IV. STUDIES IN HYPERPARASITES ON MELIOLACEAE

a) Introduction

A number of fungi are active parasites on other fungi. Relationship between two species of plants or animals in which one benefits at the expense of other usually without killing is known as parasitism. An organisms that parasitizes another an such a relationship is known as hyperparasitism. It is a attack of a secoondary parasites on a primary parasites.

Fungi occurring on other fungi are commonly termed 'Mycoparasite'. Cooke (1977) considered the term mycoparasites in appropriate as it could be used for a fungus on any organism and not only on other fungi. The term hyperparasite was employed interchangeably with mycoparasites by Boosalis (1964) and has been adopted by several mycologists (e.g. Deighton, 1969; Deighton and Pirozynski, 1972) but it was considered unacceptable by Cooke (1977) in strictly implying only a species parasites on an already parasitic organisms.

The term 'mycophilic' used by Rudakav (1978) may be unacceptable according to Cole and Kendrick (1981) where the association is obligate, but the precise physiological relationship is unclear. The term fungicolous has sometimes been used to refer to fungi macromycetes, but also more widely to embrace a very wide range of fungus to fungus relationships (Gilman and Tiffany vide Cole and Kendrick, 1981). The term fungicolous has been used as a general term by Barnett (1963); Barnett and Binder

(1973) used it where a definite nutritional relationships has not been demonstrated.

Mycoparasitism is biocontrol mechanism of fungal diseases of plants. Certain fungi and bacteria are parasitic on plant pathogens. There are also fungi which are actively parasites on other leaf fungi and such hyperparasites (Mycoparasitism) occur with several soil fungi as well as other ones.

The hyperparasitic fungi so far recorded belong to all the groups from Phycomycetes to Deuteromycetes but mostly from the Phycomycetes, Ascomycetes and Deuteromycetes and very rarely from Basidiomycetes. Hyperparasitism is wide spread in fungi particularly in certain orders such as Hypocreales, Chytridiales, Hyphomycetales (Devay, 1956) but very common on the members of the orders Uredinales, Erysiphales, Meliolales, Asterales etc.

Fungi enter into a number of mutualistic relationships with other fungi. Some are facultative (e.g. Rhizoctonia solani) while others are obligate (e.g. Eudarluca caricis) hyperparasites and some others can be antagonistic or hyperparasitic. Hyper-parasitic and phytoparasitic fungi show similarities in their host-parasitic interaction. Parasitism is just a one form of symbiosis which involves heterotrophic organisms. Among the true mycoparasities there are those which obtain nutrients i.e. necrotrophic hyperparasites atleast by those which quickly kill the invaded host cells, where as fungi which attack the shoot

of plants tend to be parasitised by biotrophic fungi. They have been classified into different groups on the basis of their cultural ability and nutritional requirements (Tarr, 1972): (1) Obligate mycoparasites, (2) Near obligate mycoparasites, (3) Ecological obligate mycoparasite and (4) Facultative mycoparasites.

b) Review of Literature

Different degrees of morphological adaptation towards mycoparasitism may be recognised. Several plasmodiophoraceous organisms are intercellular parasites of other fungi. Woronina polycystis was the first to be discovered while W. pythi is a second species which is claimed to be an obligate parasite on Pythium. Sorodiscus cokeri is another parasite of Pythium but causes little hypertrophy, while Octomyxa achlyae and O. brevilegniae complete their life cycles in their respective saprolegniaceous hosts in ways similar to W. polycystis (Karling, 1942b; Pendergrass, 1950).

Many genera of Chytridiales are mycoparasites and these are recognised by three types viz. ectoparasites, parasites and endoparasites. But nothing is known about their nutritional requirements practically. Solutoparies pythii is an ectoparasite with rhizoids that encircle but apparently does not penetrate the hyphae of its pythiaceous hosts, which stimulates to branch abnormally. Phlyctochytrium synchytrii is parasitic on the resting sporangia of Synchytrium endobioticum while Chytridium

rhizophydii, Septosperma anomalum and S. rhizophydii are parasites on other chytrids. Some chytrids which parasitised on filamentous fungi e.g. Chytriomyces parasiticus on Aphanomyces laevis, while Rhizophydium carpophilum on number of water moulds. Another species of Rhizophydium, R. fungicola attacks the mycelium of the imperfect fungus Gloeosporium theobromae.

Internal mycoparasitic chytrids include species of Rozella and Olpidium. Many species of family Cladochytriaceae are parasitised by R. cladochytrii as well as many aquatic fungi are also parasitised by many species of Rozella (Karling, 1942 a). The uredinospores of several species of Puccinia overgrown (infected) by Olpidium uredinis. Allomyces spp. are infected by O. allomycetos and O. rhizophlyctidis which inhabits species of Rhizophlyctis. Other internally parasitic chytrids includes Pleotrachelus fulgens and P. zopfianus which form their sporangia within species of Pilobolus and Pringsheimiella dioica which parasitizes the Achlya species.

Catenaria allomyces was discovered growing within Allomyces anomalus in the soil and also Blastocladiella simplex (Sparrow, 1960). Species of Achlya and Saprolegnia are parasitised by Rhizidiomyces apophysatus, Rhizidiomycopsis japonicus is a parasite of the oogonia of a species of Aplanes, while third mycoparasite in this small class (Hyphochytridiomycetes) is Hyphochytrium infestans which inhabits the ascocarps of Discomycetes (Sparrow, 1960).

Hyphae of Aphanomyces parasiticus invade the mycelium, young sporangia and young oogonia of certain saprolegniaceous fungi and emerge only after they have exhausted the host hyphae. A. exoparasiticus (Couch, 1926), A. cladogamus and Plectospira myriandra (Drechster, 1943) parasitised pythiaceous hosts. Among the Ectrogellaceae, Pythiella besseyi is an endobiotic and holocarpic hyperparasite of Olpidiopsis schenkiana. The allied P. vernalis parasitizes and causes formation of galls on the filaments of certain species of Pythium. A number of endobiotic mycoparasites are known from the Laginidiales. Indeed, two species of the genus Lagenidum are mycoparasites of themselves, one L. destruens, being a particularly virulent and parasites on a species of Achlya. Further the genus Olpidiopsis is chiefly composed of parasites of fresh water fungi. Rozella inflata (= Pleolpidium inflatum) which parasitizes various pythiaceous hosts. Haskins (1963) described a species of Pythium which in laboratory trials parasitized 79 of 98 species of fungi. On 69 hosts it produced oogonia, an event which depends on the presence of particular exogenous sterols (Haskins et al., 1964).

Parasitism by 'mucors' on other fungi is common. It is accomplished (1) by its proliferation of endoparasitic mycelium as in Syncephalis, (2) by the insertion into the host of its haustoria arising from an extramatrical mycelium in species of Piptocephalis, Dispira, Dimargaris and Tieghmiomyces.

Except for Syncephalis wynnae which parasitizes the Discomycetes : Wynnea macrotis (Thaxter, 1897), all species of Syncephalis are facultative parasites of mucors. Species of Piptocephalis parasitize only mucorales except for P. xenophila which develops better on ascomycetes (Dobb and English, 1954). Dispira cornuta (= D. americana = D. circinata, fide Ayers, 1935) parasitizes only mucorales. D. parvispora likewise parasitizes only mucorales, but D. simplex is known to parasitise only ascomycetes viz. Chaetomium bostrychodes (Benjamin, 1961 and 1963). Species of Parasitella and Chaetocladium are morphologically specialised but culturable parasites. Burgeff (1924) concluded that parasitism of Absidia glauca and A. caerulea by Parasitella and Chaetocladium was strictly sex-limited, in that a single strain of the heterothallic parasite attached only complementary strains of these two heterothallic hosts. However, Satina and Blakeslee (1926) concluded that the parasitic reactions were not truely sex-limited since there found numerous exceptions. A few members of the Kickxellaceae occur in association with other fungi and may prove to be mycoparasitic (Benjamin, 1959).

A few basidiomycetes which are known to be mycoparasitic are all hymenomycetes e.g. Claudopus subdepluens fruits on the pores and stipe of Polyporus perennis. Boletus parasiticus attacks the fruit bodies of Scleroderma species, while Asterophora lycoperdoides and A. parasitica live and fruit on a number of agarics (especially species of Russula and Lactarius).Stropharia

epimyces parasitizes Coprinus comatus and C. atramentarius. There are also examples of Hymenomycetes attacking non-basidiomycetous fungi. Barnett (1963) recently recorded that in laboratory tests some wood rotting Polypores and agaricus penetrate and damage the endoconidia of Ceratocystis species. He suggested that mycoparasitism would have some survival value for these fungi.

A number of fungi are reported to be mycoparasitic on members of the Agaricaceae and other higher fungi. Many ascomycetes are mycoparasitic too (Hansford, 1946, Nicot, 1962). Among those which attack basidiomycetous fructifications are species of Hyphomyces. H. chrysosperma is common on boletes. The genus Cordyceps contains five species (including the familiar C. ophioglossoides and C. capitata) which live upon the subterranean ascocarp of Elaphoglossum and two which live upon the sclerotia of Claviceps (Kobaysi, 1941). Battarina inclasa is another parasites of ascocarp of Tuber puberulum. Eudarluca caricis (= E. australis) in both pseudothecial and pycnidial (= Darluca filum) stage, a cosmopolitan mycoparasite of many macrocyclic and microcyclic rusts. Its perfect state is generally found on Puccinia species on members of the family Poaceae and Cyperaceae (Eriksson, 1966). Keener (1934) showed that isolates of this easily cultured parasite differed in their virulance towards different species of rusts. A few discomycetes are mycoparasitic e.g. Micropyxis geoglossi which grows and fruits on the living ascocarps of another discomycetes Trichoglossum. A

well known other mycoparasites - viz. Hypomyces papulasporae Rogerson & Samuels var. Americanus Rogerson & Samuels and its conidial state viz. Papulaspora candida saccardo which parasitized several spp. of Trichoglossum hirsutum (Pers. ex Fr.) studied from our own school, (Patil, 1991).

Ampelomyces quisqualis (= Cicinnobolus cesatii) is a mycoparasite which forms pycnidia on the conidiophores, ascocarps and even vegetative cells of powdary mildews. It is possible that the hyperparasites overwinter as a saprophyte on the leaves bearing the midews. A. quisqualis grows and sporulates on various nutrients agar media (Emmons, 1930). A number of other hyperparasitic species of Ampelomyces have been described, but it seems doubtful that they are distinct from A. quisqualis (Hansford, 1946). Coniochytrium minitahs is a parasites of the Sclerotia and sometimes the apothecia of certain species of Sclerotinia. A number of other pycnidial fungi parasitize leaf habiting ascomycetes (Hansford, 1946) and other higher fungi (Seeler, 1943).

Various hyphomycetes are capable as mycoparasites but for many of these, it is probably not their predominant habit. This is probably true for certain species of Trichoderma, Penicilium and Cephalosporium. T. lignorum parasitizes a number of different soil fungi in artificial cultures. T. viride in artificial culture on acid media parasitizes the hyphae of Armallaria mellea and Polyporus scheveinitzii. This sort of para-

sitism evidently occurs under more natural conditions too. Boosalis (1956) found that Trichoderma species was able to parasitise the mycelium of Rhizoctonia (= Corticium) solani in unsterilised field soil as also could Penicillium vermiculatum. A species of Penicillium is parasitic upon Aspergillus (Thom & Raper, 1945). Species of Penicillium and Aspergillus have also been observed to invade the sporangiophores of Mucoraceous fungi, just as species of Cephalosporium invade the hyphae, conidiophores and conidia of certain species of Helminthosporium (Kenneth & Isaac, 1964). A greater degree of physiological specialisation for mycoparasitism is shown by Gonatobotryum fuscum (Shigo, 1960), G. simplex (Whaley and Barnett, 1963) and Calcarisporium parasiticum (Barnett & Lilly, 1958). A rather differently a specialised form of mycoparasitism is known by Dactylella spermatophaea and Trinacrium subtile, which invade the oospores of root rotting and other soil inhabiting Oomycetes (Drechsler, 1938). Several hyphomycetes which parasitize the cultivated mushroom are economically important e.g. Mycogone perniciosa is an important pest which causes enlargement of the stipe, reduction or suppression of the cap and eventually, rapid decomposition of the flesh of the mushroom. Other hyphomycetes which parasite on mushrooms include Verticillium malthousei and Cephalosporium costantinii, both of which can deform the host, though not like Mycogone causing rapid decomposition; and C. lamellaecola which causes fasciation and mildewing of the gills (Smith, 1924; Ware,

1933). Under natural conditions, too many hyphomycetes are associated with the fruit bodies of higher basidiomycetes (Nicot, 1962). Although harmless saprophytes sometimes grow on perennial or coriaceous fruit bodies, the relationship of many hyphomycetes is undoubtedly a parasitic one. Parasitism of larger ascomycetous fruit bodies is also known e.g. Fusidium parasiticum attacks the stromata of Xylaria species. Many hyphomycetes which parasitized leaf inhabiting ascomycetes were studied by Hansford (1946).

Like so many true fungi, Myxomycetes too, can be attacked by many fungi. These are mainly hyphomycetes. Stilbum tomentosum is a common and forms abundant white coremia on the fructifications of Trichia and other slime molds (Petch, 1945). No study on their basic nutritional requirements in cultures have been attempted, an essential requirement to confirm their parasitism as well as other behaviours.

There are endless reports of supposed to be mycoparasitic or hyperparasitic fungi and their occurrence in their natural habitat. But their real significance especially in terms of nutritional requirements, nature of parasitism, cultural studies, their role as an agent of biological control have been poorly known and studied. An attempt has been made here in the present investigation to study the mycoparasitic fungi of the members of the family Meliolaceae which provides a very favourable ground (substrate) for the growth and development of many different

types of fungi especially the members of Ascomycetes, Coelomycetes and Hyphomycetes are the major ones; but never tried to isolate and culture them on important requirement. It is kept reserve for further work.