tropical foliicolous fungi), Regensburg (REG, collection of W. Helfer), Tartu (TAA, collection of K. Pöldmaa), and Weimar (now University of Jena, JE, collection of G. Arnold). The richest collection of living cultures is preserved in the Centraalbureau voor Schimmelcultures, Utrecht.

Geographic Distribution and Diversity

In contrast to the mostly cosmopolitan soil fungi (see Chapter 13), the distributions of SCIF are determined largely by the presence of their substrata. Macromycete species themselves are more strongly localized as a consequence of continental barriers and differences in climate, soil, and vegetation than are other saprotrophic fungi. Therefore, some of the SCIF are localized considerably over continents and units of vegetation.

Although many fungicolous Hypocreales, particularly their teleomorphs, are found mainly in the tropics, other species are distributed mainly in temperate regions. *Cosmospora* (*Nectria*) *episphaeria*, for example, is common at temperate latitudes but less so in the tropics. Of the other species in *Cosmospora*, however, about 25 species have tropical distributions and 21 species have warm-temperate distributions (Samuels et al. 1991; Rossman et al. 1999). Although species diversity for the genus

Hypomyces is higher in temperate regions, several species, including anamorphic *Cladobotryum* species, have been found only from the tropics. The impression that polyporicolous species of this genus are more numerous in the tropics, but that the agaricicolous are not, may be explained by the distributions of their hosts and the short lives of the host sporocarps. *Hypomyces aurantius* is very common in north- and south-temperate regions but rare in tropical regions. The similar *H. subiculosus* is a species of warm regions, being one of the most common tropical and subtropical species in the genus (Rogerson and Samuels 1993). Many of the species of *Hypomyces* (e.g., *H. aurantius*, *H. semitranslucens*, *H. rosellus)* are probably cosmopolitan. The "cause" of the common lobster mushroom, *H. lactifluorum*, and two other agaricicolous species (*H. banningiae* and *H. macrosporus)* occur only in North America. While those three species obviously have restricted distributions, *H. polyporinus* is frequent on *Trametes* species in North America but also has been found occasionally in Europe, where it has a much wider host range (Põldmaa and Samuels 1999). Several species of *Hypomyces* are known as single records from different regions. They cannot be considered as endemics, however, because of the scarcity of data. However, species reported only from New Zealand are probably endemics. Approximately a dozen species from *Cladobotryum* and closely related anamorphic genera have been described from the tropics, mainly from Cuba (Castañeda 1986; Arnold 1987; Arnold and Castañeda 1987, Bastos et al. 1982), and the same number from Europe (Arnold 1969, 1970; de Hoog, 1978; Helfer 1991; Põldmaa 1996, 1999). According to present knowledge, the distributions of those two groups of species do not seem to overlap.

Oberwinkler (1993) listed several tropical genera among the heterobasidiomycete mycoparasites, particularly *Cryptomycocolax* and *Kryptastrina* in the Platygloeomycetidae. The center of diversification of the Atractiellales is probably in the tropics; the genera *Atractiella* and *Helicogloea*, in particular, are mainly tropical. Similarly, a considerable proportion of the Tremellales are tropical, but their geographic distributions are still poorly known. *Holtermannia* has four tropical species and two in Japan; some species of *Syzygospora* are also tropical.

Species richness of SCIF is high, both in temperate and tropical countries, although the tropics are less well sampled. Apparently the Americas are richer in species than Europe, corresponding to higher numbers of host fungi. Rudakov (1981) found that regions of the former Soviet Union (Moldova, Ukraine, Northern Caucasus, Georgia, Central Russia, Kirgizia, some parts of Siberia, and the Far East) with a humid climate were much richer in mycoparasites growing on either macromycetes or biotrophic plant parasites than regions with a dry climate. Alexopoulos (1970) argued that the colonization of myxomycete sporocarps by filamentous fungi, which is promoted by constant high humidity, is responsible for a limited development of myxomycetes in tropical forests. In accordance with that argument, Rogerson and Stephenson (1993) observed that a very high proportion of myxomycete collections from northwest India during the wet monsoon season were colonized. Although studies of isolated species suggest a locally confined distribution of SCIF, that conclusion should be viewed with caution because sampling in most parts of the world is fragmentary, especially compared with that of macromycetes and other ecological groups of fungi. So far, known distribution patterns probably reflect the distribution of collectors.

Although seasonal variation in the presence and abundance of SCIF depends strongly on that of their hosts, their occurrence is even less regular, making them difficult to locate. Many pleomorphic ascomycetes sporulate abundantly with their anamorph on the host sporocarps, whereas the ascomata (in most cases perithecia) appear only on the strongly decayed sporocarps or on adjacent substrata (bark, mosses). Only the long-lived carpophores of polypores can serve as a substratum throughout the year.

The optimum time for the development of agaricicolous and boleticolous species of *Hypomyces* in temperate zones is usually in the autumn when fleshy fungi are abundant. For example, both *H. luteovirens* and its *Russula* hosts are most common in Norway in August (Eckblad and Torkelsen 1974). In the Moscow region, Rudakov (1981) recorded highest species richness and frequencies of SCIF in the second part of the summer. He ascribed this to the abundance of the hosts, the deposition of dew, and the presence of the inoculum in the air. He also followed the succession of SCIF on agarics, which begins with the development of anamorphs of various species of *Hypomyces*; those forms then are followed by *Calcarisporium arbuscula*, *Acremonium species*, and others. On almost decayed sporocarps, species of *Mucor*, *Mortierella*, *Penicillium*, *Trichoderma*, *Alternaria*, and *Cladosporium* generally supersede the more specific SCIF. Undamaged overwintering of the mycoparasites was observed only after a dry autumn (Rudakov 1981).

Quantification and Relative Importance

A quantitative census of SCIF ideally would involve regular observation of permanent plots. To our knowledge, however, only qualitative inventories of the species present in particular areas, with only rough quantitative estimates, have been carried out.

With some parasites, such as *Hypomyces chrysospermus*, an investigator can tell at a glance whether the host population (many diverse boletes and *Paxillus* species) in an area is infested heavily. The occurrences of other fungicolous taxa, such as species of *Asterophora*, *Squamanita*, and *Volvariella surrecta*, are geographically and seasonally so erratic that their detection requires an extended search over large areas. *Asterophora*, moreover, seems to be affected strongly by environmental pollution and is declining significantly in the Netherlands (Nauta and Vellinga 1995).

Microscopic SCIF, although probably not rare, are usually hardly visible and impossible to identify in the field. Assessment of such fungi would require extensive culturing. To date, however, such time-consuming quantitative methods have not been applied as widely to SCIF as they have been to soil fungi. Of the polypore carpophores studied by Rudakov (1981), 5% contained other fungi, mainly symbiotic so-called semisaprotrophs.

For 5 years Rogerson and Stephenson (1993) collected infected and normal sporocarps of myxomycetes in the Smith Mountain Lake area of southwestern Virginia and then assessed the relative abundances of myxomyceticolous fungi among different host orders. Members of the *Ceratiomyxales*, *Liceales*, and *Trichiales* turned out to be less susceptible to colonization than members of the *Physarales* and *Stemonitales*.

Lichenicolous Fungi

We use the term *lichenicolous* to refer only to those fungi that are obligate residents of lichens, excluding forms that have been found only incidental to culturing. Lichenicolous fungi live on the thalli or ascomata of lichenized fungi. Certain lichens (e.g., species of *Cladonia*, *Lobaria*, *Parmelia sensu lato*, *Peltigera*, *Pertusaria*, *Pseudocyphellaria*, *Usnea)* provide extremely rich habitats for parasites and merit increased study, whereas other lichen groups (e.g., *Pyrenula*, *Thelotrema)* are rarely hosts. As a rule, macrolichens are richer hosts than crustose lichens. In general, however, lichen thalli are resistant to colonization by most saprotrophic fungi, forming a very selective substratum. The firmer lichen ascomata support parasites that are quite different from the SCIF that parasitize nonlichenized discomycetes.

It is not always clear which of the two lichen symbionts—the mycobiont (an ascomycete or rarely a basidiomycete) or the photobiont(s) (an alga or/and a cyanobacterium)—is parasitized. Many species of lichenicolous fungi grow on only a single monophyletic group of lichenized fungi; one can assume that those species, at least, have developed a close relation with the mycobiont. In some species (e.g., *Tremella* species), specialized haustoria have been observed attacking the mycobiont, whereas haustoria of other species attack and kill the algal cells. Very specialized parasites, such as *Blarneya hibernica*, kill the mycobiont and go on to form an independent lichen with the surviving algal cells (Hawksworth et al. 1979).

A number of lichenicolous fungi (e.g., *Arthonia* species) (Fig. 17.6) are closely related to the lichenized fungi and are considered to represent lichens that have lost their ability to form their own thallus. In contrast, species in another group of parasitic, lichenicolous fungi have their own, sometimes reduced, thalli, which appear at the onset of development. Other groups of lichenicolous fungi (e.g., species of *Hypocreales)* are related to nonlichenized taxa.

Lichenicolous fungi that damage their host lichens are considered to be parasitic, whereas those that cause no visible damage are assumed to be commensals (or parasymbionts) (Hawksworth 1982, 1988b). Some lichenicolous fungi induce galls or gall-like growths to form on the lichen thallus but do not damage the lichen. Such fungi sometimes form multiple symbioses with a lichen involving one or more photobionts and two or more mycobionts.

Some lichenicolous fungi have hyperparasites. Pycnidia of the lichenicolous *Lichenoconium usneae*, for example, have been observed parasitizing ascomata of *Abrothallus usneae*, which in turn were growing on the basidiomata of *Biatoropsis usnearum* developing on the lichen; simultaneously, the basidiomata of *B. usnearum* were developing on the lichen *Usnea rigida* (Bricaud et al. 1992; P. Diederich, personal observation).

Historically, few scientists have studied lichenicolous fungi, and the group largely has been neglected. Knowledge of the European and American forms is incomplete; knowledge of such fungi in the rest of the world is nearly nonexistent. Lichenicolous fungi are collected almost exclusively by lichenologists who generally have little experience with nonlichenized fungi; other mycologists rarely collect fungi on this unusual substratum.

Methods of Study

The best way to find and collect lichenicolous fungi is to examine many thalli of different lichen species in the field. Concentrating on abnormal-looking, damaged, or dying lichens may increase the numbers of fungi located, although numerous species grow on healthy thalli without damaging them. By using a hand lens lichenicolous species can often be recognized in the field, although some intrahymenial hyphomycetes or heterobasidiomycetes are detected only after the lichen is studied under a microscope.

Techniques for studying lichenicolous fungi are normally the same as those used for studying lichens—that is, examination under a light microscope of material mounted in water, KOH (potassium hydroxide), lactophenol-cotton blue, or other mountants (see Appendix II, "Mounting Media"). Although culturing is useful for the study of many groups, lichenologists normally do not culture material. Extensive studies of cultures of lichenized and lichenicolous fungi are, however, now in progress (Hawksworth and Jones 1981; Crittenden et al. 1995). Considerable numbers of fungi were isolated from fruticose *Cladonia* species and *Stereocaulon* species in Germany, including soil or litter fungi, symbionts or pathogens of higher plants, and true lichenicolous fungi (Petrini et al. 1990).

Most descriptions of lichenicolous fungal species are, at present, based exclusively on macromorphological and micromorphological characters, and many studies of those species have been carried out on herbarium specimens. Lichenologists, who regularly encounter and collect such fungi, but do not study them, should keep them separated and send them to experts. Major host groups that have been surveyed for lichenicolous fungi are listed in Table 17.6. References for recent monographs on genera of lichenicolous fungi are listed in Table 17.7.

Identification

Major publications useful for the identification of lichenicolous fungi include Vouaux (1912–1914), Keissler (1930), Hawksworth (1983), Clauzade and colleagues (1989), Triebel (1989), and Alstrup and Hawksworth (1990). Hawksworth (1979a) reviewed 44 species of lichenicolous hyphomycetes, among which 10 genera are exclusively lichenicolous. He (Hawksworth 1981b) also recognized 44 species of lichenicolous coelomycetes, including 16 genera that grow obligately on lichens. Diederich (1996) monographed 54 species of lichenicolous heterobasidiomycetes.

Lichenicolous fungi also can be identified by comparison with voucher specimens in herbaria. The herbaria (Appendix III) in Graz (GZU), Egham (IMI), München (M), Upsala (UPS), and Luxembourg have the richest collections of lichenicolous fungi.

Since 1980, interest in the study of lichenicolous fungi has grown among lichenologists, and the most recent checklists of lichens include lichenicolous fungi. Checklists of lichenized and lichenicolous fungi have been produced for North America (Esslinger and Egan 1995, listing 219 species); Britain (Hawksworth et al. 1980,

TABLE 17.6
Lichenized Fungi That Have Been Inventoried for Lichenicolous Fungi

Host group	Reference
Arthrorhaphis	Hafellner and Obermayer 1995
Baeomyces, *Dibaeis*, *Icmadophila*	Ihlen 1998
Brigantiaea	Hafellner 1985
Foliicolous lichens	Matzer 1996; Etayo 1998; Lücking et al. 1999
Haematomma	Kalb et al. 1995
Lecideoid lichens	Triebel 1989
Lepraria neglecta-group	Kümmerling et al. 1993
Omphalina foliacea	Santesson 1989
Peltigerales (*Lobaria*, *Peltigera*, *Solorina*, *Sticta*)	Hawksworth 1980; Etayo and Diederich 1996; Hawksworth and Miadlikowska 1997; Martínez and Hafellner 1998
Thamnolia	Ihlen 1995

TABLE 17.7
Recent Monographs Dealing with Genera of Lichenicolous Fungi

Genus	Reference
Arthonia (in part)	Grube et al. 1995; Wedin and Hafellner 1998
Biatoropsis	Diederich and Christiansen 1994
Corticifraga	Hawksworth and Santesson 1990
Dacampia	Henssen 1995
Didymellopsis, *Zwackhiomyces*	Grube and Hafellner 1990
Endococcus	Hawksworth 1979b
Gelatinopsis, *Geltingia*, *Phaeopyxis*	Rambold and Triebel 1990
Hemigrapha	Diederich and Wedin 2000
Hobsonia	Lowen et al. 1986
Karschia and similar genera	Hafellner 1979
Lichenochora	Hafellner 1989; Navarro-Rosinés et al. 1998
Lichenoconium	Hawksworth 1977
Lichenopeltella	Aptroot et al. 1997
Llimoniella	Hafellner and Navarro-Rosinés 1993; Diederich and Etayo 2000
Minutoexcipula	Atienza and Hawksworth 1994
Odontotrema	Diederich et al. 2002
Phacopsis	Triebel et al. 1995
Plectocarpon	Diederich and Etayo 1994
Polycoccum	Hawksworth and Diederich 1988
Pronectria	Rossman et al. 1999; Etayo 1998
Refractohilum	Roux et al. 1997
Rhagadostoma	Navarro-Rosinés and Hladun 1994
Rhymbocarpus	Diederich and Etayo 2000
Rosellinia	Matzer and Hafellner 1990
Sagediopsis	Triebel 1993
Sarcopyrenia	Navarro-Rosinés and Hladun 1990
Skyttea	Diederich and Etayo 2000
Sphaerellothecium, *Stigmidium*	Roux and Triebel 1994
Tephromela	Rambold 1993
Weddellomyces	Navarro-Rosinés and Roux 1995
Wentiomyces	Roux et al. 1994

183 species); the Netherlands (Aptroot et al. 1999, 70 species); Belgium, Luxembourg, and northern France (Diederich and Sérusiaux 2000, 201 species), Germany (Wirth 1994, 161 species), and Norway and Sweden (Santesson 1993, 314 species), and other sites. Those publications can facilitate taxon identifications.

Geographic Distribution and Diversity

More than 1500 species of lichenicolous fungi are known. Based on recent studies, we believe that the actual number of species is probably much larger, possibly exceeding 3000 species. New taxa are being discovered and described at an increasing rate (at present, about 30 species/year; Sipman 1996a), for several reasons: (1) numerous taxa still remain to be discovered and described, even in well-explored areas; (2) outside Europe and North America, lichenicolous fungi are still poorly known, despite their extraordinary richness and diversity in some areas, including the montane tropics, especially in the Southern Hemisphere; and (3) revisions of genera based on modern techniques often lead to the division of single heterogeneous, poorly differentiated, and apparently nonspecialized species into several highly specialized species with slight morphological differences (e.g., Roux and Triebel 1994).

Many well-known lichenicolous species appear to be cosmopolitan, growing wherever the host lichens occur. A few lichenicolous fungi have much narrower distributions. *Plectocarpon macaronesiae*, for example, is specialized on widespread species of *Lobaria* but, to date, has been found only in Macaronesia (Diederich and Etayo 1994). *Stromatopogon baldwinii*, which grows on various species of *Usnea*, is known only from Tasmania and the South Sandwich Islands (Diederich 1992). So far, no well-documented species are known endemics of smaller areas. Because of directed collecting, some 50 lichenicolous heterobasidiomycetes now are known, about one-third of which come from montane forests in Papua New Guinea (Diederich 1996).

Quantification and Relative Importance

Most lichenicolous fungi are rare or rarely have been recorded, and only a few species are considered to be really abundant. *Athelia arachnoidea* can invade the epiphytic vegetation (mainly lichens and algae) of whole trees. In polluted areas of central Europe, this fungus can destroy the lichen vegetation of entire forests. Because of its intermittent appearance, particularly in autumn, only lichen species (e.g., *Lecanora conizaeoides, L. expallens, Lepraria incana, Soliciosporum chlorococcum*) that can recolonize the trees within a few months survive (see Arvidsson 1976, 1978). The little-known *Trichonectria hirta* and its *Cylindrocarpon* anamorph are frequent on bark in polluted areas and often are present on every tree in a forest. Lichens that are killed by *Athelia arachnoidea* or other agents frequently are scavenged by the coelomycete *Lichenoconium erodens*. Lichen communities of the Xanthorion in central Europe often are attacked by numerous parasites; species of *Marchandiomyces* (Fig. 17.9), especially *M. aurantiacus*, as well as *Hobsonia christiansenii*, can completely destroy thalli of *Xanthoria* species and members of the family Physciaceae. Some lichenicolous heterobasidiomycetes, such as *Tremella lichenicola* (growing on *Mycoblastus fucatus*) and *T. phaeophysciae* (growing on *Phaeophyscia orbicularis*) are present on 20% of herbarium specimens of the host and can be found in most localities where the hosts are abundant.

Mycoparasites on Biotrophic Plant Parasites

Biotrophic plant pathogens are attacked frequently by mycoparasites, many of which can penetrate the spores (or conidia) of their host fungi. Some of the mycoparasites attack specific groups of plant pathogens and are, thus, of interest as potential biocontrol agents (see "Fungicolous Fungi as Biocontrol Agents of Plant Pathogens" later in this chapter). Many of the species are obligate parasites, unknown in nature outside their hosts, although they can be grown in axenic culture. The most prominent hosts include powdery mildews, rusts, and smuts.

On Peronosporales (Downy Mildews)

The downy mildews on above-ground parts of green plants rarely are attacked, and then it is mostly by generalist mycoparasites. *Fusarium incarnatum* (synonym *F. semitectum*) has been found as a destructive mycoparasite of oospores of *Sclerospora graminicola* on *Pennisetum typhoides* in India (Rao and Pavgi 1976).

On Erysiphales (Powdery Mildews)

By far the best-known mycoparasite of the Erysiphales (powdery mildews) is *Ampelomyces quisqualis* (synonym *Cicinnobolus cesatii*), which can eradicate whole populations of its host (Emmons 1930; Sundheim 1982; Falk et al. 1995a, 1995b). Initially, it grows biotrophically, suppressing sporulation of the host; later it becomes necrotrophic (Philipp 1985). The parasite contacts the host hyphae with appressoria and forms its pycnidia inside the host cells within 5 days (Sundheim and Krekling 1982). It is grown easily *in vitro* and produces several cell-wall-dissolving enzymes (Philipp 1985). It

can penetrate developing ascomata of the host and overwinter in them on bark, but mature ascomata of the host are immune (Falk et al. 1995b). Although the species is found on many species of *Erysiphales*, it more frequently parasitizes those with well-developed and persistent superficial mycelia (e.g., *Erysiphe, Sphaerotheca*) than those with poorly developed surface mycelia (e.g., *Podosphaera, Microsphaera*); the latter sometimes are colonized inside the ascomata (Põldmaa 1966).

The nonspecific mycoparasite *Lecanicillium muscarium* (formerly identified as *Verticillium lecanii*) also commonly inhabits powdery mildews and kills the conidia (Heintz and Blaich 1990). In Crete, *Acremonium alternatum* was found commonly as a parasite when mildewed cucurbit leaves were incubated in moist chambers for 4 days; after conidia of *A. alternatum* were sprayed on the leaves, the mildew *Sphaerotheca fuliginea* was parasitized completely within 3 days (Malathrakis 1985). *Acrodontium crateriforme, Lecanicillium aphanocladii* (formerly identified as *Aphanocladium album*), *Isaria* (*Paecilomyces*) *farinosa, Ramichloridium apiculatum, Tilletiopsis minor, Trichothecium roseum*, and *Dissoconium apiculatum* also appear to be active mycoparasites on powdery mildews (Hijwegen and Buchenauer 1984). The first two species also commonly are found on rust fungi. *Isaria* (*Paecilomyces*) *farinosa*, like *Lecanicillium* species, is otherwise entomogenous and highly chitinolytic. Two species of *Dissoconium* probably also parasitize Erysiphales and other fungi in the phyllosphere (de Hoog et al. 1991).

Some species of *Tilletiopsis* and *Pseudozyma* of the Ustilaginales are efficient biocontrol agents, particularly *T. pallescens* and *T. minor*. The destructive interaction seems to be a case of hyphal interference (Hoch and Provvidenti 1979; Klecan et al. 1990). Urquhart and colleagues (1994) demonstrated that *Tilletiopsis* species produce β-1,3-glucanase, an enzyme associated with mycoparasitism in a wide array of fungi (Hijwegen 1992a). Host hyphae collapse on contact with a *Tilletiopsis* parasite (hyphal interference), without appressorium formation, leading to a drastic reduction in hyphal expansion and sporulation throughout the colony.

On Black Mildews, Sooty Molds, and Similar Leaf-Inhabiting Fungi

Numerous mycoparasites on taxonomically unrelated leaf-inhabiting fungi have been described (Hansford 1946; Deighton 1969; Deighton and Pirozynski 1972; Pirozynski 1974, 1976). Pirozynski (1976) revised many genera of parasites growing on Meliolales, including the pale-colored bitunicate ascomycetes *Melioliphila, Paranectriella, Puttemansia, Tubeufia*, and *Hyalocrea* and the unitunicate genera *Schweinitziella, Hyaloderma, Rizalia*, and *Nematothecium*. All species of *Byssocallis, Malacaria*, and *Melioliphila* and some species of *Paranectriella, Hyalocrea, Hyalosphaera*, and *Nematothecium* live on meliolaceous fungi. Species of *Dimerosporiella* (the *Nectriopsis leucorrhodina* group, Bionectriaceae) and the discomycete *Calloriopsis gelatinosa* also parasitize hyphae on living leaves (Rossman 1987). *Dimerosporiella* (*Calonectria, Nectriopsis*) *cephalosporii* with an acremoniumlike anamorph, is a widely distributed parasite of *Meliola* species in the tropics (Gams 1971; Samuels 1988).

Deighton (1969) described 10 species and Deighton and Pirozynski (1972) described 46 species of fungicolous conidial fungi from leaf-inhabiting fungi. Species of *Spiropes* are generally mycoparasitic (Ellis 1968; Katumoto 1983). Additional species commonly found on such substrata include *Pleurodesmospora coccorum* (synonym *Oospora meliolae*) and species of *Acremonium, Lecanicillium, Eriomycopsis, Titaea, Trichoconis, Sympodiophora, Chionomyces, Cylindrocarpon, Hansfordia, Cercospora, Arthrobotryum, Tripospórium, Trinacrium*, and *Tripospermum*. A key to the fungi in those genera that have elongate, septate, or nonseptate blastoconidia is provided in Braun (1995, 1998).

The biotrophic Phyllachoraceae, along with the Meliolaceae and Erysiphaceae, are among the most heavily parasitized fungus families (Parbery 1978; Hawksworth 1981a, 1981b; Cannon 1991). Parbery (1978) emphasized the risk of confusing parasitized stromata with conidial anamorphs of *Phyllachora*, which are exceedingly rare, apart from the *Linochora*-type spermatia with filiform conidia; he listed particularly the parasites *Phaeodothis winteri* and species of *Mycosphaerella, Shanoria, Discomycopsella, Seimatosporium, Cercospora*, and some other dematiaceous fungi. A parasitized *Phyllachora* can be recognized by its dull surface and the appearance of necrotized host tissue around the colony.

The sooty molds (sensu Hughes 1976) comprise at least six orders of saprotrophic leaf-inhabiting bitunicate ascomycetes. Hughes (1993) noted two parasitic ascomycetes, three hyphomycetes, and a few coelomycetes of the genus *Cicinobella* that grow on *Meliolina*. Several species of *Paranectriella, Puttemansia*, and *Hyalocrea* occur on carbonous stromata of various ascomycetes on living leaves. Long lists of conidial parasites for all these groups have been compiled by Hawksworth (1981b).

On Uredinales (Rust Fungi)

Parasites of rust fungi often have been investigated as possible biological control agents. By far the most common mycoparasite of rust fungi is *Eudarluca caricis* (for taxonomy and nomenclature, see Eriksson 1966;

anamorph the pycnidial *Sphaerellopsis filum*, synonym *Darluca filum*); it is especially destructive, growing in the sori (mostly uredinia). Its ascomata develop after the pycnidia and eventually occupy the whole sorus (Hawksworth 1981b). Unspecialized hyphae penetrate the urediniospores (Carling et al. 1976). The species has a wide spectrum of hosts, including more than 370 species of rust, worldwide (Eriksson 1966; Kranz 1974; Kranz and Brandenburger 1981). The parasite penetrates the urediniospores with an enzyme (Carling et al. 1976) and strongly inhibits their germination on wheat seedlings and the branching of their germ tubes (Stähle and Kranz 1984). *Eudarluca* is not regarded as a practical biocontrol agent of *Cronartium strobilinum* (a fungal pathogen of wheat), however, because of the short and irregular cycle of that host (Kuhlman et al. 1978).

The sporodochial genus *Tuberculina* (teleomorph *Helicobasidium*) comprises 10 species, most of which are exclusively uredinicolous (Hubert 1935; Wicker and Woo 1973; Kuhlman and Miller 1976; Hawksworth 1981b; Wicker 1981). The species *T. persicina* is known from at least 26 rust species, particularly affecting their aecial stage. Natural populations of *T. maxima* also seem to have a controlling effect on rusts, particularly *Cronartium* species. The parasite exploits the rust gall and, by destroying its nutrient source, displaces the rust (Wicker and Woo 1973; Wicker 1981). Hubert (1935) envisioned the spread of the mycoparasite by insects.

Scytalidium uredinicola (Kuhlman et al. 1976) was first found on aecia of *Cronartium fusiforme* on *Pinus* species in the southeastern United States, but later also was recorded from galls of *Endocronartium harknessii* in western Canada (Tsuneda et al. 1980). It penetrates the woody tissue of the galls and destroys the rust in the wood. It inhibits spore germination in *E. harknessii* with the metabolite maltol, a substance known to occur in some plants to which it may confer a natural resistance to some fungal pathogens (Cunningham and Pickard 1985). This parasitic fungus is distributed by Nitidulid beetles (Currie 1995).

Lecanicillium dimorphum (formerly identified as *Aphanocladium album*, a taxon different from the myxomyceticolous one with this name) is a necrotrophic parasite that efficiently invades the aecidiospores of *Puccinia graminis.* It inhibits urediniospores formation and induces precocious teleutospore formation, a phenomenon regarded as a defense reaction on the part of the fungal host (Koç et al. 1981; Koç and Défago 1983). It produces large amounts of endochitinases or exochitinases, depending on the inducing substratum (Srivastava et al. 1985a; Studer et al. 1992). Like *Verticillium muscarium*, it also produces a β-1,3-D-endo-mannanase, which lyses the germ pore plug in urediniospores of its host (Langen et al. 1992).

Other efficient mycoparasites are *Lecanicillium muscarium* (Mendgen and Casper 1980; Spencer 1980; Mendgen 1981) and *L. psalliotae* (Lim and Wan 1983; Saksirirat and Hoppe 1990b). The same isolates of *L. muscarium* can parasitize both rusts and aphids (Hall 1980); they penetrate the urediniospore wall directly (Spencer and Atkey 1981) and destroy the germ tubes of the rust (Mendgen and Casper 1980; Uma and Taylor 1987). Enzyme activities of *L. psalliotae* allow for the penetration of the urediniospores of *Phakopsora pachyrhizi* in soy beans (Saksirirat and Hoppe 1990a, 1990b). This fungus also can control coffee rust in Malaysia. Srivastava and associates (1985b) and Leinhos and Buchenauer (1992) screened other fungi for their parasitic properties and found that *L. muscarium* and *L. psalliotae* were much more efficient than their congeners and also induced early teliospore formation.

Cladosporium uredinicola and *C. gallicola* were described as specific rust parasites, but whether they are specifically distinct from saprotrophic taxa has not yet been demonstrated. *Cladosporium uredinicola* penetrates the urediniospores of *Puccinia violae* (Traquair et al. 1984), and *C. gallicola*, which originally was described from *P. violae* (Sutton 1973a), efficiently parasitizes aecial galls of *Endocronartium harknessii* (Tsuneda and Hiratsuka 1979). The otherwise saprotrophic *C. tenuissimum* (Ellis 1976) is an efficient antibiotic-producing parasite of *Melampsora larici-populina* in Australia. It also can grow epiphytically on poplar leaves, but its growth is promoted by rust pustules (Sharma and Heather 1978, 1987). Species of *Cladosporiella, Cercospora*, and other genera also parasitize rusts (Deighton 1969).

Monocillium nordinii is known to kill rust spores of *Cronartium coleosporioides* and *Endocronartium harknessii* with the toxic metabolites monorden (radicicol) and monocillin I, which also damage *Ophiostoma ulmi* and *Alternaria alternata* (Ayers et al. 1980; Tsuneda and Hiratsuka 1980). Additional rust parasites include *Ramichloridium schulzeri* (Uma and Taylor 1987), *Acrodontium crateriforme, Fusarium bactridioides* on blister rusts (Wollenweber and Reinking 1935), the ascomycete *Scopinella gallicola* in galls of *Endocronartium harknessii* (Tsuneda and Hiratsuka 1981), species of *Paranectriella* and *Uredinophila* (Tubeufiaceae; Rossman 1987), and *Colletoconis aecidiophila* on *Puccinia* in warmer regions (CBS, unpublished data). Many other potential parasites are listed by Hawksworth (1981a).

On Ustilaginales (Smut and Bunt Fungi)

Reports of mycoparasites on smuts and bunts are relatively scarce (Hawksworth 1981a). An oomycete para-

sitized *Ustilago bullata* on the grass *Bromus mollis* in the field. *Pythium vexans* was isolated from the same host and was mycoparasitic in culture but not when the host was growing in a plant (Roberson et al. 1990). Several species of *Fusarium* have been reported from *Ustilago* hosts (Wollenweber and Reinking 1935). Although the galls caused by *Ustilago maydis* and other species are used as food in some places, infections by toxinogenic *Fusarium* species can render them poisonous (CBS, unpublished data). Species of *Itersonilia* and *Tilletiopsis* have been found growing on lesions caused by *Entyloma* (Brady 1960). *Itersonilia perplexans* and its congeners in turn can be parasitized by the chytrid *Rozella itersoniliae* (Barr and Bandoni 1979).

Methods of Study

Attacks by mycoparasites are normally inconspicuous, except when *Ampelomyces quisqualis* or other species cause large patches of powdery mildew to disintegrate. Whitish flakes of mycoparasites on rust fungi are rarely conspicuous. Mycoparasites usually are located by a directed search in which voluminous collections from the field are screened under a dissecting microscope, often after incubation in a moist chamber. *Eudarluca caricis* and other mycoparasites grow readily on ordinary agar media *in vitro* (Calpouzos et al. 1957).

To selectively isolate *Tilletiopsis* species from field material of powdery mildews, Urquhart and colleagues (1994) used the active spores shed from mildewed mats onto a dichloran-containing CMA. Spore fall is also successful for the isolation of *Dissoconium* species, which shoot off their conidia (de Hoog et al. 1991).

Identification

There is no comprehensive treatment of biotrophic plant pathogens and their parasites. Most papers deal with individual groups of host fungi (see the respective sections under "Taxonomic Groups of Fungicolous Fungi and Fungus-like Organisms," earlier). Those data taken together suggest that about 70 parasite species are known, plus an additional ca. 75 from black mildews and others (Deighton and Pirozynski 1972; Rossman 1987). In tropical countries, mycoparasites of black mildews and other leaf-inhabiting fungi are particularly abundant.

Major publications by Hansford (1946), Deighton (1969), and Deighton and Pirozynski (1972) and keys to hyphomycete genera with holoblastic conidiogenesis by Braun (1995:46, 1998:7) are helpful for identifying leaf-inhabiting mycoparasitic fungi.

Geographic Distribution, Biodiversity, and Ecology

The best-studied representatives of this group (e.g., *Eudarluca caricis*) are cosmopolitan. Such mycoparasites develop best under moist tropical conditions. Not surprisingly, then, these parasites of rusts and other leaf-inhabiting ascomycetes are particularly common in tropical countries. In temperate regions, parasites of rusts and powdery mildews most frequently are found in habitats characterized by a higher-than-average relative humidity, such as those in the vicinity of water bodies and in bogs (Põldmaa 1966). Similarly, species of rusts on cultivated and wild grasses growing on raised places usually lack parasites, whereas those near water bodies or in moist places frequently are colonized by several species of parasites (Rudakov 1981). Black mildews and sooty molds that are highly susceptible to mycoparasites are distributed most widely in the tropics (Jeffries and Young 1994:37). Field studies generally have been confined to a qualitative assessment of the parasitic association.

Abundance of *Ampelomyces quisqualis* on powdery mildews varied among mildew species found on different plants in the Eurasiatic countries (Rudakov 1981). In material collected from Northern Estonia, 60% of 370 specimens belonging to 24 species of *Erysiphe* and 30% of 140 specimens of eight species of *Sphaerotheca* appeared to be infected (Põldmaa 1966). *Ampelomyces quisqualis* appeared at the beginning of summer and spread widely later in summer. Infections on colonies of powdery mildews that had overwintered declined considerably in the spring as a result of overgrowth by saprotrophs (Rudakov 1981).

Mycoparasites on Mycelia, Ectomycorrhizae, Sclerotia, and Spores in Soil

Fungi of divergent taxonomic groups that parasitize or otherwise antagonize the hyphae, vegetative propagules, or survival structures of nonlichenized fungi in the relatively moist soil environment are included under this heading. Both biotrophic and necrotrophic relationships are observed in the soil. Some necrotrophs invade any host structure that they encounter, but most are specialized and colonize only certain structures such as vegetative hyphae, sclerotia, or spores of particular host fungi (Whipps 1991; Lumsden 1992; Jeffries 1995). The highly specialized biotrophic mycoparasites of zygomycetes treated earlier (see "Zygomycota" under "Taxonomic Groups of Fungicolous Fungi and Fungus-like Microorganisms") belong in this section, as do the mycoparasitic species of *Pythium*. *Trichoderma* and *Clonostachys* (*Gliocladium*) species are particularly

well-known mycoparasites that are destructive, little-specialized, and highly successful in biocontrol (see "Fungicolous Fungi as Biocontrol Agents of Plant Pathogens," later in this chapter).

On Oomycetes

Species of *Pythium* often are antagonized by congeners, particularly *P. oligandrum, P. periplocum*, and *P. acanthicum*, which have spiny oogonia (Deacon 1976; Vesely 1977; Deacon and Henry 1978; Lutchmeah and Cooke 1984; Martin and Hancock 1987; Berry et al. 1993), and the more distant *P. nunn* and *P. mycoparasiticum* (Deacon et al. 1991). *Pythium oligandrum* is the most common (Ribeiro and Butler 1992). The density of *P. nunn*, which suppresses *P. ultimum*, can be increased by adding crumbled dried bean leaves to the soil (Lifshitz et al. 1984; Paulitz and Baker 1988); *P. nunn* is less aggressive than *P. mycoparasiticum* and *P. oligandrum* (Laing and Deacon 1990) but is better at competing for nutrients (Elad et al. 1985). These parasites cause hyphal interference (see "Types of Fungicolous Associations," earlier) and induce a rapid hyphal lysis in many hosts (Elad et al. 1985). *Pythium oligandrum, P. mycoparasiticum*, and *P. nunn* needed an average of 4.5, 4.8, and 13.3 minutes, respectively, after a first contact to stop a host hypha; penetration occurred after about 50 minutes, disrupting the hypha up to 1.2 mm ahead of the point of contact. However, *Stachybotrys chartarum* parasitizes *P. oligandrum* (Deacon and Henry 1978), and *Olpidiopsis gracilis* also attacks certain species of *Pythium* and *Phytophthora* (Pemberton et al. 1990).

Soil-borne species of *Pythium* and *Phytophthora* are affected negatively by numerous other antagonistic fungi. The toxinogenic *Trichoderma virens* efficiently suppressed *Pythium ultimum* in cotton fields (Howell 1991). *Geomyces pannorum* var. *pannorum* is a very common soil-borne fungus that also has been recorded from *Ramaria* and *Trametes* (Helfer 1991); its varieties *asperulatus* and *vinaceus* were found to antagonize *Pythium ultimum* in cucumber cultivation. A peat substratum strongly colonized by this fungus suppressed *P. ultimum* (Danielsen and Wolffhechel 1991).

On Oospores

The oospores of certain Oomycetes, particularly *Pythium* and *Phytophthora* are, because of their persistence in soil, a special substratum for a diversity of mycoparasites. Conidial fungi of the genera *Dactylella* (some formerly in *Trichothecium*) and *Trinacrium* have been described from *Pythium* oospores (Drechsler 1938, 1943, 1952, 1962, 1963). *Microdochium fusarioides* was found in oospores of *Phytophthora* syringae (Harris 1985). The hyphochytridiomycete *Hyphochytrium catenoides* (Ayers and Lumsden 1977) and the Chytridiomycete *Catenaria anguillulae* are common endobiotic colonizers of *Phytophthora* oospores (Humble and Lockwood 1981; Daft and Tsao 1984). The epibiotic *Rhizidiomyces japonicus*, and species of *Fusarium, Acremonium, Verticillium, Humicola*, and *Clonostachys* colonized buried oospores of several genera (Sneh et al. 1977; Wynn and Epton 1979). *Hyphochytrium catenoides* is one of the most active parasites of *P. cinnamomi* and *P. parasitica*, as well as of *Humicola fuscoatra* and *Anguillospora pseudolongissima* (Daft and Tsao 1983). Oospores of *P. ultimum* also are attacked by *Fusarium merismoides* (Hoch and Abawi 1979a).

On Zygomycetes

Besides some nonspecific zygomycete parasites of *Chaetocladium, Parasitella*, and some other *Mucorales* (mainly *Rhizopus*), *Curvularia* species, *Bipolaris spicifera, Alternaria alternata*, and *Exserohilum* (*Drechslera*) *rostratum* have been found on the sporangiophores of Mucoraceae (El Shafie and Webster 1979; Gupta et al. 1983). Also, species of *Aspergillus, Penicillium, Myrothecium, Trichoderma*, and *Fusarium* may penetrate the sporangiophores, but whether these are mycoparasitic associations remains doubtful (Hawksworth 1981b). For biotrophic parasitism, see under "Taxonomic Groups, Zygamycota."

On Spores of Glomales

The resting spores of the arbuscular mycorrhizal fungi (order Glomales) are particularly susceptible to necrotrophic parasites (reviewed in Paulitz and Linderman 1991b). Large proportions of spores extracted from field soils usually are parasitized and nonviable. Their walls are perforated by fine radial canals, often with internal projections (Bhattacharjee et al. 1982; Lee and Koske 1994). Both amoebae and fungi can make radial pores in the thick spore walls (Boyetchko and Tewari 1991). Such pores first were described, apparently, from spores of *Glomus microcarpum* and were associated with an acremonium-like fungus (Malençon 1942). Necrotrophic mycoparasitism by chytrids and other zoosporic fungi that sporulate either inside or on the surface of spores is probably widespread and may limit populations of mycorrhizal fungi in wet soils (Sylvia and Schenck 1983). A heavy infestation with *Phlyctochytrium* can reduce soil populations of *Glomus macrocarpum* and *Gigaspora gigantea* (Ross and Ruttencutter 1977). In contrast, the colonization of dead spores of *Gigaspora* species by *Spizellomyces* (*Phlyctochytrium*) *punctatus* is regarded as a saprotrophic relationship and does not reduce the mycorrhizal population (Paulitz and Menge

1984). A species of *Labyrinthula* also parasitized the arbuscular fungus *Gigaspora gigantea* in sand dune soils (Koske 1981). Many mycoparasites, easily isolated from the spores of arbuscular mycorrhizal fungi, appear to be facultative parasites that are to some degree saprotrophic and not dependent on the presence of the spores for survival (Paulitz and Menge 1986). *Trichoderma virens* does little harm to Glomales (Paulitz and Linderman 1991a), but *T. harzianum* does (Rousseau et al. 1996). Species of Glomales with pigmented spores are less susceptible to parasitism than those with hyaline spores (Ross and Ruttencutter 1977; Bhattacharjee et al. 1982). *Humicola fuscoatra* and *Anguillospora pseudolongissima* were found to be highly parasitic on *Glomus epigaeum* and *G. fasciculatum* in California (Paulitz and Menge 1980, 1986; Paulitz and Linderman 1991b). *Stachybotrys chartarum* is also an efficient parasite (Siqueira et al. 1984). In a maritime sand dune soil, 44 species of higher fungi, most belonging to the genera *Acremonium, Verticillium, Chrysosporium, Exophiala*, and *Trichoderma*, were found on *Gigaspora gigantea* (Lee and Koske 1994). An experiment with healthy, surface-disinfected spores of *G. gigantea* showed that species of *Acremonium* and *Verticillium* were the most pathogenic. The mycorrhizal colonization of citrus trees can be diminished considerably by mycoparasites (Daniels 1981; Jeffries 1995). Nonsporulating fungi also may be common inside the spores but may not be recognized without culturing. Contrasting with the Glomales, the subterranean sporocarps of Endogonales often are colonized by species of *Mortierella* (W. Gams, personal observation).

On Sclerotia

Several soil-borne plant pathogens of ascomycetes and basidiomycetes form sclerotia in soil. Fungal sclerotia provide a rich source of nutrients for the fungi that are capable of attacking them. Most sclerotial parasites are necrotrophs, although an initial biotrophic phase has been observed in some species.

On Ascomycete Sclerotia. Species of *Sclerotinia* frequently have been examined for their parasites, many of which also attack the related white-rot fungus (*Sclerotium cepivorum*) of onion (Jackson et al. 1991). The most common and best-studied parasite of *Sclerotinia* species is the pycnidial *Coniothyrium minitans*, which is distributed worldwide (Turner and Tribe 1976; Whipps and Gerlagh 1992; Sandys-Winsch et al. 1993). It does not form appressoria (Huang and Kokko 1988). *Coniothyrium minitans* significantly inhibits *Sclerotinia sclerotiorum in vitro* on nutrient-poor media (Whipps 1987). *Microsphaeropsis centaureae*, a related fungus from British Columbia, causes necrotic lesions on *Centaurea diffusa* and attacks the sclerotia of *S. sclerotiorum* (Watson and Miltimore 1975). These fungi are unable to parasitize sclerotial basidiomycetes, which appear to produce toxic metabolites (Whipps et al. 1991).

Three biotrophic hyphomycetes, *Sporidesmium* (or *Teratosperma*) *sclerotivorum* (Uecker et al. 1978; Ayers and Adams 1979), *Teratosperma oligocladum* (Uecker et al. 1980), and *Laterispora breviramosa* (Uecker et al. 1982), are more specialized. *Sporidesmium sclerotivorum* penetrates host cells by means of branched haustoria that, nevertheless, do not penetrate the plasmalemma of infected cells (Bullock et al. 1986). None of these parasites infects sclerotial fungi in other families (Ayers and Adams 1979, 1981).

A few strains of *Trichoderma koningii*, *T. harzianum*, and *T. pseudokoningii* parasitize and have been isolated from the sclerotia of *Sclerotinia sclerotiorum* (Dos Santos and Dhingra 1982). *Clonostachys* (*Gliocladium*) *rosea* f. *catenulata*, isolated from sunflower field soil, is an efficient destructive parasite of *S. sclerotiorum* and several *Fusarium* species, which it contacts with pseudoappressoria (Huang 1978). *Trichoderma virens* also destroys sclerotia of *S. sclerotiorum* and related fungi (Tu 1980; Phillips 1986). *Trichothecium roseum* attacks the sclerotia on bean plants in the field with a slightly lower frequency than *Coniothyrium minitans*; because it is potentially harmful to plants, however, it has not been considered as a control agent (Huang and Kokko 1993). *Dictyosporium elegans* is one of the most active parasites on *S. sclerotiorum* in West Australia (McCredie and Sivasithamparam 1985). In a screening of 10 known mycoparasites, *Trichoderma virens* and *C. minitans* singly and in combination were the most efficient control agents (Whipps and Budge 1990).

Talaromyces flavus is an aggressive parasite of many kinds of sclerotia and one of the most successful biocontrol agents against *Verticillium dahliae* (Boosalis 1956; Dutta 1981; McLaren et al. 1986, 1989; Madi et al. 1992; Fahima and Henis 1995; Nagtzaam 1998; Nagtzaam et al. 1998). Additional efficient parasites of *V. dahliae* are *Clonostachys rosea* and *C. rosea* f. *catenulata* (Keinath et al. 1991). *Talaromyces flavus* produces antibiotic metabolites, including glucose oxidase, which has been identified as the main antifungal agent (Kim et al. 1990). That enzyme releases hydrogen peroxide from glucose, which is highly toxic to *V. dahliae*. The mycoparasite also produces β-1,3 glucanase and chitinase. When *C. minitans* was applied in combination with *T. flavus* against *Sclerotinia*, it had a nearly equivalent effect (McLaren et al. 1994).

Paecilomyces lilacinus, a pathogen of nematodes, also colonizes sclerotia of *Aspergillus flavus* and *A. parasiticus* in soil and thus shortens their survival. It also has been reported to parasitize *Sclerotinia* species (Wicklow and Wilson 1990). Sclerotia of *Phymatotrichopsis*

(*Phymatotrichum*) *omnivora* buried 50-cm deep in soil were attacked by *Clonostachys rosea*, *C. rosea* f. *catenulata*, and *Trichoderma* species (Kenerley and Stack 1987).

Fusarium heterosporum can parasitize the sclerotia of the ergot fungus *Claviceps purpurea* and also attacks its mycelium in culture (Wollenweber and Reinking 1935; Hornok and Walcz 1983). Mower and colleagues (1975) proposed that it be used as a biological control agent against ergot. *Neobarya* (*Barya*) *aurantiaca* also grows on *Claviceps purpurea* (Ellis and Ellis 1988; Eriksson 1992).

On Basidiomycete Sclerotia. A different spectrum of parasites colonizes sclerotia of the important plant pathogens *Rhizoctonia solani* (teleomorph *Thanatephorus cucumeris*) and *Sclerotium rolfsii* (teleomorph *Athelia rolfsii*). Some 30 species of mycoparasites have been recorded for *R. solani* (Butler 1957; Chand and Logan 1984; Jeffries 1995). *Trichoderma* species are both common and efficient mycoparasites (Elad et al. 1980, 1984; Lewis and Papavizas 1985; Howell and Stipanovic 1995). Hyphae of *Trichoderma* species exhibit directed growth towards *R. solani*, mostly coiling around the host, sometimes forming appressoria, and penetrating the host hyphae; antibiotic action has been detected only in *T. virens* (Chet et al. 1981; Elad et al. 1982). *Trichoderma harzianum* has a complex method of action, involving chitinase and β-1,3-glucanase (Elad et al. 1984), whereas *T. virens* affects host fungi mainly with its toxic metabolites gliotoxin and gliovirin (Tu 1980; Howell and Stipanovic 1983; Howell 1991). *Trichoderma virens* also forms appressoria, penetrates host hyphae, and forms intracellular hyphae in *R. solani*, which eventually lead to its collapse and prevent it from forming sclerotia (Tu and Vaartaja 1981). Antibiotic effects also prevail in *Gliocladium viride* (synonym *G. deliquescens*), which disorganizes the cell walls and organelles of *R. solani* (Hashioka and Fukita 1969). When *G. viride* or *T. harzianum* are cultured together with *R. solani*, high β-1,3-glucanase and chitinase activities are observed. The localization of these enzymes at points of contact has been observed by means of fluorescein-conjugated lectins (Elad et al. 1983c).

Verticillium biguttatum is a very efficient biocontrol agent of *R. solani*. It is an obligate parasite and has many biotrophic traits (van den Boogert and Deacon 1994). It is found only on *Thanatephorus cucumeris* (*Rhizoctonia solani*) and related fungi (van den Boogert et al. 1989; Morris et al. 1995b) and strictly is associated with host fungi under natural conditions. It does, however, grow easily and axenically *in vitro* (van den Boogert et al. 1990). This fungus requires biotin and grows best with mannitol or galactose as carbon sources and glutamine or ammonium salts as nitrogen sources (van den Boogert 1989). Various other species of *Verticillium* and *Lecanicillium* (in fact, anamorphs of three ascomycete families) interact with the hyphae of *R. solani* by appressed growth, coiling, and sometimes penetration (Kuter 1984). *Pythium oligandrum* also can attack *Rhizoctonia solani* (Hoch and Fuller 1977), suppressing its cellulolytic activity and sclerotium formation (Al-Hamdani and Cooke 1983).

The sclerotial, strand-forming basidiomycete *Laetisaria arvalis* (Burdsall et al. 1980) is a potent biocontrol agent against *Rhizoctonia solani* and *Pythium ultimum* (Hoch and Abawi 1979b). The former fungus seems to be closely related to a still incompletely identified "sterile red fungus" (Dewan and Sivasithamparam 1988, 1989), which has similar capacities. Another unidentified basidiomycete first recognized as a mycoparasite of *Macrophomina phaseolina* on pine seedlings was found to parasitize several other fungi by coiling, invasion, and lysis (Cerrato et al. 1976). *Rhizoctonia solani* also is controlled by nonpathogenic conspecific isolates and by binucleate isolates of *Rhizoctonia* species (now *Ceratorhiza*; e.g., in sugar beet) even better than it is by *Laetisaria arvalis*. The mechanism is not well understood, although it may involve competition (Ichielevich-Auster et al. 1985; Herr 1988; Lewis and Papavizas 1992).

The nematophagous *Arthrobotrys superba*, *A. oligospora*, and *A. cladodes* are also contact mycoparasites. *Arthrobotrys oligospora* acts on *Rhizoctonia solani* by hyphal interference (Udagawa and Horie 1971; Tzean and Estey 1978a, 1987b), which involves an accumulation of membranous vesicles and greatly increased proteolytic activity in the coiling cells (Persson et al. 1985; Persson and Friman 1993). That species also can attack *Aphanomyces euteuches*; *Mucor silvaticus*; *Penicillium spinulosum*; and its own relatives, *A. superba* and *Dactylellina* (*Monacrosporium*) *haptotyla* (synonym *Dactylella candida*). The mycoparasitic effects of *A. oligospora in vitro* are strongest on a dilute CMA or on water agar with 0.2 g/liter glucose (Persson and Bååth 1992). The fungus excretes chitinase in liquid culture with cell walls of *R. solani* but not in culture with colloidal chitin (Persson 1991). Twigs are often densely covered with *A. superba*, which apparently overgrows corticiaceous fungi as a mycoparasite (Corda 1839).

A strain of *Stachybotrys elegans*, isolated from soil in Turkey (Turhan 1993), efficiently destroyed *R. solani*, but only the anastomosis groups 1–6 were susceptible (Benyagoub et al. 1994, 1996). Although the host cells were killed on contact, no inhibition zone was observed in dual culture. Mortality seemed to be caused by chitinases and β-1,3-glucanases, which are induced by the substratum (Tweddell et al. 1994).

Additional parasites of *R. solani* and *P. ultimum* include *Fusarium oxysporum* (Gupta et al. 1979), *Neo-*

cosmospora vasinfecta var. *africana*, *Acrophialophora levis* (Turhan and Turhan 1989), *Stachybotrys chartarum*, *Trichothecium roseum*, and *Verticillium luteo-album* (Turhan 1990). Conversely, some isolates of *R. solani* also parasitize other fungi, such as species of *Rhizopus*, *Mucor*, *Pythium*, *and Amblyosporium*, by hyphal penetration (Butler 1957). Sclerotia of *Athelia* (*Sclerotium*) *rolfsii* usually are parasitized by similar fungi. Some isolates of *Trichoderma harzianum* can attack this pathogen; others cannot (Wells et al. 1972). That difference has been ascribed to differences in enzyme production; both β-1,3-glucanase and chitinase are required for successful parasitism (Elad et al. 1984). *Aspergillus terreus* also efficiently parasitizes and penetrates sclerotia of *A. rolfsii* (Shigemitsu et al. 1978). Parasites have not been found on sclerotia of *Typhula* species, apart from one instance of the widely distributed *Cylindrobasidium parasiticum* (Woodbridge et al. 1988).

On Conidiophores and Hyphae of Conidal Fungi (Biotrophic Parasites)

Cladosporium cladosporioides can be parasitized by an epibiotic chytrid, *Caulochytrium protostelioides* (Powell 1981). *Gonatobotrys simplex* sometimes is found on its *Alternaria* hosts during analyses of soil and litter. Biotrophic contact mycoparasites of hyphomycetes commonly are found among the Ceratostomataceae and associated *Papulaspora*, *Harzia*, *Gonatobotrys*, and *Olpitrichum* anamorphs. Host specialization varies, even among closely related species (Jordan and Barnett 1978; Cannon and Hawksworth 1982). *Harzia acremonioides* grows easily without a host fungus, but it parasitizes *Stemphylium botryosum* with lobed, sometimes branched contact cells that function as appressoria, causing little damage (Urbasch 1986). In contrast, *H. velata* can grow on species of *Verticillium*, *Fusarium*, and *Cylindrocarpon* and is strongly dependent on a host fungus (G. Fischer and W. Gams, unpublished data). Similar observations apply to several species and strains of *Melanospora* and *Papulaspora*. The possibly related hyphomycete *Gliocephalis hyalina* also is biotrophic and can grow *in vitro* only with a host such as *Cylindrocarpon destructans* (G. Fischer and W. Gams, unpublished data).

On Ectomycorrhiza

In contrast to sporocarps, ectomycorrhizal mantles are usually little affected by mycoparasites, and the array of secondary invaders isolated from this substratum is similar to that of mycorrhiza-free root tips (Summerbell 1989). Only occasionally do species of *Trichoderma* inhibit the establishment of *Laccaria bicolor* mycorrhiza on *Picea mariana* (Summerbell 1987). *Pochonia* (*Verticillium*) *bulbillosum*, which commonly is isolated from forest soils and tree roots, also can parasitize the hyphae of *Laccaria laccata* (Girlanda et al. 1995). The frequently observed adjacent fructification of *Gomphidius roseus* and *Suillus bovinus* has been traced to the mycorrhizal mantle where *G. roseus* grows partially within the *Suillus* mycorrhiza (Agerer 1991).

Methods of Study

Methods used to isolate soil mycoparasites are often the same as those used to isolate soil fungi (e.g., Gams 1992; Chapter 13). The methodological problems are also similar, particularly the difficulty of extrapolating *in vitro* results to the situation in the soil. In suspension plating, the soil material usually becomes so thoroughly dispersed that the associations between biotrophic parasites and their hosts are broken. The likelihood of keeping them together is higher when washed soil particles, or even fragments of unwashed soil or root material, are plated. When the latter method was used, *Gliocephalis* species, *Harzia velata*, and *Gabarnaudia* species were found in soil in parasitic associations with *Cylindrocarpon destructans*, and *Heterogastridium pycnidioideum* was found in association with *Plectosphaerella cucumerina* (G. Fischer and W. Gams, unpublished data). *Heterogastridium pycnidioideum* hitherto had been found only on species of the *Russulaceae* and associated *Hypomyces* and on various litter-inhabiting fungi (Seeler 1943; Bandoni and Oberwinkler 1981).

"Drechsler's soil plate" method used to study nematophagous fungi (see "Drechsler's Technique" in Chapter 19 and "Drechsler's Method" in the Appendix of Chapter 13) is also useful for the observation of mycoparasitic associations (particularly of Mucorales); on water agar or other transparent media inoculated with soil, dung, or other organic material, a dense mosaic of sparsely growing fungi develops. The opportunity for parasites to encounter their hosts increases in such a mat.

The incubation of dung samples in moist chambers (Appendix I) is usually an efficient way to obtain biotrophic members of the Zoopagales and Dimargaritales for observation. The spores they produce are transferred onto *Cokeromyces recurvatus*, which is a convenient host for their maintenance (Benjamin 1959); *Mycotypha microspora*, *Umbelopsis (Mortierella) longicollis*, and *M. isabellina* are also suitable for certain species (Richardson and Leadbeater 1972). Choosing a substratum on which the parasite can overgrow the host efficiently is important. *Piptocephalis* species and their host fungi were detected from soil crumbs spread on potato-carrot agar with streptomycin (Richardson and Leadbeater 1972). Jeffries and Kirk (1976) improved the

technique by inducing the formation of yeast-phase cells of *Cokeromyces recurvatus* in peptone-glucose liquid medium at 25°C. When the yeast-phase cells are spread on malt extract-yeast extract agar, vegetative hyphae grow within a few hours, providing excellent sites for infection by parasites originating from a soil sample.

It is generally impossible to assess the effects of mycoparasites in the soil because of the difficulty of direct observation (Jeffries 1995). Only in special cases is such an assessment possible; for example, hyphal swellings induced in *Rhizopus oryzae* by *Syncephalis californica* indicate levels of parasite activity (Hunter et al. 1977). Lumsden (1981) emphasized the need for developing imaginative techniques to study mycoparasitism in natural systems, such as enumeration on improved selective media, trapping methods for examining mycohosts, and direct observation by scanning electron microscopy.

Because of the roles that mycoparasitic fungi may play in natural, or biological, control of plant pathogens (see "Fungicolous Fungi as Biocontrol Agents of Plant Pathogens," later in this chapter), it is important to quantify them in the soil. Use of a target organism as bait makes a directed search for specific mycoparasites possible in many cases. Sclerotia or spores of the bait organism can be recovered easily either by physical extraction from field soil or by trapping them in a membrane filter or nylon gauze sandwich in which the bait organism has been buried in the soil. The colonization by mycoparasites of oospores of *Pythium* or *Phytophthora* (Ayers and Lumsden 1977; Sneh et al. 1977; Hoch and Abawi 1979a; Wynn and Epton 1979; Daft and Tsao 1984), microsclerotia of *Verticillium dahliae* (Keinath et al. 1991), or the large spores of *Glomus* or *Gigaspora* (Lee and Koske 1994) has been studied with the latter technique. Sneh and colleagues (1977) observed parasitism by *Rhizidiomycopsis*, *Canteriomyces*, *Leptolegnia*, and *Hyphochytrium* species as well as some hyphomycetes on oospores of *Phytophthora*, *Pythium*, and *Aphanomyces* species buried in soil. Harris (1985) buried apple leaves colonized with oospores of *Phytophthora syringae* and later recovered them from soil. Oospores enclosed between membrane filters can be examined microscopically after embedding the membrane in water agar (Sneh 1977). Colonization of *P. megasperma* by *Hyphochytrium* species was observed in that way.

Sclerotia often have been used for the selective isolation of mycoparasites after recovery from soil and superficial disinfection (Chand and Logan 1984; McCredie and Sivasithamparam 1985; Woodbridge et al. 1988). A mycoparasite population also can be enriched by the repeated addition of the host fungus to the soil—for example, *Rhizoctonia solani* for *Verticillium biguttatum* (van den Boogert and Jager 1983) and *Sclerotinia sclerotiorum* for *Coniothyrium minitans* (Gerlagh and Vos 1991). Ayers and Adams (1979) and Adams and associates (1984, 1985) quantified *Sporidesmium sclerotivorum* and other sclerotial parasites in relation to the number of host sclerotia retrieved from soil (naturally infected or buried artificially as bait) after incubation on moist filter paper.

The sclerotial parasite *Verticillium biguttatum* can be quantified in soil particles that are spread over Petri dishes colonized with *Rhizoctonia solani* (van den Boogert and Gams 1988). Morris and colleagues (1995a) refined the method using suspension plating on *R. solani* plates with potato-dextrose agar pH 4 (APDA, Appendix II). Mulligan and Deacon (1992) extended the method using PDA plates overgrown with various other host fungi and recovered *P. oligandrum* on *Fusarium culmorum*, *Trichoderma* species on *R. solani*, and *Papulaspora* species on *Botrytis cinerea*; *Clonostachys* (*Gliocladium*) *rosea* appeared on all three hosts. For the selective isolation of *Talaromyces flavus* from soil, a PDA medium was amended with 0.1% lactic acid, antibacterial antibiotics, 4 mg pimaricin, 30 mg nystatin, and 0.5 g oxgall per liter (Marois et al. 1984).

Selective techniques for the isolation of *Pythium* species are described in Chapter 13 (see "Media" under "Isolation Techniques for Filamentous Fungi"). *Pythium oligandrum* and related species are more sensitive than other congeners to the inhibitors commonly used in isolating *Pythium* species (particularly pentachloronitrobenzene). Placing soil crumbs on a Petri-dish culture of a potential host, such as *Phialophora* species, as a bait is an alternative method for recovering their mycoparasites (Deacon and Henry 1978; Foley and Deacon 1985). Sclerotia of *Sclerotinia sclerotiorum* can serve as baits for mycoparasitic species of *Pythium* (Ribeiro and Butler 1992). Conversely, Petri dishes colonized with a *Pythium* have been used to isolate parasites of their oospores (Drechsler 1943).

The isolation of fast-growing and heavily sporulating colonies of *Trichoderma* is usually easy, but semi-selective techniques can be used to quantify the species of this genus in soil (Elad et al. 1981; Elad and Chet 1983; Chet 1987; Askew and Laing 1993). Elad and Chet (1983) modified a previously published formula for the isolation medium (see *Trichoderma* Isolating Medium, Appendix II) by adding 20 mg/liter captan after autoclaving. Askew and Laing (1993) replaced the fenaminosulf with propamocarb or metalaxyl, which suppressed oomycetes even more efficiently. To isolate *Clonostachys rosea* and *Trichoderma virens* selectively, Park and associates (1992) used a medium with benomyl, sodium propionate, rose bengal, and antibacterial antibiotics, supplemented with either 1 mg gliotoxin and 60 mg acriflavine or 20 mg gliotoxin (per liter), respectively.

Laetisaria arvalis was isolated selectively by placing soil pellets, or table beet seeds that had been buried in soil, on a medium containing an ethanol solution of phenol, dichloran, benomyl, and thiabendazol with antibacterial antibiotics (Papavizas et al. 1983). Concentrations of down to seven propagules per gram of soil thus could be detected.

The large spores of the Glomales are extracted from soil by a wet-sieving procedure (see "Particle Filtration" under "Principal Isolation Methods" and in the Appendix in Chapter 13). Plating of the surface-disinfected spores allows the isolation of many mycoparasites, as noted earlier (see "Methods of Study" under "Mycoparasites of Mycelia, Ectomycorrhizae, Sclerotia, and Spores in Soil").

Identification

For the identification of Zygomycota, see Zycha and colleagues (1969). The genera of the biotrophic parasites have never been monographed exhaustively, but Benjamin (1959) provided much information on species of those genera. Benjamin (1965) also published a key to the species of *Dimargaris*. For other soil fungi, readers should refer to the literature compiled in Chapter 13.

Geographic Distribution and Diversity

Soil-inhabiting mycoparasites form a very heterogeneous group that has never been surveyed as a whole. About 50 species of biotrophic zygomycetous mycoparasites are known, as are about 50 parasites of Glomales, besides the other groups outlined earlier. The true numbers are undoubtedly much higher.

Most fungi discussed in this section are cosmopolitan in distribution, although most records are from temperate regions. The biotrophic parasites of Mucorales include seven tropical and three cosmopolitan species of the *Dimargaritales*. Two of 20 species of *Piptocephalis* are strictly tropical, at least two are temperate, and two are cosmopolitan; little information is available for the others (Kirk 1993). *Coniothyrium minitans* is distributed worldwide (Whipps and Gerlagh 1992; Sandys-Winsch et al. 1993). *Sporidesmium sclerotivorum* has been found so far in Australia, Canada, the United States, Finland, Hungary, Japan, and Norway but not in other European countries (Adams and Ayers 1985). *Laterispora brevirama* is known only from Australia, Canada, Finland, and Japan. The distribution of *Verticillium biguttatum* apparently follows the worldwide distribution of its host fungus, *Rhizoctonia solani*, when associated with potatoes (van den Boogert and Saat 1991).

Distribution patterns of species of *Hypocrea* and *Trichoderma* are correlated with temperature (e.g., Domsch et al. 1980; Samuels et al. 1994).

Quantification and Relative Importance

Biotrophic parasites of Mucorales commonly are found on dung that is rich in mucoralean host fungi. Richardson and Leadbeater (1972) reported that *Piptocephalis* also could be isolated frequently from litter and humus horizons, particularly in woodland and pasture habitats, if the material were examined systematically.

The majority of the spores of Glomalean arbuscular mycorrhizal fungi retrieved from soil are parasitized and nonviable. For example, large numbers of empty spores (ghosts) were observed during an assessment of the abundance of arbuscular mycorrhizal fungi on various crops in different agricultural soils of Northern Greece. Ghosts usually outnumbered intact spores up to fivefold (Jeffries et al. 1988). Few other calculations of the relative proportions of parasitized spores in field soils have been published (Jeffries 1995).

Mycoparasitic species of *Pythium* have been recovered from most soil samples taken in California, regardless of vegetation cover, soil pH, or soil texture (Ribeiro and Butler 1992), exemplifying their wide distribution in temperate zones. *Coniothyrium minitans* colonized host sclerotia on and in roots more successfully than it reached those inside the stems of sunflower (Huang 1978). The population dynamics of *Verticillium biguttatum* tracks the population fluctuations of its host after a lag period (van den Boogert et al. 1990; van den Boogert and Velvis 1992).

Aquatic Fungi and Fungus-like Microorganisms

Fungicolous organisms in aquatic environments include representatives of the zoosporic fungi in the Oomycota, Plasmodiophoromycota, and Chytridiomycota, as treated in "Taxonomic Groups of Fungicolous Fungi and Fungus-like Microorganisms," earlier. They often parasitize hosts from the same orders. The intracellular, often wall-less, thalli of certain Chytridiomycota and Oomycota in particular commonly grow inside other zoosporic fungi. Most records of associations between mycoparasites and aquatic fungi are based on single observations, and we cannot generalize about their distributions.

The hyphae of several Saprolegniaceae and algal cells serve as hosts to *Phlyctochytrium planicorne*, a chytrid with an epibiotic thallus, and endobiotic apophysis and rhizoids (Milanez 1967). In aquatic environments, *Woronina* species (Plasmodiophorales) parasitize *Saprolegniaceae*; the zoospores of the parasite encyst on the hypha of the host, and the contents of the cyst pass into the hypha via a penetration tube (Jeffries and Young 1994). Zoospores of *Olpidiopsis incrassata* encyst on and penetrate the hyphae of *Saprolegnia* (Slifkin 1961,

1963); those of *Rozellopsis inflata* attack *Pythium* species (Prowse 1954). Surprisingly, the chitinolytic (not cellulolytic) *Mortierella alpina* can penetrate and disintegrate the cellulosic hyphae and oogonia of *Saprolegnia* species (Willoughby 1988) as can certain stemphylium-like and acremonium-like parasites (Moreau 1939). Chytrids themselves can act as hyperparasites. *Chytridium parasiticum* grows on *C. suburceolatum*, which itself parasitizes *Rhizidium richmondense* (Willoughby 1956). The rotifer-capturing *Zoophagus insidians* can be parasitized by naked thalli of *Rozellopsis inflata*, which also can grow in species of *Pythium* (Prowse 1954). We found no recent literature about galls induced in *Pilobolus* by the chytrid *Pleotrachelus fulgens*.

The mostly aquatic Ingoldian hyphomycetes, the conidia of which float in water (see "Summary of Existing Knowledge," under "Mitosporic Fungi," in Chapter 23), can be parasitized by a few specialists. *Sphaerulomyces coralloides* parasitizes conidia of the aquatic hyphomycetes *Anguillospora crassa* and *Trichocladium splendens* (Marvanová 1977); it is characterized as a biotrophic contact parasite, cannot be grown in culture, and apparently causes little harm to its host. The tetraradiate anamorph fungus *Crucella subtilis* (teleomorph *Camptobasidium hydrophilum*, Atractiellales) cannot grow on leaf material without a host fungus, for which several species of Ingoldian hyphomycetes are suitable; *in vitro* it coils around the hyphae of the host and behaves like a biotrophic mycoparasite. Growth and sporulation of the host were reduced considerably when host and parasite were coinoculated on leaf material (Marvanová and Suberkropp 1990; Howe and Suberkropp 1993). *Naiadella fluitans* (probably also a heterobasidiomycete anamorph) produces tremelloid haustorial branches on agar media, suggesting mycoparasitic activity (Marvanová and Bandoni 1987). *Nectriopsis indigens* regularly is associated with the small pyrenomycete *Naetrocymbe saxicola* on mats of algae and cyanobacteria in slightly polluted streaming water (Molitor and Diederich 1997).

Zoosporic mycoparasites usually are discovered in specially devised studies. Baiting with substrata suitable for the host in combination with samples of water (see "Collection, Identification, and Deposition of Specimens" under "Chytridiomycetes and Hyphochytridiamycetes," in Chapter 23 and "Isolation Methods" in Chapter 24) or soil (see "Baiting" and "Selective Baiting and Enrichment Techniques for Isolating Soil Chytrids" in Chapter 13) from nature often also yield the parasites. Fuller and Jaworski (1987) have provided detailed descriptions of methods that can be used to observe the host-parasite combinations of *Olpidiopsis varians-Achlya*, *Woronina pythii-Pythium*, and *Rozella allomycis-Allomyces arbuscula*.

FACTORS DETERMINING HOST SPECIFICITY

Host specificity requires that a mycoparasite recognize its host (see the reviews by Barak and colleagues [1985]; Baker [1987, 1991]; and Manocha and Sahai [1993]). Recognition appears to depend on interactions of surface sugars of the parasite and lectins or agglutinins (often two specific glycoproteins) of the host that control attachment and appressorium formation in biotrophic zygomycetes (Manocha 1991) as well as necrotrophic mycoparasites such as *Trichoderma* (Elad et al. 1983a). Lectin probes have been developed to study those interactions (Manocha and Sahai 1991). Nylon fibers impregnated with concanavalin A or *Athelia rolfsii* agglutinin induced coiling in the appropriate strain of *Trichoderma* (Manocha and Sahai 1993). When a mycoparasite is paired with a resistant host, the parasite elicits increased wall deposition in the host, a defense reaction that prevents a nutritional relationship from developing between the two. A nonhost species does not even induce attachment by the parasite (Manocha 1981; Manocha and Golesorkhi 1981; Manocha and Graham 1982; Manocha 1987; Manocha and Sahai 1993). *Phascolomyces articulosus* is a resistant host (Manocha 1981, 1987; Manocha and Graham 1982), which, when infected by *Piptocephalis unispora*, prevents further development of the parasite (Jeffries and Young 1978).

Manocha and Golesorkhi (1979, 1981) studied the ultrastructure of compatible and incompatible interactions. Growth of the germ tubes of parasites toward suitable hosts such as *Umbelopsis* (*Mortierella*) *vinacea* and *Mycotypha microspora*, but not the equally suitable host *Circinella mucoroides*, is directed along diffusible factors (proteinaceous compounds) from the host (Evans et al. 1981; Evans and Cooke 1982). Germ tubes of the parasite attach to protoplasts of host, but not to those of nonhost, fungi (Sundari and Manocha 1991). In the case of the combination *Parasitella-Absidia*, which functions only between complementary sexual mating types, the sexual hormone trisporic acid is likely involved in recognition (Wöstemeyer et al. 1995). Isolates of *Trichoderma harzianum* antagonize different plant pathogens by producing different enzymes (Elad et al. 1984). An interaction with *Rhizoctonia solani* led to increased production of an extracellular fibrillar polysaccharide (Elad et al. 1987). Different strains of *Trichoderma virens* produce either gliotoxin (Q strains), which acts against *R. solani*, or gliovirin (P strains), which acts against *Pythium* species (Howell 1999).

Only a few decomposer fungi are able to attack lichens, presumably because of the presence of noxious lichen metabolites. Nonlichenicolous species of *Nectria* and

Pronectria thus are unable to grow on various lichens, whereas their lichenicolous relatives can (Lawrey et al. 1994).

FUNGICOLOUS FUNGI AS BIOCONTROL AGENTS OF PLANT PATHOGENS

Pesticides needed to control plant pathogens or pests easily can upset the natural equilibrium. Many of the side effects of pesticides are quite undesirable, particularly in soil (Bollen 1979); others, in contrast, may enhance a control action (Hofman and Bollen 1987; Bollen 1993). Regardless, with growing consciousness of the negative environmental effects of these substances, the application of pesticides is being increasingly restricted. As a result, the importance of biological control of plant pathogens is growing. Fungicolous mycoparasitic fungi often make suitable biocontrol agents, their many antagonistic effects reducing the populations of pathogens in artificial (agricultural) systems as they do in natural systems. Biocontrol with fungi, which was started by Weindling (1932), has been reviewed many times (e.g., Baker and Cook 1974; Burge 1988; Deacon 1988b; Philipp 1988; Lumsden and Lewis 1989; Whipps and Lumsden 1989; Adams 1990; Hornby 1990; Harman 1991; Lumsden 1992). Organisms used for this purpose have been tabulated by Jeffries and Young (1994).

Soil-Borne Plant Pathogens

Biological control is particularly appropriate in soil; the most successful cases concern mycoparasites of fungal mycelia and sclerotia. Sclerotia normally survive in the soil for years and are difficult to control with other methods. Normally, it is hardly possible to establish a microorganism in a soil where it was not present previously or only reached low densities. If a host organism is present, however, introduced parasites are at an advantage. Biocontrol agents usually are applied at high densities, the inundative approach, to reach a sufficient proportion of the target propagules. Another important criterion for the selection of control agents is their capacity to colonize the rhizosphere. *Talaromyces flavus*, for example, is rhizosphere-competent (Marois et al. 1984; Nagtzaam 1998). In *Trichoderma*, in contrast, rhizosphere competence varies among strains (Ahmad and Baker 1987). Strains that are good colonizers have been combined successfully with those that are highly antagonistic by protoplast fusion (Sivan and Harman 1991).

Indirect control may be achieved when a pesticide suppresses certain organisms and favors others that are able to control a disease. For example, when pimaricin or thiram was used instead of the banned mercury products to control *Fusarium oxysporum* basal rot in cultivated *Narcissus* in the Netherlands, populations of *Penicillium janthinellum* and *Cylindrocarpon destructans* increased; the latter two species then controlled the disease (Langerak 1977). *Trichoderma harzianum* and *T. virens* most often are used to control fungal plant pathogens (Elad et al. 1982; Papavizas 1985; Chet 1987). By means of nonvolatile and volatile toxic metabolites, enzymes, and direct mycoparasitism, they limit many soil-borne plant pathogens. *Trichoderma* species are particularly effective because they are excellent at recolonizing fumigated or otherwise decontaminated soils and are highly antagonistic.

Pythium oligandrum can be used against damping-off caused by *P. ultimum* (Deacon 1976; Vesely 1977); its oospores are mass-produced in liquid culture and air-dried (McQuilken et al. 1990) and then are applied as a seed coating (Lutchmeah and Cooke 1985; Martin and Hancock 1987). *Harpophora* (*Phialophora*) *radicicola* is the host most susceptible to *P. oligandrum*; other fungi are less affected by it or not affected at all (Deacon 1976; Laing and Deacon 1990, 1991; Berry et al. 1993).

Control of Pathogenic Sclerotial Ascomycetes

Various potential mycoparasites of *S. sclerotiorum* sclerotia have been tested to determine their efficacy as biocontrol agents of that species. *Coniothyrium minitans* was tested because it had been observed that when it was abundant in the phyllosphere of oilseed rape, *S. sclerotiorum* was suppressed (Whipps et al. 1993a). In fact, among several potential antagonists, *C. minitans* and *Trichoderma virens* were the most active (Whipps and Budge 1990). *C. minitans* is the most successful agent against *Sclerotinia* species (Whipps and Gerlagh 1992; Lewis et al. 1995), however, because it attacks the sclerotia and also can grow inside the hyphae and thus follow the host into plant tissue (Huang and Hoes 1976; Huang 1978; Trutmann et al. 1982; Phillips and Price 1983; Tu 1984; Huang and Kokko 1988; Whipps and Gerlagh 1992; Whipps et al. 1993a, 1993b). A successful preparation of this agent is now on the German market (Lüth 1998). *Trichoderma virens*, which is abundant in soil, is most efficient in preventing carpogenous germination (Mueller et al. 1985).

Talaromyces flavus is also effective against *S. sclerotiorum*. Once introduced into the soil, its effect, as with that of *C. minitans*, lasts for more than 2 years,

conferring suppressive properties on the soil (Whipps et al. 1993a, 1993b).

The more specialized biotrophic *Sporidesmium sclerotivorum* (Uecker et al. 1978; Ayers and Adams 1979) is a highly successful biotrophic mycoparasite, despite its poor growth on synthetic media and its reproductive difficulties (Adams et al. 1984; Adams 1990). It deprives sclerotia of food and eventually kills them. Five conidia per gram of soil can be sufficient to infect the host sclerotia present; the fungus then multiplies enormously, producing thousands of conidia from one infected sclerotium (Adams et al. 1984).

The aggressive parasite *Talaromyces flavus* has been applied successfully against the microsclerotia of *Verticillium dahliae* (see "On Sclerotia," earlier). Applications in potato fields led to a concentration-dependent reduction of microsclerotium formation on potato stems. The effect lasted for 2 years after the introduction into the soil of ascospores incorporated in alginate wheat-bran pellets (Nagtzaam 1998). *Clonostachys rosea* has been applied with some success against *Phomopsis sclerotioides* cucumber black root rot (Moody and Gindrat 1977).

Control of Pathogenic Basidiomycetes

An isolate of *Trichoderma harzianum* that efficiently controls *Athelia rolfsii* (anamorph *Sclerotium rolfsii*) produces large amounts of protease and lipase (Elad et al. 1982).

Verticillium biguttatum can attack both hyphae and sclerotia of *Rhizoctonia solani*. It controls its host by draining away nutrients and preventing sclerotium formation. Its use on a large scale has been limited because of the relatively high minimum temperature (13°C) required for its activity in the soil and its dependence on a host fungus for multiplication; it has been used successfully, however (Jager and Velvis 1985; van den Boogert and Velvis 1992). Recently a new harvesting technique ("green-crop harvesting") has considerably improved its potential as a biocontrol agent. Conidia are sprayed onto freshly harvested potatoes, which then are covered again with soil and left on the field for a couple of weeks to harden (Mulder et al. 1992). The fungus also can be applied in combination with certain fungicides (van den Boogert et al. 1990; Jager et al. 1991).

Rhizomorphs of *Armillaria* species provide a suitable substratum for many fungicolous fungi (CBS, unpublished data), including *Pseudographiella rhizomorpharum* (Helfer 1991). So far, however, no efficient direct biological control agent has been found for those pathogens. Nevertheless, various chemicals stimulate the mycoparasitic *Trichoderma* species to attack *Armillaria* species, leading to indirect control (Bliss 1951; Ohr and Munnecke 1974; Fox et al. 1991).

Antagonists of *Heterobasidion annosum* have been studied intensively (e.g., Lundborg and Unestam 1980). Freshly cut stumps can be inoculated with one of its most successful competitors, *Phlebiopsis* (*Peniophora*) *gigantea* (Rishbeth 1963), which outcompetes it (primary resource capture) or displaces it, killing the host hyphae by hyphal interference (secondary resource capture) (Ikediugwu 1976b).

Above-Ground Plant Pathogens

Eudarluca caricis has been applied with some success against certain rust fungi, particularly *Cronartium strobilinum*, and less against *C. fusiforme* (Kuhlman and Matthews 1976; Kuhlman et al. 1978); the natural infestation already provides considerable control.

Control of powdery mildews with *Ampelomyces quisqualis* has been attempted in many places (Sundheim 1986; Philipp 1988). The fungus requires high moisture for germination and penetration of its host; adding paraffin compounds to the conidial suspension protects the germinating conidia (Philipp et al. 1990). Falk and colleagues (1995a) used inoculated cotton wicks suspended over grapevines as a lasting source of inoculum, which was successful during wet weather only. *In vitro*, the fungus sporulated well in submerged, shaken cultures on potato-dextrose broth at 20–25°C; sporulation was best if glucose was omitted from the culture medium. Sztejnberg and associates (1990) recommended this method for mass production of the control agent.

Other suitable agents for the control of powdery mildews are found among species of *Tilletiopsis* and *Pseudozyma*. *Tilletiopsis pallescens* and *T. washingtonensis* efficiently controlled *Sphaerotheca fuliginea* in greenhouse tests with three weekly applications of a conidial spray (Urquhart et al. 1994). Sprays with *Tilletiopsis* also eradicated the host population both *in vitro* on cucumber leaves (Hoch and Provvidenti 1979) and in the field on barley (Klecan et al. 1990). *Pseudozyma* (*Stephanoascus*) *flocculosa* and *P. rugulosa* kill mildew conidia without penetration (Jarvis et al. 1989); *P. flocculosa* acts on *Sphaerotheca* mainly by antibiosis and less by chitinase (Hajlaoui et al. 1992). *Tilletiopsis* species and *Pseudozyma* species are easier to handle, demand less moisture, and control the host more efficiently than *Ampelomyces* (Jarvis et al. 1989; Klecan et al. 1990; Urquhart et al. 1994).

The success of many fungal biocontrol agents against leaf pathogens is hampered because of lack of sufficient moisture. Exceptions may be the successful application of *Trichoderma harzianum* against *Botrytis cinerea* infec-

tions (eye rot) in apple (Tronsmo and Ystaas 1980) and foliar application of *Hansfordia pulvinata* against *Passalora (Mycovellosiella, Cladosporium) fulvo (Mycovellosiella, Cladosporium) fulva* (Dubos 1987).

In the phyllosphere, some yeastlike fungi and a few hyphomycetes normally compete with plant pathogens (Fokkema 1978; Williamson and Fokkema 1985; Roberts 1990). Foliar application of fungicides can damage those yeast populations, which control several plant pathogens in the phyllosphere, thus causing undesired side effects above ground (Andrews and Kenerley 1978; Cullen and Andrews 1984; Dik and van Pelt 1992).

Cladobotryum amazonense, which produces high levels of antibiotic, was used experimentally to control witches' broom (*Crinipellis perniciosa*) in cacao (Bastos et al. 1982, 1986). Witches' broom of cacao also can be controlled by strains of *Trichoderma stromaticum* (Samuels et al. 2000) that grow as a direct parasite on the mycelium of the pathogen (Bastos 1996). The *Trichoderma* prevents the formation of new inoculum through the suppression of basidioma formation.

Modes of Application of Mycoparasites

Mycoparasites can be applied to the plant or to the soil. For soil applications, material propagated in wheat bran (e.g., Elad et al. 1980) or in spore suspensions immobilized in alginate pellets (e.g., Magan and Whipps 1988) are suitable. When seeds are coated with fungal material, the control agent can become active in the soil during germination of the plant. *Trichoderma* species are particularly used for seed-coating (e.g., Chet 1987; Howell 1991). *Pythium oligandrum* (reviewed by K. Lewis et al. 1990) now is used mainly to coat seeds of cress and sugar beet against *Pythium ultimum* and *Aphanomyces.*

Solid matrix priming is another successful procedure in which germination of both the seed and the control agent is induced before seeding (Harman 1991). *Coniothyrium minitans* also is applied as a solid substratum preparation (wheat-grain inoculum) for celery, lettuce, and other greenhouse crops (Whipps et al. 1993b; Gerlagh et al. 1995; Lüth 1998). *Sporidesmium sclerotivorum* (Adams 1990) can be spread using infected sclerotia of *Sclerotinia minor*, or low concentrations of conidia can be sprayed on infected lettuce fields and then plowed into the soil. For the production of biomass, a formulation on a vermiculite base has been developed by Ayers and Adams (1983).

Successful application of *Tilletiopsis* and other control agents to above-ground plant parts requires relatively high moisture levels in greenhouses. Lipophilic additives to the suspension can compensate for lack of moisture (Hijwegen 1992b).

General Considerations

Biocontrol has many constraints that so far have limited its large-scale use. The effects are usually less reliable and less complete than those with chemical treatments. Environmental factors have a greater effect on the success, and only under certain conditions can the application of particular strains assure the desired control effects (Lumsden and Lewis 1989). Biocontrol programs require a much more refined system of monitoring of target organisms and selecting the control agent than do conventional chemical applications. The fact that *T. harzianum* also can be recommended for improving plant growth (Baker 1988) probably makes it more attractive in practice than its role as a control agent. At the moment, about 10 *Trichoderma*-based products are on the market or on the verge of being introduced worldwide.

Biological agents have the advantage of building up an antagonist population that may survive for some years. Antagonists usually can cope with only a limited density of pathogens and are inefficient at high degrees of infection. Nevertheless, the integration with low concentration of chemicals often can give sufficient results. Overall, studies of the application of biocontrol agents are progressing rapidly and such agents rapidly are gaining importance. A strategy to promote the research required to identify appropriate biocontrol agents and understand their functions has been proposed by Whipps (1992).

RECOMMENDATIONS FOR THE INVENTORY OF FUNGICOLOUS FUNGI

Each individual group of terrestrial and aquatic fungicolous fungi requires special techniques for detection, many of which have been described in preceding sections. No general technique will recover a good number of them in one step. It is important to look for mycoparasites under ecological conditions suitable for each group of host organisms. We confine ourselves here to give some suggestions for the SCIF and lichenicolous groups. Mycoparasites of soil-borne plant pathogens normally are investigated with methods devised for each host individually as described under Major Groups of

Fungicolous Fungi: Mycoparasites of Mycelia, Ectomycorrhizae, Sclerotia, and Spores in Soil.

For fungi growing on sporocarps, an inventory is possible. It must be carried out in the right season, particularly when fungi fruiting on soft and caducous hosts are involved. Because of the often rather unspecific host relationships, it may suffice to examine sporocarps of abundant species, which are likely to show all SCIF of the area and their relative frequencies. With the more persistent Aphyllophorales, a detailed investigation, also in deeper layers of the sporocarp, is worthwhile to detect a wider spectrum of microscopic species. To study SCIF, cooperation with mycologists collecting macromycetes is profitable and helps in the determination of host fungi. More SCIF can be collected when experienced agaricologists point to probable infections so that a first sorting of infected material can be done in the field.

For the lichenicolous group, an inventory is carried out by lichenological fieldwork (study of numerous lichen thalli and apothecia of numerous species) and by the study of lichen herbaria as described under Major Groups of Fungicolous Fungi: Lichenicolous Fungi.

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