15. Entomogenous Fungi and Development of Mycoinsecticides

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SUMMARY Fungi growing on insects have been often thought of as possible biocontrol agents for various pests. A glimpse of floristics, ecology and biology of entomogenous fungi belonging to various taxonomic groups studied over a period of time has been presented in this article. Efforts made to convert entomopathogenicity into field reality as mycopesticides have been identified and elaborated. Future researches needed in this direction have been discussed.

Introduction

Fungi are considered as the second largest group among living organisms, after insects. After careful and critical analysis, Hawksworth (2002) suggested that his earlier proposition of 1.5 million fungi on earth surface (Hawksworth, 1991) is an underestimate. Fungi live on a variety of substrates and habitats and one specialized group among them growing on insects is called 'entomogenous' or 'entomo-pathogenic fungi'. Though less known, this group, in recent days, has gained considerable importance in view of its potential as biocontrol agents of insect pests (Rossman, 1994).

Most subdivisions of Eumycota are represented by entomogenous fungi (Agarwal and Rajak, 1988). Over 700 species in 90 genera of fungi were reported to be pathogenic to insects and mites. Several reviews dealing with their taxonomy, biology, host range and economic importance are available (Burges, 1981; Roberts and Humber, 1981; Samson et al. 1988; Boucias and Pendland, 1991; Lacey and Goettel, 1995; Evans and Hywel-Jones, 1997; Tzean et al. 1997; Evans, 1999; Goettel et al. 2000; Roy and Pell, 2000; Lacey et al. 2001; Klingen et al. 2002a, b, c, d). Many species of fungi are known to grow on and regulate insect population (Butt et al. 2001; Inglis et al. 2001; Pell et al. 2001).

The potential of fungi as biocontrol agents in vector control programs has been recognized since the time of Pasteur. Although not used so far on a measurable scale, reports of mass production of fungal spores aiming at control of insects are available in the literature (Agarwal and Rajak, 1988). In this work, an attempt has been made to review the taxonomy and biology of some of the entomogenous fungi known for their bio-control potential.

The salient features of genera of hyphomycetes and coelomycetes are given in Table 1.

Coelomomyces Keilin

While describing *Coelomomyces*, Keilin in 1921 suggested its affinity to Chytridiales. In 1945, Couch, amending the genus, accommodated *Coelomomyces* in Blastocladiales. About 25 species are accommodated in *Coelomomyces* (Hawksworth et al. 1995).

The life cycle of members of *Coelomomyces* alternates between mosquito larvae and copepods or

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Table 1. Salient features of genera of entomopathogenic hyphomycetes and coelomycetes

Genus	Condiophores	Conidiogenous cells	Conidia	Teleomorphs known
Akanthomyces	Synnematous, terminally tapering synnema	Arranged in a hymenial layer over synnema, denticulate	Catenate, aseptate, pleomorphic, ellipsoidal to elongated.	*Cordyceps*
Aspergillus	Mononematous with swollen terminal vesicle	Arranged in uni or biseriate over the vesicle	Catenate, aseptate, globose to subglobose.	*Emericella*
Beauveria	Mononematous	Clustered on lateral cells, sympodially denticulate	Solitary, aseptate, smooth, thin-walled, globose.	*Cordyceps*
Gibellula	Synnematous to mononematous, rough-walled and pigmented, conidiophores with a terminal vesicle	One-celled metulae and phialides over the vesicle	Catenate or solitary, aseptate, smooth-walled and ellipsoidal	*Torrubiella*
Hirsutella	Synnematous to mononematous, terminally tapering	Arranged laterally, swollen at the base and with a long slender neck, monophialidic	Solitary, aseptate, ellipsoidal to cylindrical conidia	*Cordyceps*
Hymenostilbe	Synnematous, terminally tapering	Arranged in a hymenial layer, denticulate	Solitary, aseptate, pleomorphic, ellipsoidal to elongated	Nectriaceae
Metarhizium	Mononematous, penicillate	One-celled metulae and monophialides	Catenate, aseptate, pale to olive green, ovoid to cylindrical,	*Cordyceps*
Nomuraea	Mononematous to synnematous	Verticillately arranged below the septum	Catenate to solitary, aseptate, hyaline to green, ovoid to cylindrical	–
Paecilomyces	Mononematous, penicillate or solitary	Terminal and intercalary	Catenate, aseptate, hyaline to green, globose to ellepsoidal	*Byssochlamys*
Verticillium	Mononematous, Verticillately branched	Verticillately arranged monophialides	Solitary, aseptate, hyaline, ovoid to ellipsoidal	*Hyphomyces* and *Torrubiella*
Tolypocladium	Mononematous, sparingly branched	Swollen phialides	Solitary in slimy balls, aseptate, globose to cylindrical	*Cordyceps* and *Hyphomyces*
Aschersonia	Pycnidia in the stroma, slender, branched simple pycinidiophores	Slender, awl-shaped	Hyaline, mostly fusoid, smooth, one-celled conidia	*Hypocrella*

ostracods (Whisler, 1985). In most species, the haploid gametes that emerge from copepods are isogametes of two mating types. Whisler (1979) confirmed meiosis in resting sporangia of *Coelomomyces* and presumed that segregation of different mating types occurs during meiosis. Isogametes fuse to form zygotes which eventually settle on the inter-segmental membranes of mosquito larva. Flagella are retracted in zygotes and adhesion vesicles attach it to the host. A cyst wall develops around the zygote. An appressorium from which a narrow penetration tube enters through a cuticle into the epidermal cells of the host. The fungus ramifies the epidermis, depletes nutrients in the haemocoel and thereby kills the mosquito larva. Resting sporangia are produced at swollen ends of hyphae. Federici and Chapmann (1977) estimated 10000 to 60000 resting sporangia in a single 4th instar larva depending on the species of host. The fungus over-winters as resting sporangia. Usually larvae die in the 4th instar stage and spores are released from the decomposing cadaver. Posteriorly uniflagellated meiozoospores emerging out from the resting spores, infect appropriate copepod or ostracod host and establish haploid heterothallic gametophytic stage which develops in the haemocoel.

In adult female *Aedes aegypti*, the infection is mostly localized in ovaries. During enlargement of ovaries, hyphae in the haemocoel get transferred to interstitial spaces of the ovaries and penetrate epithelial cells of the ovaries (Lucarotti, 1992). Following a sumptuous blood meal, fungal hyphae in the ovaries develop into resting sporangia (Lucarotti and Klein, 1988). Resting sporangia are laid down, in place of eggs, when female mosquitoes (infected with *Coelomomyces stegomyiae*) attempt to oviposit. Meiozoospores emerge out from the resting spores infect copepod host and complete the life cycle (Padua et al. 1986).

Coelomomyces spp. have a life cycle involving an intermediate crustacean host, which helps in maintaining a viable progeny. Development in an intermediate host provides the fungi a launching pad to invade mosquito larvae. The gametes are released simultaneously when copepods and mosquito larvae are both near the water surface (Apperson et al. 1992) which facilitates mating between two types of gametes and helps the resultant zygote to interact with mosquito larvae. Species of *Coelomomyces* have the potential for use in natural control because they can cause epizootics. These can cycle in the environment and infect adult female mosquitoes and thereby effect their potential dispersal (Lucarotti and Andreadis, 1995).

Lagenidium giganteum Couch

Lagenidium giganteum (Lagenidiales: Oomycetes) is a facultative parasite on mosquito larvae, first observed by Couch in 1935. Umphlett (1973) reisolated the fungus from the host and recognized its biocontrol potential. *L. giganteum* is the only fungus that attained operational stage in mosquito control. Biflagellate motile zoospores are the effective phase of the fungus that adheres to the larval cuticle. Infection is initiated by mechanical and enzymatic activity of encysted zoospores allowing entry of the fungus into larva and resulting in death of the latter within 24-72 hours. On maturation, the fungus reproduces either sexually or asexually. Asexual reproduction amplifies infection, with a new round of zoospore release occurring every 24-72 hours depending upon the mosquito host and environmental conditions. Sexual reproduction results in the formation of oospores that can survive desiccation, environmental extremes and mechanical abrasion. Oospores can be stored for at least 7 years in a viable condition in the laboratory or the field (Kerwin et al. 1994).

Three formulations of *Lagenidium giganteum* consisting of various combinations of sexual and asexual spores have been registered by the US Environmental Protection Agency (USEPA Regulation Nos. 56984-1, 56984-2 and 56984-3) with Department of Health Service as registrant (Kerwin et al. 1994). The fungus can be commercially grown on a large scale and applied by ground or air appliances (Kerwin and Washino, 1986, 1987, 1988). Its host specificity and safety has been evaluated using a variety of non-target organisms (Kerwin et al. 1988). Temperature intolerance (>3°C) of zoospores, absence of any toxin production, safety against mammals and birds makes the fungus very lucrative for pest control management (Siegel and Shadduck, 1987; Kerwin et al. 1990).

Entomophthorales

The Order Entomophthorales is placed in the Subdivision: Zygomycotina, Class: Zygomycetes. Six families are recognized in the Order. These include, Entomophthoraceae, Neozygitaceae, Completoriaceae, Ancylistaceae, Meristacraceae and Basidiobolaceae (Humber, 1989). Entomogenous fungi are accommodated in Entomophthoraceae and Neozygitaceae. About 200 species in Entomophthoraceae and 15 in Neozygitaceae are known (Keller, 1997). Several of the Entomophthorales regulate host population through epizootics. They have a narrow host range exhibiting close associations with foliar insect or mite hosts (Evans, 1989).

The members of Entomophthorales have complex life cycles with two or more types of spores. *Entomophthora muscae* is a typical example. To increase the efficiency of out-reaching insect hosts, many show deviation from the basic pattern of life cycle. Conidia are infective units in ideal conditions. Conidiophores of *E. muscae* arise through membranous regions of the host integument and large amounts of primary conidia are actively discharged (Soper et al. 1976; Samson et al. 1979). The mitospores are fragile, short-lived and germinate instantly. A primary conidium can produce and actively discharge a secondary conidium and the latter may produce and discharge a tertiary conidium. The size of successive conidia diminishes while the shape remains the same.

In species of *Neozygites*, primary conidia are not effective whereas secondary conidia produced are infective and differ in shape and size from the former. In *Zoophthora*, successive conidia are produced on fine capilli-conidiophores. The capilli-conidium is a sticky propagule borne at the tip of the conidiophore some distance above the surface and readily attaches to the host. Spherical appressoria are produced for host penetration although it is not a prerequisite (Brobyn and Wilding, 1977; Lambiase and Yendol, 1977). Entomophthorales grow as protoplasts lacking sugar rich cell walls within the haemocoel. Lack of cell wall is presumed to help in escaping detection by the host's immune system (Beauvais et al. 1989). Reduced feeding, negative geotaxis are some of the symptoms of infection. Physiological starvation and short-lived cells are factors reported as cause of host death (Hajek,1997b).

Entomophthorales survive hostile periods as resting spores. The zygospores or azygospores are thick-walled and remain dormant for several months before germination (Hajek, 1997a). These germinate any time when hosts are present in the field and produce one to several actively ejected infective germ conidia or capilli-conidia as in case of *Neozygites* spp.

Entomophthora muscae

E. muscae was the first Entomophthoralean fungus described (Cohn, 1855). The biology and biocontrol potential of this fungus against adult flies, especially housefly, *Musca domestica*, has been studied (MacLeod et al. 1976). The fungus is apparent as dead flies get attached to vegetation, walls, etc. by rhizoids emerging through the proboscis and by the legs of the dead flies. *E. muscae* is known from a range of dipteran hosts. Keller (1984, 1987) demonstrated that *E. muscae* is a complex of species. Recently *E. muscae* sensu stricto has been described (Keller et al. 1999).

E. muscae is not confined to one host species but may be transmitted to other dipteran species and epizootiology of the fungus involves several hosts (Kramer and Steinkraus, 1981; Mullens et al. 1987; Mullens, 1989; Eilenberg et al. 1990; Jensen and Eilenberg, 2000). The entire life cycle, including production of resting spores in the field population, has been studied (Wilding and Lauckner, 1974; Carruthers et al. 1985; Thomsen and Eilenberg, 2000). In other species, resting spores were observed occasionally (Steinkraus et al. 1993b). The natural epizootics caused by *E. muscae* are reported in the populations of *M. domestica, Delia* spp. and *C. rosae* (Carruthers and Haynes, 1985; Mullens and Rodriguez, 1985; Eilenberg, 1987a; Bellini et al. 1992; Moller, 1993; Six and Mullens, 1997).

Behavioural fever was observed in *E. muscae* infected *M. domestica* in which they prefer higher temperatures than uninfected flies, with the result that the fungus dies and the fly survives (Watson et al. 1993). Females

of *C. rosae* infected with *E. schizophorae* do not recognize their hosts, though they are capable of depositing eggs (Eilenberg, 1987b). This behaviour influences the effect of *E. schizophorae* on *C. rosae* populations, since infected females do not contribute to population growth. Towards the end of the infection, flies attach themselves to the vegetation with their abdomen exposed. The fungus discharges primary conidia after death of the host. (Krasnoff et al. 1995). Recent works in host-pathogen interactions include that of Thomsen et al. (2001) and Thomsen and Jensen (2002).

Neozygites fresenii

Isolated from aphids, the fungus was originally recognized as *Empusa fresenii* Nowakowski (Nowakowski, 1883). Witlaczil (1885) described it as *Neozygites aphidis*. Thaxter (1888) placed *E. fresenii* in a new subgenus, *Triplosporium*. Giard (1888) noted that the genera *Triplosporium* and *Neozygites* were synonymous. Remaudiere and Keller (1980) replaced *Triplosporium* with *Neozygites*. About 15 *Neozygites* species are currently recognized (Keller, 1997). More undescribed species of *Neozygites* from Collembola have recently been discovered (Dromph et al. 2000; 2001). *N. fresenii* has a worldwide distribution with reports of infected aphids from Africa, Australia, Europe, India, Israel, the South Pacific and North America (Kuntz, 1925; Gustafsson, 1965; Ramaseshiah, 1968; Thoizon, 1970; Bitton et al. 1979; Milner and Holdom, 1986; Thaxter, 1888; Silvie and Papierok, 1991; Keller, 1997). The fungus is considered as the most common aphid pathogen of tropical regions (Remaudiere, 1977). *Neozygites floridana* was reported from Brazil, India, Israel, Poland, USA and the West Africa (Ramaseshiah, 1971; Kenneth et al. 1972; Brandenburg and Kennedy, 1981; Smitley et al. 1986; Mietkiewski et al. 1993; Yaninek et al. 1996).

Members of Neozygitaceae are specialized as pathogens of small arthropods such as mites, springtails, thrips and aphids (Keller, 1997). Because the hosts are of small size, *Neozygites* spp. may not have been well studied. *N. fresenii*, *N. cinarae* and *N. microlophii* attack only aphids, whereas *N. cucumeriformes* and *N. parvispora* are known only from Thysanoptera (Balazy, 1993) and *N. sminthuri* only from Collembola (Keller and Steenberg, 1997). *N. floridana* and *N. tetranychi* are restricted to mites in the Tetranychidae (Keller, 1997).

Neozygites spp. are recognized as important natural control agents of cassava green mite, *Mononychellus tanajoa*, and mites on groundnuts cotton and lima beans (Carner and Canerday, 1968; Brandenburg and Kennedy, 1983; Boykin et al. 1984; Keller, 1997; Elliot et al. 2000). A very short life cycle, ability to attack all stages except eggs of the hosts, production of a large number of primary conidia per host make them very effective as natural control agent (Steinkraus et al. 1993a). There are a number of published reports dealing with life cycle and epizootiology of *Neozygites* spp. (Bitton et al. 1979; Steinkraus et al. 1991, 1993a, 1995, 1996, 1999; Steinkraus and Slaymaker, 1994; Keller, 1997; McLeod et al. 1998).

Entomophaga maimaiga

Although said to be native to northern Asia, *E. maimaiga* has been reported from North America (Andreadis and Weseloh, 1990; Hajek et al. 1990). Molecular studies have disclosed that *E. aulicae* is a 'species complex', with *E. maimaiga* included in one of the four groups. Fungi in the other three groups currently retain the name *E. aulicae* (Walsh, 1996). *E. maimaiga* was initially differentiated from the *E. aulicae* complex based on the fact that it is the only member able to infect *Lymantria dispar* (Soper et al. 1988). Host range of this species has been extensively studied in view of its potential as biocontrol agent (Hajek et al. 1995a, b; Bidochka and Hajek, 1996, 1998).

Entomophaga grylli

E. grylli was first collected on a *Gryllus* sp. by Fresenius (1858) from Europe and has been referred as *Entomophthora grylli*, *Empusa grylli* and *Conidiobolus grylli* (Carruthers et al. 1997). *E. grylli* exists as a

complex of pathotypes. *E. grylli* sensu stricto is distributed mainly in Europe (Carruthers et al. 1989; Humber, 1989). All members of the '*E. grylli* species complex' are pathogens of grasshoppers and locusts (MacLeod, 1963; Carruthers et al. 1989). North American pathotypes of the two species have a different host range (Pickford and Riegert, 1964; Carruthers and Soper, 1987; Ramoska et al. 1988; Streett and McGuire, 1990). Both pathotypes have resting spores which produce infective germ-tubes to initiate the infection cycle in their hosts. The pathotype 1, produces actively discharged conidia or resting spores in the host whereas pathotype 2 has only resting spores in all infected hosts (Carruthers et al. 1997).

Infection with *E. grylli* is commonly called 'summit disease' as infected and dying insects exhibit abnormal behaviour and climb to the top of vegetation, dying in a head up position, grasping the plant stems (Evans, 1989). Insect death occurs in the late afternoon and early evening, synchronizing sporulation and infection with optimal conditions of high humidity, cool temperatures and zero ultraviolet radiation during the night (Carruthers and Soper, 1987; Carruthers et al. 1988, 1992). *E. grylli* sporulates within hours of host death. If abiotic conditions are not favourable, the cadaver desiccates but the fungus remains viable for extended periods of time, with ability to rehydrate, sporulate and desiccate repeatedly (Sawyer et al. 1997).

Grasshoppers and locusts are highly mobile insects, and infection has little impact on their mobility during early stages. Though dispersing grasshoppers are likely to carry infection with them, at least over moderate distances. Carruthers et al. (1997) suggested that long range migration by hoppers may be a way of disease escape, particularly when the fungus can survive at a site for several seasons as resting spores. They also noted that some species leave favored feeding sites to lay eggs in more open areas, which may separate susceptible early instars from over-wintering sites of the fungus.

Erynia neoaphidis

E. neoaphidis has a wide distribution, being recorded from Europe, Asia, Africa, North and South America and Australia (Wilding and Brady, 1984; Glare and Milner, 1991; Hatting et al. 1999). Besides *Erynia* (Keller, 1991), the species was earlier assigned to *Pandora* (Humber, 1989) and *Zoopthora* (Balazy, 1993). *E. neoaphidis* has been recorded from more than 70 species of aphids on annual and perennial crops, weeds and wild flowers (Pell et al. 2001). Epizootiology of *Erynia neoaphidis* has been the subject of several publications (Milner et al. 1984; Morgan, 1994; Brown et al. 1995; Morgan et al. 1995; Roy, 1997; Tromph et al. 1997, 2001; Nielsen et al. 1998; McLeod et al. 1998; Hemmati, 1999; Roy et al. 1998, 1999, 2001).

Zoophthora radicans

Z. radicans was originally described from *Pieris brassicae* (Brefeld, 1870) as *Empusa radicans*. With a worldwide distribution, it has been recorded from members of Coleoptera, Diptera, Hemiptera, Hymenoptera, Lepidoptera, Orthoptera, Thysanoptera and Trichoptera (Glare and Milner, 1991). Individual isolates are better adapted to infect taxonomically related insect hosts (Papierok et al. 1984; Milner and Mahon, 1985; Mietkiewski et al. 1986; McGuire et al. 1987a; Magalhaes et al. 1988; Goettel et al. 1990). Infection may have an impact on host behaviour (Furlong et al. 1997; Reddy et al. 1998). Under certain circumstances, persistent resting spores (azygospores) are produced within the host in response to changing climatic factors, particularly low temperature and high humidity, high inoculum density, host age or inappropriate hosts (Ben Ze'ev and Uziel, 1979; Perry et al. 1982; McCabe et al. 1984; McGuire et al. 1987b; Glare et al. 1989). Resting spore production has not been observed in all isolates (Glare et al. 1989; Pell et al. 1993). Literature regarding effects of temperature and circadian rhythm on production and discharge of conidia (Milner and Lutton, 1983; Yamamoto and Aoki, 1983; Milner et al. 1984; van Roermund et al. 1984; Glare et al. 1987; Wraight et al. 1990; Pell et al. 1993; Sawyer et al. 1994; Leite et al. 1996b), effects of host or substrate (Wraight et al. 1990; Leite et al. 1996a, c), and effects of nutrients and pH

(van Roermund et al. 1984; Magalhaes et al. 1990, 1991a, b) on germination and subsequent development are available.

Ascomycetes

Several entomogenous fungi reported to date belong to Ascomycetes. The genera such as *Cordyceps* (Fr.) Link, *Hypocrella* Sacc., and *Torrubiella* Bound. of Sphaeriales and members of Laboulbenniales are discussed.

Cordyceps Link

Typified by *C. militaris* (Fr.) Link, the genus *Cordyceps* accommodates more than 300 species (Mains, 1958). Host range comprises Coleoptera, Hymenoptera, Homoptera and Lepidoptera. *C. ophioglossoides* attacks deer truffle, *Elaphomyces* sp. The classic Japanese book on *Cordyceps* and related genera, by Shimizu and Kobayasi (ISBN 4-259-53866-7) contains colour paintings of these fungi. Tzean et al. (1997) described 6 species of *Cordyceps* from Taiwan. The genus is characterized by stalked stromatic fruit body with a fertile head. Those arising from insect larvae or pupae are known as 'vegetable caterpillars' and are used in traditional Chinese medicine for various ailments. Masses of hyphae usually fill the host body, emerging out in the form of stalks of hyphae through the exoskeleton. The perithecia are formed either superficially or immersed in the stalks. Thin-walled asci with 8 ascospores are typical of the genus with ascospores being long, filiform and sometimes end as part-spores at maturity (Evans and Hywel-Jones, 1997). The development of part-spores can be seen as adaptation to increase targeting-efficiency. Both shooting of spores into air and oozing into water films are reported. Usually each of the 8 long ascospores break into 128 part-spores, often while within the ascus. The number of part-spores in *Cordyceps* varies. Kendrick (2002) estimated that a single stroma of *Cordyceps* species can produce as many as 614,400,000 propagules. Anamorphic genera of *Cordyceps* belong to *Akanthomyces, Hirsutella, Hymenostilbe, Paecilomyces, Metarhizium* and *Verticillium. Tolypocladium niveum,* producer of cyclosporin, was recently discovered as the anamorph of *Cordyceps subsessilis* (Kendrick, 2002).

Torrubiella Boudier

The genus, typified by *Torrubiella arachnida* Boudier (Petch, 1923), accommodates about 54 species (Kobayasi and Shimizu, 1982). Fruiting body is distinguished from that of *Cordyceps* by absence of an erect stalk and the perithecium is borne directly on the host. Host range comprises of homoptera and spiders (Evans and Hywel-Jones, 1997). Peritheicial ascocarps, with wall covered by anamorphic conidial structures, long cylindrical asci with 8-spores, with thickened ascal apices penetrated by a fine canal, filiform multiseptate ascospores which break into several part-spores at maturity characterize the genus. Tzean et al. (1997) lescribed 6 species of *Torrubiella* from Taiwan.

Hypocrella Saccardo

Typified by *Hypocrella discoidea* (Berk. & Br.) Sacc. (Petch, 1921), this genus accommodates about 38 species (Petch, 1921; Evans and Hywel-Jones, 1997). The genus *Hypocrella* is one of the most specific of entomopathogenic genera being restricted to the members of the Aleyrodidae and Coccidae (Evans and Hywel-Jones, 1997). Stroma exosclerotium, cushion-like, brightly coloured, irregular and undulating due to semi-erumpent perithecia. Asci are cylindrical to filiform, with prominent apical thickening, 8-spored. Ascospores are filiform and break into part-spores at maturity. Blackening of otherwise brightly coloured fruiting bodies is observed while drying herbarium collections. Anamorphs of *Hypocrella* belong to *Aschersonia.* Anamorph and teleomorph can be found on the same stroma adjacent to each other.

Laboulbenniales

Laboulbenniales are most interesting of all entomogenous fungi, named after French mycologist Alexandre Laboubene. The group contains around 2000 described species. The fungi usually are ectoparasitic, superficially penetrating the host cuticle and evidence for deleterious effects against host is wanting. Therefore, this group has received little attention as agents of biological control (Weir and Beakes, 1995).

The fungal body consists of a fixed number of cells and organs arranged in a definite pattern. The main axis supporting the reproductive organs is called a receptacle. Lower foot cell of the ascospore attaches to the host cuticle and gives rise to a primary receptacle, which further extends to a secondary receptacle to form secondary axis which may bear one or more peritheica. The structural complexity of the receptacle is the key criterion in the taxonomy of Laboulbenniales. Upper spore segment gives rise to primary appendages. Secondary appendages are also formed in some genera. Sometimes antheridia are produced in the septate columns of these appendages. It is assumed that spermatia are produced either exogenously like conidia (e.g. *Ceratomyces* sp.), endogenously in flask-shaped structures (e.g. *Laboulbenia* sp.) or compound antheridia in which antheridial cells discharge spermatia into a common antheridial cavity (e.g. *Eucantharomyces* sp.). Perithecial ascocarp is an outgrowth of receptacle comprising of stalk cells and a procarp which later develops into trichogyne, ascogonium and related cells. Arrangement of perithecial wall cells has importance in delineating families and subfamilies. Ascospores are usually 4 or rarely 8, elongated, spindle shaped and always two-celled.

The exact nature of host specificity, position specificity on the host body and sex specificity of the host is poorly understood. Transmission of the fungus seems to be by direct contact among host individuals. The fungus can be gathered round the year by collecting exact hosts. The fungus appears as short bristles either darkly pigmented or pale-coloured on the host body which can be seen microscopically.

Deuteromycotina

Hyphomycetes

***Akanthomyces* Lebert**

The genus *Akanthomyces,* typified by *A. aculeata* Leb., was established by Lebert in 1858 (cited from Mains, 1950b). An anamorph of *Cordyceps* (Seifert, 1985), the genus is diagnosed by cylindrical, terminally tapering synnemata, conidiogenous cells in a hymenium and unicellular conidia in chains. The host range includes members of Lepidoptera, Coleoptera, Diptera, Orthoptera, and Arachnida (Mains, 1950b). Mains (1950b) described 4 species of *Akanthomyces*. Tzean and co-workers (1997) have described 13 species of *Akanthomyces* from Taiwan. Other useful references include Samson and Brady (1982), Vincent et al. (1988) and Hywel-Jones (1996).

***Aspergillus* Micheli**

Species of *Aspergillus* such as *A. flavus, A. fumigatus, A. parasiticus* and *A. sclerotium* were reported from insects and spiders (Lisansky and Hall, 1983; Tzean et al. 1997; Evans and Hywel-Jones, 1997). Erect conidiophores with terminally swollen vesicles bearing uniseriate or biseriate phialides and 1-celled, catenate conidia characterize the genus *Aspergillus* (Gams and Samson, 1985). *A. fumigatus* is found to be infective to mammals and hence excluded from biocontrol studies (Lisansky and Hall, 1983).

***Beauveria* Vuillemin**

The genus, typified by *Beauveria bassiana* (Bals.) Vuill., is important as a source of biocontrol agents and novel metabolites (Ferron, 1981). The type species is an insect pathogen and recorded from more than 500

insect hosts (Hall and Papierok, 1982; Ekesi et al. 1998; Hallsworth and Magan, 1999; Dromph, 2001; Dromph and Vestergaard, 2002; Bruck and Lewis, 2002; Klingen et al. 2002a,b). Altogether 49 species of *Beauveria* are so far recorded. Seven of them were found to be synonymous with *B. bassiana*, 2 with *B. brongniartii* and one with *B. felina*. Many of the recorded species have been transferred to and accommodated in related genera -5 in *Tolypocladium*, 2 each in *Acrodontium* and *Tritirachium* and 1 each in *Engyodontium*, *Nomurae* and *Pleurodesmospora*. Sympodial conidiophores with a zig-zag appearance; densely clustered conidiogenous cells, one-celled, hyaline, smooth, thin-walled, globose conidia characterize the genus (Tzean et al. 1997). According to Samson (1995), although there are considerable variations among isolates, 6 species can be recognized in the genus based on morphology and biochemical analysis. Though there are reports of allerginicity to *Beauveria bassiana* (Lisansky and Hall, 1983), several formulations of the fungus are available commercially from Mycotech, Troy Bioscience (USA), NPP (France), and Nitto Denko (Japan).

***Gibellula* Cavara**

Though species of *Gibellula*, anamorphs of *Torrubiella*, are generally encountered as parasites of spiders, they have not been tested for their biocontrol efficacy. The genus is typified by *Gibellula pulchra* (Sacc.) Cavara. The species range from synnematous to mononematous with septate, rough-walled and pigmented conidiophores bearing terminal vesicular, hyaline, smooth-walled zone with one-celled metulae and phialides. Conidia are one-celled, smooth-walled, ellipsoidal and hyaline. About 35 species have been recorded so far (Petch,1932; Mains,1950a; Evans and Samson, 1987; Samson and Evans,1992; Tzean et al.,1997).

***Hirsutella* Pat.**

The genus, typified by *H. entomophila* Pat., has been studied by Minter and Brady (1980). Altogether 87 records of species belonging to this genus can be found in literature. Several species have their perfect stages in *Cordyceps*. Synnematous or mononematous conidiophores, with monophialidic conidiogenous cells that are swollen at the base and with slender necks. One celled, ellipsoidal to cylindrical conidia covered with mucus characterize the genus. *H. thompsonii* attacks only mites and is well-known for its epizootics among eriophyid mites, particularly citrus rust mite (*Phyllocoptruta oleivora*), citrus bud mite (*Eriophyes sheldonii*) and coconut mite (*Eriophyes guerreronis*). It is known to have considerable potential as an acaricide (Mc Coy and Couch, 1978; Hall et al. 1980).

***Hymenostilbe* Petch**

The genus is established by Petch in 1931 to accommodate *Hymenostilbe muscaria* Petch, an inhabitant on flies. Similar to *Akanthomyces*, *Hymenostilbe* produces synnema with phialides on lateral branches. *Hymenostilbe* however differs in having solitary conidia whereas *Akanthomyces* is characterized by catenate conidia (Mains, 1950b). In all, 25 species have been recorded under the genus.

***Metarhizium* Sorokin**

The genus, typified by *M. anisopliae* (Metschn.) Sorokin, is characterized by mononematous and penicillate conidiophores, monophialidic conidiogenous cells, basipitally developing conidial chains and ovoid to cylindrical, aseptate, pale to olive green conidia in mass. *M. anisopliae* is one of the best studied entomopathogenic fungi. It was the first fungus to be produced in a large scale from a biological control perspective. Besides mosquitoes, *Metarhizium* spp. infect wide range of insects including members of Coleoptera, Collembola, Lepidoptera, Diptera and Homoptera (Prior, 1990; Hallsworth and Magan, 1999; Arthurs and Thomas, 2001a,b; Butt et al. 2001; Dromph, 2001; Ekesi et al. 2001; Hunter et al. 2001; Dromph and Vestergaard, 2002; Klingen et al. 2002a,b). Lately, *M. anisopliae* has been licensed for indoor control of cockroaches (Ward et al. 2000).

***Nomuraea* Maublanc**

Botrytis rileyi Farlow, the basionym of *Nomuraea rileyi* (Farl.) Samson, typifies the genus. Following is the diagnostic feature of the genus. Conidiophores mononematous to synnematous, with verticillately arranged cylindrical to oval conidiogenous cells, aseptate, hyaline to green, smooth, ovoid to cylindrical conidia (Samson, 1974). The members of the genus are well-known for their epizootics among Lepidoptera, though they were reported from Homoptera, Diptera and spiders. Currently 6 species are accommodated in the genus, viz. *Nomuraea anemonoides* A.D. Hocking, *N. atypicola* (Yasuda) Samson, *N. cylindrosporae* (Chen and Guo) Tzean, Hsieh, Chen and Wu, *N. prasina* Maubl., *N. rileyi* (Farl.) Samson and *N. viridula* Tzean, Hsieh, Chen and Wu. *Nomuraea prasina* was however recognized as a synonym of *N. rileyi*.

***Paecilomyces* Bainier**

Typified by *P. variotii* Bainier, the genus is cosmopolitan in distribution as saprophyte in soil and as pathogen on nematodes or insects. Although 119 species have been recorded, many are synonyms of *Acremonium, Acrophialophora, Gabarnaudia, Mariannaea, Penicillium, Sagenomella, Scopulariopsis, Septofusidium, Sesquicillium* and *Verticillium*. The species have their teleomorphs in the genus *Byssochlamys*. *Paecilomyces fumosoroseus* and *P. farinosus* were studied from the biocontrol utility point of view (Ekesi et al. 1998; Hallsworth and Magan, 1999).

***Verticillium* Nees**

The genus, typified by *V. tenerum* (Nees. Ex Pers.) Link, has erect, slender, branched, tapering conidiophores, verticillately branched phialides, 1-celled, smooth, hyaline, ovoid to ellipsoid, conidia which are solitary or sometimes in chains. The genus is heterogenous with species usually saprophytic or parasitic on plants but also mycoparasitic and entomopathogenic. Altogether 261 species have been recorded for the genus. Many have been later accommodated in genera such as *Acremonium, Acrostalagmus, Cladobotryum, Clonostachys, Gliocladium, Paecilomyces, Phaeostalagmus, Phialophora, Sesquicillium* and *Trichoderma*.

V. lecanii, originally described from scale insects, has a broad host range among Arthropoda. There is a great deal of variation among the isolates of the fungus from different hosts making *V. lecanii* a 'species complex' (Yun et al. 1991). As a consequence, the species of *Verticillium* has an impressive list of synonyms (Evans and Hywel-Jones, 1997). *V. lecanii* has its teleomorph associated with *Torrubiella*, although remaining species have it with *Hyphomyces*.

Verticillium lecanii has been used successfully to control aphids and white flies in glass houses (Lisansky and Hall, 1983). It was the first fungus to be registered for commercial use and produced in a controlled and standardized conditions. Three products of *V. lecanii*, Vertilac against whiteflies, Mycotal against aphids and Thriptal against thrips, produced by Microbial Resources Ltd. were in the market in early 1980's (Evans and Hywel-Jones, 1997). *V. chlamydosporium* is well-known for its efficacy against cyst nematode of cereals. Chlamydospores of this fungus are able to infect the target in soil, whereas the conidia are helpful in survival and dispersal (Lisansky and Hall, 1983).

***Tolypocladium* Gams**

The genus contains anamorphs of *Cordyceps* and *Hyphomyces*. *Tolypocladium* was established by Gams in 1971, typified by *Tolypocladium inflatum* W. Gams. Sparingly branched conidiophores, swollen phialides, and small, one-celled conidia borne in slimy phialides (Bisset, 1983) characterize the genus. *Tolypocladium niveum*, producer of cyclosporine, is the anamorph of *Cordyceps subsessilis* (Kendrick, 2002). *Tolypocladium* spp. are wide spread as soil fungi, some of which are pathogenic on insects (Bisset, 1983; Samson and Soares, 1984). Some strains of *T. cylindrosporum* are considered as potential candidates for control of mosquitoes and other insect pests (Lam et al. 1988; Samson and Soares, 1984; Klingen et al. 2002a, b). The

fungus causes epizootics in mosquito larval population (Weiser and Pillai, 1981). The susceptible mosquitoes include species of *Aedes, Culex, Culiseta, Anopheles, Maorigoeldia, Opifex,* etc. (Pinnock et al. 1973; Soars et al. 1979 and 1985; Yu et al. 1980; Weiser and Pillai, 1981; Gardner et al. 1986; Goettel, 1987a,b). *Tolypocladium* spp. produce a wide range of metabolites including cyclosporins, efrapeptins, elvapeptins and the antibiotic LP237-F8 (Dreyfuss et al. 1976; Jackson et al. 1979; Krasnoff et al. 1991; Tsantrizos et al. 1996). However, the effect of these compounds during infection of mosquitoes is not known so far.

Laboratory studies have shown that relatively high dosages of *T. cylindrosporum* are required to elicit a response in mosquitoes (Pinnock et al. 1973; Goettel, 1987a). It is unlikely that such high doses occur in the field under natural conditions. Conidia are produced only on floating cadavers whereas blastospores are produced in the haemolymph of insects. Action of the fungus is said to be slow and possibilities of using the fungus as a biocontrol candidate is yet to be ascertained.

Coelomycetes

Aschersonia Montagne

The genus *Aschersonia*, typified by *A. taitensis* Montagne (Petch, 1921), is characterized by production of pycnidia containing conidiophores and/or paraphyses, formed in hemispherical or cushion-shaped centrum; conidiophores are slender, branched consisting of thin-walled usually awl-shaped conidiogenous cells with hyaline, mostly fusoid, smooth, one-celled conidia. Species of *Aschersonia* are parasitic on homopteran insects and have *Hypocrella* teleomorph (Tzean et al. 1997). Rolf and Fawcett (1913) first described their entomogenous nature. Reports on their biocontrol value are given by Ramakers and Samson (1984); Frasen et al. (1987), and Rombach and Gillespie (1988). Petch (1921) examined the herbarium specimens then available for *Aschersonia* and recognized 25 species. Mains (1959a,b, c) reviewed species of *Aschersonia* described from America. Recent works on ecology, *in vitro* growth and biocontrol aspects are reported by Hywel-Jones and Evans (1993), Evans (1994) and Meeks et al. (2002).

Mycoinsecticide Development

Development of mycoinsecticides is a complex process demanding enormous capital, technology, infrastructure, manpower and organizational inputs in order to make them environment-friendly principles. Promising fungi have not been researched much despite known advantages. A potential biocontrol organism can be realized only by obtaining fungi from different habitats and testing them for insecticidal activity. Lacey and Brooks (1997) advocated isolation of microfungi from insects and arachnids from as many geographical locations and climatic conditions as possible and maintenance in culture collections, as a priority area of research. Selection of a candidate requires evaluation for its ability to withstand adverse field conditions. Screening of fungi for insecticidal activity can be done by following relatively simple procedures (Kerwin and Petersen, 1997).

Conventional genetic crossing, mutation and molecular cloning can be of some help (Deshpande, 1999). Mass production of virulent and live propagules of fungi is another step in the process for which many standard methods are available (Jenkins and Goettel, 1997). Fungal entities need to be viable at the time of application (Bateman and Chapple, 2001; Wraight et al. 2001). Once cultivated on a suitable substrate, spores have to be collected and concentrated. Optimum drying rate and desired moisture level for each fungus has to be determined. Spore concentration will have to be formulated for stability during storage and application. Further, the formulation has to be stored for months to sustain agricultural market and pest control programs (Couch and Ignoffo, 1981). Desired physical characteristics need to be rendered by augmenting with wetters, stickers, dispersants, UV protectants etc. (Wraight et al. 2001). Identification of host pathogen recognition factors has major implications for commercial development of fungal principles.

Host specificity can be conferred to otherwise non-specific virulent isolates, by incorporating host specific antigens to fungal propagules. By incorporating different antigenic elements specific to different insect hosts, the host range of an isolate can be widened to a greater extent (Rath et al.,1996; St. Leger and Screen, 2001).

Ability of a biocontrol agent to persist on its host will have far-reaching implications in the efficacy of naturally occurring and introduced pathogens (Jacques, 1983; Meekes et al. 2000; Magan, 2001). The impact of rain on persistence of fungal propagules on hosts and their habitats has not been given much attention. Fate of fungal entities following field application can be investigated by variety of protocols that have been developed in recent times (Goettel et al. 2000; Bidochka, 2001).

The benefit of using a biological control agent on a target organism should always be linked with biosafety of non-target organisms (Goettel et al. 2001). Fungi have a wide spectra of host ranges among insects. Adverse effect on non-target organisms, competitive displacement of microorganisms and allergy to humans are matters of concern linked with utilization of microbes for pest control (Cook et al. 1996; Goettel and Jaronski, 1997; Hajek and Goettel, 2000; Goettel and Hajek, 2001; Holt and Hochberg, 2001; Waage et al. 2001; Strong and Pemberton, 2001; Lynch et al. 2001; Gassmann and Louda, 2001; Lonsdale et al. 2001; Hajek and Markham, 2001). The risk of consumption of pathogens is addressed by standard maximum challenge tests which require acute mammalian oral toxicity/pathogenicity tests. Safety tests being observed for chemical pesticides are irrelevant for biopesticides. Stringent regulations have posed impediments to the development and use of microbial agents since these are required as components of IPM (Lacey and Goettel, 1995; Hajek and Goettel, 2000; Hopper 2001). Most regulatory authorities are following a 'tier' system of biosafety testing (Goettel and Jaronski, 1997). In the USA, fungi are tested in 5 tiers and those that clear the 1st tier are approved for sale. Some of the fungi cleared at first tier of tests include *Lagenidium giganteum* (Kerwin et al. 1994), *Hirsutella thompsonii* (Ignoffo et al. 1973), *Nomuraea rileyi* (Ignoffo, 1981) and *Verticillium lecanii* (Lisansky and Hall, 1983).

Although production of infective structures is not expensive, many additional downstream processes such as formulation, storage, packing and delivery substantially add to the cost (Wraight et al. 2001). Lately, bacterial *Bt* and *Bs* formulations, to some extent, are placed in a more lucrative position than representative fungi (Federici, 1995) with cost effective control in the field. Advantage of using fungi over *Bt* or *Bs* is that of effective development of resistant structures of fungi which can persist and recycle in the field. It appears that in many habitats only a single application is required per season. Large-scale field trials have not been conducted with fungi, so production costs and rates of application cannot be related to level and length of vector control.

Epilogue

Hitherto research has resulted in a treasure of knowledge on the occurrence, basic biology and biocontrol potential of numerous viruses, bacteria, fungi, protozoa and nematodes that are encountered as pests in nature. In case of fungi, the major advantage is their recycling ability. Search has to be intensified for isolation of newer strains that have better potential than already known fungal vector control agents. Newer combinations of existing candidates have to be tested through biotechnological means to overcome adverse field conditions and to increase the efficacy of these agents.

Efforts must be made to identify the fungal biocontrol agents correctly. Genera such as *Cordyceps, Aschersonia, Verticillium, Beauveria* and *Metarhizium* need urgent revision (Samson, 1995). The complete life cycle of species of these genera has to be elucidated as part of safety procedure, before they are released as mycoinsecticides. Destruction of habitats and ecosystems of these fungi has resulted in the disappearance of fungal germplasm of potential value. Therefore, the need to assess the biodiversity and creativity of these fungi on a priority basis cannot be overemphasized.

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