The University of Manitoba

NEMATOPHAGOUS FUNGI OF MANITOBA

BY

© GILDETTA VALENTE-ESPOSITO

A thesis submitted to the Faculty of Graduate Studies

in partial fulfilment of the requirements for the degree

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Note to the reader: the letter u has been used to represent the symbol for micron (μ).

Abstract

An investigation into the occurrence of nematophagous fungi in Manitoba showed that they are abundant and widespread.

From 120 samples collected at 23 different sites, 106 isolations yielded 31 different species of nematode-destroying fungi. The various species were referrable to the subdivisions Zygomycotina, Basidiomycotina, and Deuteromycotina, and comprised twenty-three predators, five endoparasites, and three members of the Agaricales.

Sixteen species were new to Manitoba, and the lignicolous basidiomycetes Panus rudis Fr., Pleurotus elongatipes Pk., and Pluteus aurantiorugosus (Trog.) Sacc. were tested for nematophagous ability for the first time in Manitoba.

The 31 species belonged to the following genera: Arthrobotrys Cda., Dactylaria Sacc., Dactylella Grove, Duddingtonia R.C. Cooke, Geniculifera Rifai, Monacrosporium Oudem., Harposporium Lodhe, Verticillium Nees, Stylopage Drechs., Nematoctonus Drechs., Panus Fr., Pleurotus (Fr.) kumm. and Pluteus Fr.

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INTRODUCTION

Nematophagous fungi are a taxonomically diverse group of organisms that have ecologically similar habitats and share a pronounced predilection towards utilizing microscopic animals, especially nematodes, as food source. They can be assigned to many fungal subdivisions: the Mastigomycotina, Zygomycotina, Deuteromycotina and Basidiomycotina. The nematophagous fungi have not recently evolved, since "Fossil nematodes in pieces of Mexican amber, approximately 25 million years old appeared to have been parasitized by fungi showing a striking resemblance to present-day nematophagous species" (Jansson 1986). This long coevolution between host and parasite has resulted in a variety of modifications in certain fungal spores and hyphae for capturing nematodes (Mankau 1980).

The nematode-destroying fungi can be divided into two broad groups: (1) endoparasitic and; (2) predaceous fungi. Endoparasitic species do not exhibit extensive mycelium development outside the body of the host, nor can they usually be active without a host. For example in the Chytridiomycete Catenaria anguillulae Sorokin only the evacuation tubes of the zoosporangia protrude from the nematode body, thus allowing for the release of the zoospores. In other endoparasitic species, such as Harposporium helicoides Drechs. (Fig. 1), only the conidiophores and conidia project externally into the air or trail on the substrate. The endoparasitic species rapidly complete their life cycle and persist in the form of resting spores when conditions are unfavorable for active growth. The infective agents are usually spores which make contact with the prey in different ways. In C. anguillulae, the flagellate zoospores swim to the prey and encyst on the host cuticle prior to penetration. Haptoglossa heterospora Drechs. (Davidson and Barron 1973) has a peculiar way of infecting nematodes; a tertiary spore, representing an infection unit, is injected from a secondary glossoid spore into the cuticle of a passing nematode. Only those tertiary spores that pass directly

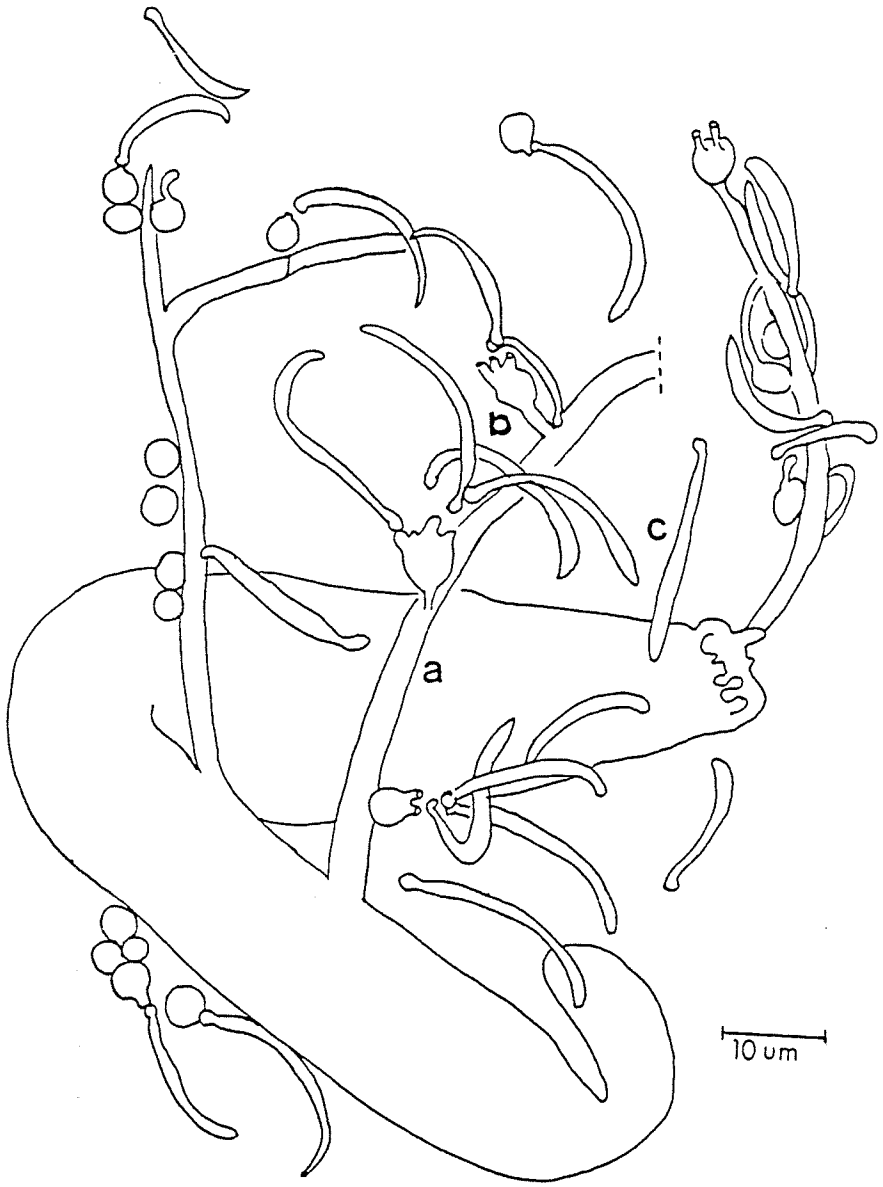

Figure 1. An endoparasitic development inside a nematode with conidiophores protruding from its cuticle (Harposporium helicoides Drechs.):
a. A conidiophore
b. A polyphialide
c. A conidium
Camera lucida drawing.

through the integument and the hypodermis of the nematode germinate into a single thallus. Spores may adhere to the cuticle of the nematode prior to germination and penetration in fungi such as Meria coniospora Drechs., or they may be ingested by the nematodes, as is the case in Harposporium species.

In contrast to the endoparasitic species, the predaceous species generally live as saprophytes. Once established, they colonize the substrate and, in the presence of nematodes, will produce the trapping device typical of the individual species. The term predaceous is applied to those fungi that can capture, kill and consume microscopic animals (Duddington 1955d), their specific trapping mechanisms have been described by Drechsler (1941b), Duddington (1962), Barron (1977b; 1981) and Gray (1987). These mechanisms are:

a) Adhesive hyphae: found in fungi such as Stylopage grandis Dudd. (Fig. 2A), in which an adhesive material produced on hyphal surfaces entraps the prey. A large area of the fungal hyphae can thus serve for nematode capture.

b) Adhesive branches: these consist of morphologically specialized branches which alone are covered with an adhesive material. The most common species in which such branches occur is Dactylella cionopaga Drechs. (Fig. 2B). Adhesive branches generally consist of one to several cells, but occasionally, a bridging hypha may join two adjacent branches and as a result of such anastomosis form a loop.

c) Adhesive net-works: these are the most common trapping mechanism. The net-works are covered with an adhesive matrix and develop from short lateral branches which curve and anastomose with the main hypha and with other branches. While Arthrobotrys musiformis Drechs. forms simple two dimensional net-works consisting of single loops, complex three dimensional net-works are more commonly formed by repeated development of single loops at one point.

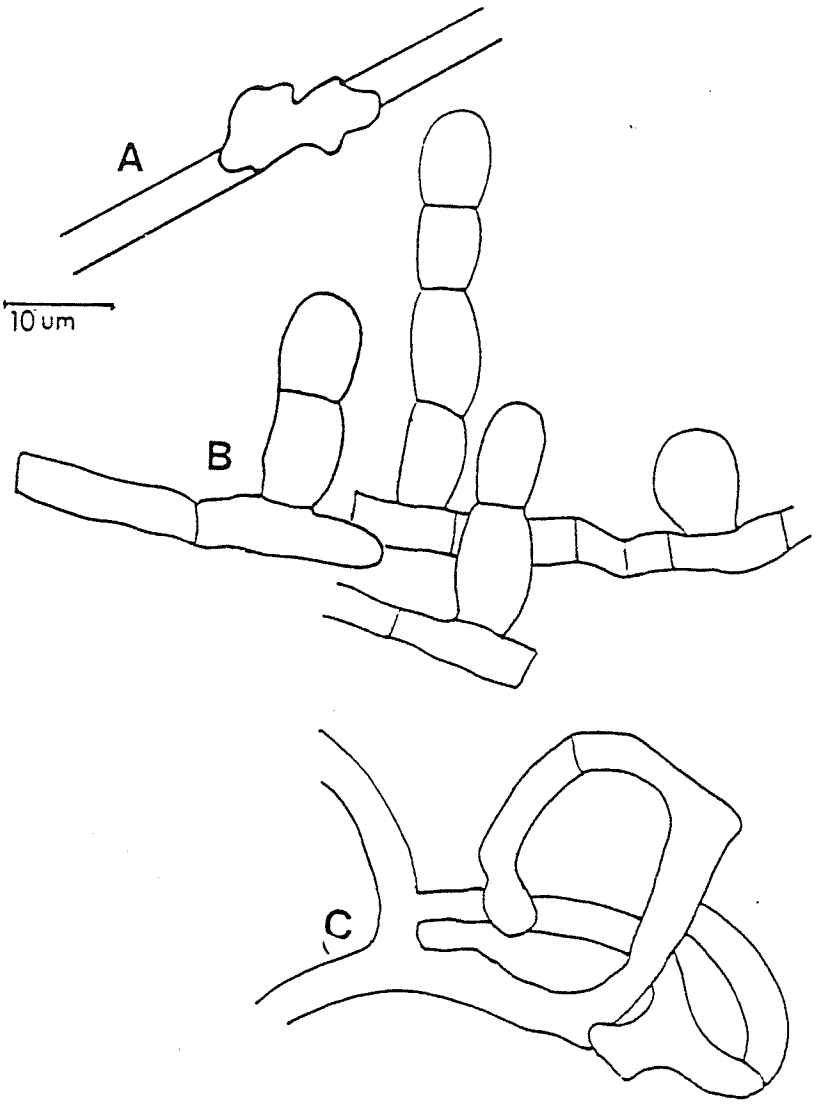

Fig. 2. Examples of trapping mechanisms of predaceous fungi:
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B. Adhesive branches (Dactylella cionopaga Drechs.).
C. An initial stage in the development of adhesive net-works (Arthrobotrys oligospora Fres.).
Camera lucida drawings.

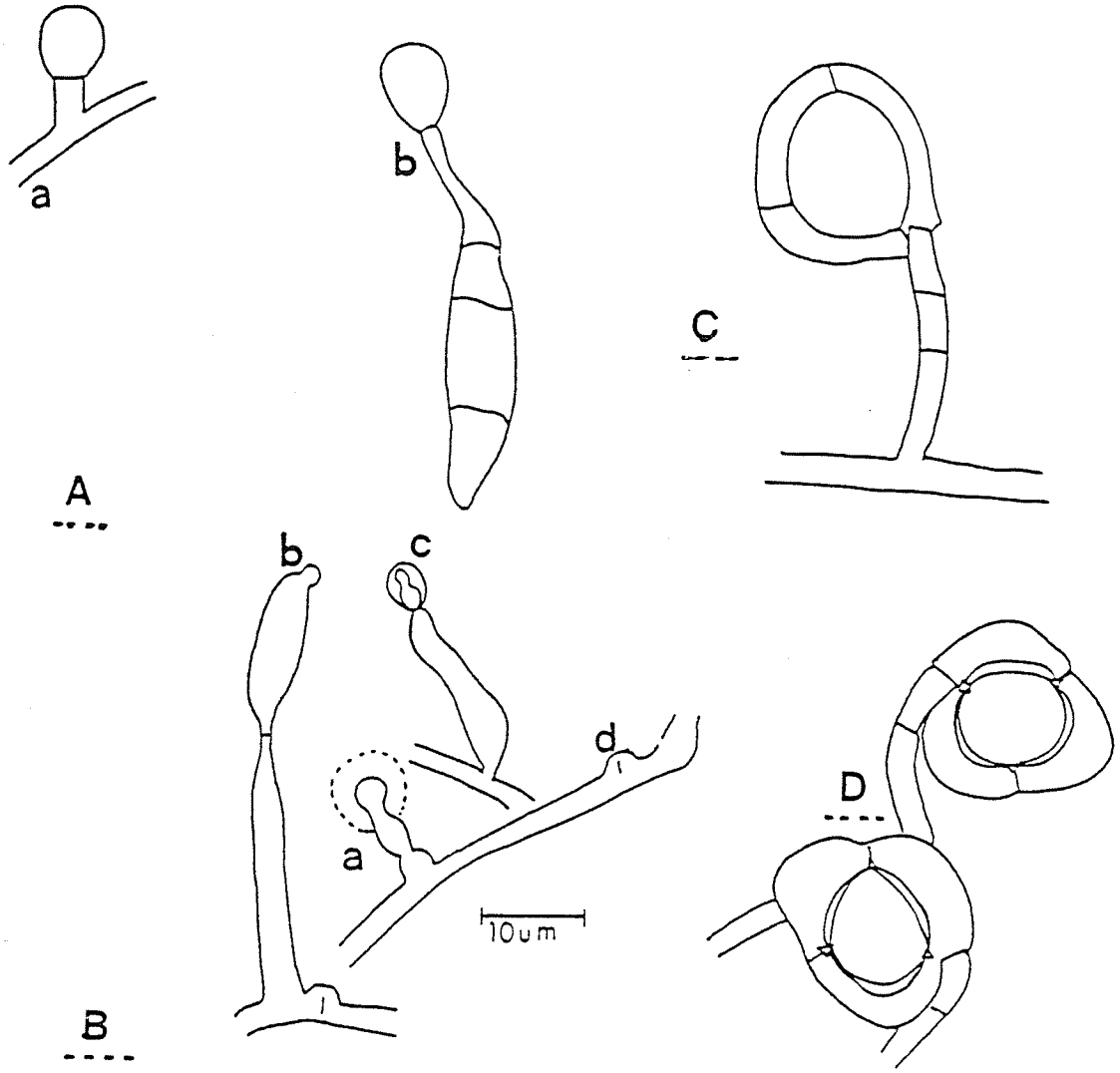

Figure 3. Examples of trapping mechanisms of predaceous fungi:
- A. Adhesive knobs (Dactylella drechsleri Tarjan),
  - a. An adhesive knob on hypha
  - b. An adhesive knob on a conidium.
- B. Adhesive hour-glass knobs (Nematoctonus amatus Thorn and Barron),
  - a. An adhesive hour-glass knob on hypha
  - b. An initial stage of hour-glass knob on a conidium
  - c. An hour-glass knob on a conidium
  - d. A clamp connection.
- C. A non-constricting ring (Dactylaria candida (Nees) Sacc.),
- D. Constricting rings (Arthrobotrys dactyloides Drechs.). Camera lucida drawings.

These are seen in A. oligospora Fres. (Fig. 2C), and nematodes are caught by entanglement and adhesion to the net-works.

d) Adhesive knobs: typical of predaceous species of the Deuteromycotina and Basidiomycotina, either sessile or stalked and covered by adhesive material. Nematodes are trapped when they come in contact with one or more knobs. It is not uncommom to see a nematode struggling to free itself, but even when the knobs are detached from the hyphae, they remain attached to the nematode's cuticle and initiate subsequent infection. Dactylella drechsleri Tarjan is an example of a fungus which produces such trapping devices (Fig. 3 A). The conidia of such fungi not only produce typical hyphae on germinating, but can also give rise to an adhesive knob in the presence of nematodes (Fig. 3Ab). Species of the genus Nematoctonus Drechs. which possess typical hour-glass shaped knobs covered by a large drop of adhesive material are the only fungi currently said to have non-detachable knobs (Fig. 3B).

e) Non-constricting rings: here a nematode is caught when it enters the lumen of a three-celled ring, and becomes tightly wedged therein. Such structures are produced in species assignable to the Deuteromycotina. However, it is not unusual for fungi which produce non-constricting rings, to also produce sticky knobs e.g. Dactylaria candida (Nees) Sacc. (Fig. 3C). Detached rings with are viable and can initiate infection of entrapped nematodes.

f) Constricting rings: produced by such fungi as Arthrobotrys dactyloides Drechs. (Fig. 3D) are the most sophisticated trapping mechanism to be found amongst the predaceous members of the Deuteromycetes. When a nematode enters the lumen of the three-celled ring, there is a rapid, irreversible inward expansion of the three cells comprising the ring with sufficient force to constrict the body of the nematode. Drechsler (1950a) described how the constricting rings developed from the main hyphae in Dactylella aphrobrocha Drechs. He reported

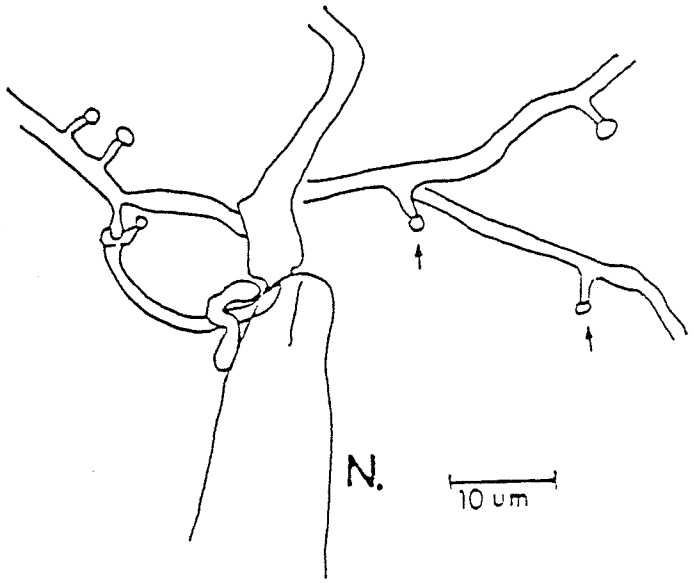

Figure 4. Stalked secretory cells for the release of nematoxin (arrows) (Pleurotus species).
N. A nematode immobilized by nematoxin and penetrated by the fungal hyphae.
Camera lucida drawing

that the ring arose as a curved branch from a prostrate vegetative hyphal element. Septa were formed in the part of this branch that became the stalk of the ring. Then, as the curving branch approached the stalk, a small bud grew out from the stalk and anastomosed with the tip of the curved branch. The branch tip continued to grow and then anastomosed with the base of the first ring cell. A septum then formed across this anastomosis and another septum formed to separate the third cell from the stalk.

Recently, Barron and Thorn (1987) have described another mechanism whereby some fungi can trap nematodes. Some species of the genus Pleurotus (Fr.) Kumm. produce stalked secretory cells which, on contact with nematodes, release a powerful toxin capable of quickly immobilizing them (Fig. 4).

Distinguishing between endoparasitic and predaceous fungi is a useful practice and generally one can assign fungi to one or the other group quite easily. However, there are species of Nematoctonus, eg. N. amatus Thorn and Barron which produce adhesive knobs on both the hyphae and the conidia. The adhesive knobs of the hyphae enable the fungus to catch, kill and consume their prey, while those produced by the conidia enable the fungus to start a new infection on a passing nematode, this pattern seems to form a bridge between predation and endoparasitism.

The purpose of this thesis is to describe and illustrate some of the nematophagous fungi which occur in Manitoba. Particular attention was given to the habitat and to the nature of the samples collected in an attempt to isolate the largest variety of organisms consuming nematodes. Nematophagous fungi are generally present in undisturbed habitats where nematodes are abundant, but individual species tend to have a favorite habitat. Samples were collected with a view to explore associations with particular soil types, other substrates, vegetation and specific environments.

LITERATURE REVIEW

Occurrence of nematophagous fungi

The endoparasitic fungus Harposporium anguillulae was the first fungus recorded as nematophagous (Lohde 1874). Fresenius (1852) had already named a fungus producing tall conidiophores with clusters of two-celled conidia Arthrobotrys oligospora, but he was not aware of its predatory ability. Nearly twenty years later, improved plating techniques employed by Woronin (1870) allowed for the observation of net-works produced on the hyphae of A. oligospora, but even then the function of these structures was not understood. Finally in 1888, Zopf observed nematodes caught in these net-works and saw the fungal hyphae penetrating the nematode cuticle and initiating an infection. The discovery did not attract great interest because it was thought that fungi would trap and consume nematodes only in times of starvation.

Fifty years later, Charles Drechsler (1933a; 1933b; 1933c and 1933d) using clear media observed that not only were nematodes caught by entanglement in the loops, but they were held there by a powerful adhesive produced by the fungus over the surface of such net-works. This began a long series of outstanding publications by Drechsler in which he described new genera and species and also pointed out the differences between the predaceous and endoparasitic fungi. As a result of his life-long interest in this group of organisms, Drechsler described approximately 100 new species distributed in many genera. Several species belonging to genera assignable to the subdivisions Zygomycotina or Mastigomycotina appeared to subsist on nematodes or on species of rhizopods. A few revealed a sexual life cycle, for e.g. Acaulopage rhicnospora Drechs. where sexual reproduction occurs by fusion of gametangia and results in the production of thick walled zygospores.

Predaceous Hyphomycetes were described by Drechsler in the following publications: 1936; 1937a, 1937b; 1940a; 1940b; 1943a; 1944a; 1944b; 1947; 1950a; 1950b; 1952; 1954b; 1962; and 1975. Most of these species belonging to the genera Arthrobotrys Cda., Dactylaria Sacc. and Dactylella Grove preyed on nematodes. Drechsler (1941a; 1942; 1946b; 1946c; 1950c and 1959a) also described endoparasitic hyphomycetes of the genera Acrostalagmus Cda., Harposporium Lohde, Cephalosporium Cda. and Spicaria Hasting that form conidia from phialides. All these genera of predaceous and endoparasitic Hyphomycetes are assignable to the subdivision Deuteromycotina.

Drechsler (1941a) also encountered predaceous fungi with clamp connections on their hyphae. He erected a new genus: Nematoctonus Drechs., for the first two endoparasitic species N. tylosporus Drechs. and N. leiosporus Drechs. which produced the typical hour-glass shaped adhesive knobs on conidia. Later, he reported two other endoparasitic species with adhesive knobs on conidia (Drechsler 1943b) and three predaceous Nematoctonus spp. with adhesive knobs on the hyphae (Drechsler 1946a; 1949; 1954a). This genus is assignable to the subdivision Basidiomycotina. The fact that nematophagous fungi are found in the four different subdivisions Zygomycotina, Mastigomycotina, Deuteromycotina and Basidiomycotina, confirms that the predaceous habit has arisen many times in more than one evolutionary line of fungi.

Another major contribution to the study of nematode trapping fungi was made by the British mycologist C. L. Duddington. Duddington (1940; 1946; 1949; 1950; 1951a; 1951b; 1951c; 1951d; 1953; 1954 and 1955c) recorded nematophagous fungi and described new species occurring in Britain. Duddington (1955a) wrote about techniques for handling predaceous Hyphomycetes and Duddington (1955b, 1955d, 1956, 1962 and 1963) addressed such topics as the physiology and taxonomy of

this group of fungi and the inter-relationship between the nematophagous fungi and the nematodes.

Other British mycologists have also contributed to the literature of the nematophagous fungi by describing new species of endoparasitic or predaceous Hyphomycetes: Goodey (1951), R.C. Cooke (1964; 1969a; 1969b), R.C. Cooke and Dickinson (1965), R.C. Cooke and Satchuthananthavale (1965) and Rifai and R.C.Cooke (1966). Jones (1964) added Nematoctonus robustus Jones, isolated from leaf litter in Ghana, to the seven species described by Drechsler. In 1972, Giuma and R.C.Cooke described and illustrated Nematoctonus tripolitanus Giuma and R.C. Cooke, a new species collected in Libya.

Since early times, French researchers have been interested in the study of nematophagous fungi as biological control agents of nematodes parasitic on plant and animals (Comandon and De Fonbrune 1938, 1939; Descazeaux and Capelle 1939; Deschiens 1939a, 1939b). In 1946 Dollfus described all the species known at that time to attack nematodes, while Virat (1977) and Peloille and Cayrol (1979) added Candelabrella javanica Rifai and R.C.Cooke, Duddingtonia flagrans (Dudd.) R.C. Cooke. and A. oviformis Soprunov to the French records

Another outstanding contributor to the knowledge of the predaceous fungi was the Russian mycologist Soprunov, who in 1958 published descriptions of all the then-known and of several new predaceous Hyphomycetes isolated in Turkmenistan. The new species included A. oviformis Soprunov and A. dolioformis Soprunov, and Trichothecium pravicovi Soprunov.

Jarowaja (1968; 1971), a Polish mycologist, described two constricting-ring trappers, Dactylaria effusa Jarowaja and Dactylella inquisitor Jarowaja.

Unquestionably, the major Canadian contributor to our knowledge of the nematophagous fungi is G.L. Barron, who, alone and in collaboration with a series of co-workers, has investigated many aspects of the biology and taxonomy of the

nematode-destroying fungi. In (1970), Barron noted that conidia of Harposporium helicoides Drechs. were ingested intact, and germinated in the nematode gut causing infection. He also pointed out (Barron 1973a) that Rhophalomyces elegans Cda. parasitizes both larval and adult stages of a species of Rhabditis, as well as nematode eggs and recorded important observations on special structures such as constricting rings and chlamydospores of the predaceous Hyphomycetes (Barron 1975b, 1979a). Barron (1977b) also published a book on the nematophagous fungi and presented an up to date overview (Barron 1981) on the most important features of the nematode-destroyng fungi.

Barron (1973b; 1975a; 1976a; 1976b; 1985) and Barron and Percy (1975) has described many new species of endoparasitic nematophagous fungi of the subdivisions Mastigomycotina and Zygomycotina. Other new species described by him were endoparasitic Hyphomycetes (Barron 1977a; 1979b; 1980) and the predaceous Hyphomycete Arthrobotrys botryospora Barron (1979c) with aseptate conidia. Barron and Davidson (1972) described A. anomala Barron and Davidson, an adhesive net-work trapper with narrow cylindrical conidia.

Barron and Dierkes (1977) showed that a Hohenbuehelia sp. was the perfect state of an Ontario isolate of Nematoctonus.

Thorn and Barron (1984) studied the ability of lignicolous Basidiomycetes to attack and consume nematodes. Testing 27 species they found five of Hohenbuehelia, five of Pleurotus and one of Resupinatus capable of destroying nematodes. Thorn and Barron (1986), in an Ontario based study, isolated five species of Nematoctonus and described a few more new species obtained in culture derived from basidiospores of several Hohenbuehelia spp.

Schenk et al. (1977) described Arthrobotrys amerospora Schenk, Kendrick and Pramer, a new species with aseptate conidia trapping nematodes by adhesive net-works.

The isolation of new species continued, Stirling and Mankau (1978) described Dactylella oviparasitica Sterling and Mankau, parasitic on eggs of Meloidogyne incognita Chitwood. McCulloch (1977b), during a survey of nematophagous fungi of Australia, isolated A. pauca McCulloch, a species similar to A. entomopaga, but with conidia produced on peg like sterigmata, Monacrosporium robustus McCulloch, a species capturing nematodes by means of sessile adhesive knobs, and two parasitic forms, Entomophthora vermicola McCulloch and Meristacrum pendulatum McCulloch.

In 1984, Tubaki and Yamanaka described a new species isolated from pine sap in Japan: Arthrobotrys ellipsospora Tubaki and Yamanaka, with small conidia and trapping by adhesive branches, and in 1985, Kuthubutheen et al. isolated in Malaysia a new nematode trapping synnematous species Arthrobotrys dendroides Kuthubuteen, Muid and Webster.

Previous isolations in Manitoba

Perhaps the first nematophagous fungus recorded from Manitoba was Harposporium anguillulae Lohde (Bisby et al. 1929). Subsequently, Bisby (1938) reported the occurrence of Arthrobotrys superba Cda. and A. superba var. oligosora (Fres.) Coemans, but the descriptions he provided of these latter two organisms are not in agreement with those of Cooke and Godfrey (1964). Sutton (1973) in his account of the Hyphomycetes of Manitoba and Satskatchewan recorded A. dolioformis , but the organism was described as having unbranched conidiophores with a single whorl of conidia at the top, while Soprunov (1958) states this organism has branched conidiophores with many whorls of conidia.

Pearn (unpublished, 1981) isolated Dactylaria scaphoides Peach and Dowsett et al. (1982) recorded Cephalosporium balanoides Drechs., both from Delta Marsh. Dowsett et al. (1984a) isolated an undescribed predaceous Hyphomycete which produced constricting rings and possessed subapical proliferation of the conidiophores; it was described as Arthrobotrys constringens Dowsett, Reid and Kalkat. Dowsett et al. (1984b) also isolated a Dactylella similar to D. leptospora Drechs., but differed therefrom in important features such as the trapping mechanism; considered an undescribed species, it was named D. multiformis Dowsett, Reid and Kalkat.

During the last ten years isolates of: A. oligospora, A. arthrobotryoides (Berl.) Lindau, A. cladodes Drechs. var. cladodes, A. cladodes Drechs. var. macroides Drechs., A. musiformis Drechs., Dactylella cionopaga Drechs., Dactylaria candida (Nees) Sacc., Dactylaria brochopaga Drechs. and D. sclerohypha Drechs. have been reported by students and

researchers from soil samples collected in Manitoba, however, information on the occurrence and distribution of nematophagous fungi in Manitoba is still quite sparse. Given the variety of sites, one would expect a considerable increase in recorded species if additional surveys were to be carried out.

Distribution and habitat

Nematode-destroying fungi are of world-wide distribution. In addition to the already cited reports of Drechsler (U.S.A.), Duddington (England), and Barron (Canada), nematophagous fungi were recorded in Ireland (Gray and Duff 1982; 1983); Poland (Jarowaja 1963); Russia (Soprunov and Galiulina 1951; Soprunov 1958); France (Comandon and De Fonbrune 1938; Peloille and Cayrol 1979); Italy (Verona and Lepidi 1970); Australia (McCulloch 1977a; 1977b); New Zealand (Fowler 1970; Wood 1973); India (Das-Gupta et al. 1964; Sachchidananda 1967); Uruguay (Gazzano 1973); Antartic (Duddington et al 1973); maritime Antartic (Gray et al. 1982; Gray and Smith 1984); Japan (Matsushima 1975), Canada (Estey and Olthof 1965; Alger 1980) and in many other parts of the world.

The variety of nematode-consuming fungi occurring in suitable substrata is easily demonstrated by the routine processing of a random collection of samples. Certain species, e.g. A. oligospora and D. cionopaga, appear to be very widely distributed, having been commonly found in a variety of samples from many different countries. Other species, e.g. A. robusta Dudd. appear more restricted in distribution; it was very frequently isolated by Duddington in Britain, but not by Drechsler in the U.S.A. On the other hand, A. musiformis has been recorded in several countries, but seldom in England, while Dactylella gephyropaga Drechs. has been isolated frequently in the U.S.A., but rarely elsewhere. The specificity in distribution of certain species may also reflect the very small numbers of samples taken by reseachers.

Gray (1985a) explored the effect of organic matter, soil moisture, pH, and the nematode density on the distribution of nematophagous fungi in 206 soil samples from Ireland. He concluded that the presence of predatory fungi was influenced more by pH and moisture than other soil factors. When he divided the group into non-spontaneous trap and spontaneous trap forming predators, he found that the

former were isolated from soils with lower organic matter and moisture content, while the latter were found in soils with relatively higher organic matter and moisture content. Gray felt that the non-spontaneous trap forming species can compete saprophytically under low nutrient and moisture conditions, but when nutrients and moisture content increase, they maintain their competitive advantage by utilizing the expanding nematode population. In contrast, the spontaneous-trap forming species are only competitive in soil rich in nematode populations. Furthermore, Gray associated the presence of conidia-forming endoparasites with the organic content of the soil and the presence of obligate parasites with high soil nematode densities.

The examination of vertical distribution by Gray and Bailey (1985) in a deciduous woodland indicated the presence of constricting ring, adhesive branch and adhesive knob trappers in the upper litter and humus layers only, while net-work forming and endoparasitic species were found in all layers. However the latter were most abundant in the lower mineral content rich layer.
In a further study, Gray (1987) pointed out that in temperate areas the presence of nematode-attacking fungi is influenced by the abundance and type of nematodes and by the soil pH, soil moisture and amount of N, P, K present in the specific soil layer. He found the greatest fungal diversity in the upper 10 - 30 cm layer of soils.

In the maritime Antarctic, where favorable condition for plant growth last only a few hours daily at the height of the summer period, Gray (1985b) found that endoparasitic fungi were far more abundant than predaceous fungi. He felt that these endoparasitic forms were more efficient in attracting prey and more rapid in completing the infection cycle than predaceous forms and, this could explain their relative abundance. The predaceous fungi he encountered were species which spontaneously produce traps and whose conidia can germinate to produce

traps. Gray also examined the effect of abiotic and biotic factors in the distribution of predaceous fungi and endoparasitic species in the maritime Antarctic and found that their presence was largely independent of abiotic soil parameters, but was directly related to the abundance of their potential prey.

Duddington (1951b) investigated habitats other than soils and he concluded that nematode-destroying fungi are common where nematodes and other microorganisms are abundant. His most productive substrate was moss; from twenty collections he recorded thirty nine nematophagous fungi. He suggested that the reason for the high yield was the moisture content of the samples and the presence of nematodes. He also found a large number of species in rotting wood and dung. Dixon (1952) isolated two new species from rotting wood: Dactylella mammillata Dixon and Harposporium lilliputanum Dixon.

Juniper (1953; 1957) isolated a substantial number of species from dung including the new species Dactylaria pyriformis Juniper. In her 1957 paper Juniper pointed out that the condition of the dung appears to have an important effect on the number of predaceous organisms present. Old dung in contact with soil was rich in predaceous fungi, and even frozen dung contained predaceous organisms. The moisture content of the dung was important, as few or no isolations were made from dry dung. While studying Hyphomycetes from dung, Seifert et al. (1983) isolated several Arthrobothrys, Dactylella, Dactylaria and Nematoctonus species, as well as endoparasitic genera such as Harposporium and Meria.

Duddington (1954) did a survey on the natural occurrence of predaceous fungi in agricultural soils generally infested with potato or tomato root nematodes. He recorded fifteen species from such fields, with the commonest being A. oligospora.

Barron (1977b) suggested that the investigation of undisturbed areas, such as old manure, rotting wood, leaves, decayed material, and agricultural soils would prove to be most rewarding in number of species isolated.

Other environments, such as fresh water ponds have proven to be very interesting. Peach (1950, 1952 and 1954) recorded many terrestrial species on decaying leaves in pond water, but also two new aquatic species: Dactylella reticulata Peach and Dactylaria scaphoides Peach.

Occurrence of nematophagous fungi in the rhizosphere has been investigated by Peterson and Katznelson (1964). A. oligospora was the only fungus regularly isolated, Harposorium species were seldom observed and there was evidence of species producing constricting rings. The authors noted that in repeated experiments, A. oligospora was found in greater abundance in the rhizosphere of soybean plants than it was in that of wheat. They could explain this result with other work in their laboratory that showed that under certain conditions, the soil of the soybean rhizosphere contained four times more nematodes than the soil of the wheat rhizosphere. The result of these studies strongly suggested that the type of crop growing in the sampled field, indirectly influenced the abundance of A. oligospora in the field.

Wingfield (1987) did a study in Wisconsin on fungi associated with the pine wood nematode Bursaphelencus xylophilus Steiner and Buhrer and recorded the presence of the predaceous Hyphomycetes A. superba Cda. and A. cladodes var. cladodes.

Taxonomy

Most predaceous and endoparasitic fungi are probably ana-holomorphs and classified in the subdivision Deuteromycotina. For only a few of these fungi are teleomorphic states known.

The criteria employed in classifying fungi have changed since Saccardo (1886) classified fungi on morphological features such as spore colour and septation. To day, the majority of authors tend to follow modifications of systems in which priorities are given to the manner in which conidia develop in determining relationships (Hughes 1953), but even this has not resulted in a stable taxonomic system. The accumulation of developmental data (Kendrick 1981) has led to the conclusion that developmental criteria cannot serve as the sole basis for a natural classification, but they do give an additional taxonomic dimension.

Early researchers, placed the predaceous Hyphomycetes in three genera: Arthrobotrys Corda (1839), Dactylaria Sacc. (1880) and Dactylella Grove (1884). The genus Arthobotrys was established by Corda in 1839 for A. superba with the original description being emended by Rifai (1968). In this genus, Drechsler placed all predaceous Hyphomycetes which have generally uniseptate conidia formed on denticles, and arranged in whorls at the tip and at nodes of the conidiophores. The genus Dactylaria was erected by Saccardo for a saprophytic species D. purpurella Sacc. and emended by Rifai (1968). In this genus, Drechsler placed all the predaceous Hyphomycetes which developed a cluster or clusters of multiseptate conidia on denticles along the conidiophore. Grove (1884) erected the genus Dactylella Grove for a saprophytic species Dactylella

which produced a solitary single conidium at the end of the conidiophore. In certain species of the latter, more conidia are produced at the ends of branches originating at lower points along the conidiophores.

Later, additional studies uncovered nematophagous species not referrable to the previous genera. Consequently Rifai and R.C. Cooke (1966) created the new genus Candelabrella Rifai and R. C. Cooke typified by the species C. javanica Rifai and R.C.Cooke. This new genus would include those species having conidiophores which proliferate subapically resulting in a small branching system similar to a candelabrum. Conidia are produced singly as the blown out ends of the successively produced branches. They also erected the genus Genicularia Rifai and R. C. Cooke, typified by Genicularia cystosporia (Dudd.) Rifai and R.C. Cooke, for species whose conidiophores become geniculate due to repeated subapical proliferations that follow the production of a single terminal conidium. Rifai (1975) proposed Geniculifera nom. nov. to replace Genicularia Rifai and R.C. Cooke. Cooke (1969a) erected the genus Duddingtonia R. C. Cooke, typified by Duddingtonia flagrans (Dudd.) R. C. Cooke (= Trichothecium flagrans Dudd.) because this species differed from Trichothecium roseum by having a capitate head of conidia instead of the catenulate cluster typical of this species. In the genus Duddingtonia, the conidiophores are simple, elongating or enlarging slightly at the tip for repeated subapical growth. Conidia are produced singly and after a first conidium is formed a new growing point appears to one side or just below the first conidium. Conidia are generally one septate and have a wide truncate base. Virat (1977) reported that the two Russian mycologists Mekhtieva and Sydorova in 1964 proposed the transfer of Trichothecium flagrans to Arthrobotrys, but that he was in favour of keeping it in the genus Duddingtonia.

Subramanian (1963) discussed the two closely related genera of Monacrosporium Oudemans and Dactylella and he concluded that the differences in conidial shape and septation were a logical separation between the two genera. Species in the genus Monacrosporium produce a more or less fusoid conidium with a large central cell, species in the genus Dactylella, a conidium divided in almost equal cells. Thus the genus Monacrosporium would accomodate most species of nematophagous fungi previously described in Dactylella. Subramanian transferred eleven species of Dactylella to Monacrosporium and he also included Dactylaria eudermata Drechs. and more species were transferred in this genus (Cooke and Dickinson 1965). Rifai (1968) proposed to limit the genus Dactylaria to the non predaceous organisms and Barron (1968) thought that the separation of Candelabrella from Arthrobotrys was not justified, because he had seen Arthrobotrys which had denticles similar to those of Candelabrella.

Cooke (1969b) pointed out that all the nematode trapping species of Dactylaria then known, were similar in conidial ontogeny to that of described for species of Candelabrella, Genicularia or Arthrobotrys and, furthermore, in the genus Dactylaria there were several darkly pigmented saprophytic species which differed from the predaceous Hyphomycetes in important characteristics, such as the nature of conidia formation, conidium shape and pigmentation.

Matsushima (1975) described several predaceous Hyphomycetes and placed the various species in the genera Arthrobotrys and Dactylella. He moved A. musiformis Drech. and Dactylaria brochopaga Drech. into the genus Dactylella.

Shenk et al. (1977) examined Dactylaria and Arthrobotrys and proposed only one genus Arthrobotrys Corda emend. Schenk, Kendrick and Pramer with type species A. superba be used for all predaceous forms of Arthrobotrys, Dactylaria, Duddingtonia, Geniculifera and Candelabrella, but they did transfer Dactylaria eudermata and D. psychrophila Drechs. to Monacrosporium.

De Hoog (1985) reported on a study of the Dactylaria complex in which he discussed the taxonomic position of the type species D. purpurella, and stressed that a revision of the genus is necessary. Van Oorschot (1985) placed thirty eight species of accepted predaceous Hyphomycetes in three genera: Arthrobotrys, Geniculifera and Duddingtonia. Van Oorschot limited the genus Arthrobotrys "to species forming blastic conidia, asyncronously on short denticles at differentiated conidiogenous heads or on pronounced denticles at a single locus, conidiophores often proliferating to form additional conidiogenus loci. In principle conidiogenesis is sympodial, leading to either swelling or proliferation of the conidiophore apex"(Fig 5, A-E). Most Dactylaria species (Fig 6, A) were thus transferred to the genus Arthrobotrys. The genus Duddingtonia is differentiated from Arthrobotrys by the sessile conidia (Fig 6, D) and the genus Geniculifera Rifai, "is similar to Arthrobotrys, but produces conidia on tubular denticles which are several microns long; the conidiophores frequently proliferate subapically at almost right angles and thus conidia are widely spaced" (Fig 6, E). Dactylella and Monacrosporium differ by having determinate conidiophores (Fig 6, B and C) .

Duddington (1955d) had pointed out that the Arthrobotrys series are an homogeneous group, in all of them, hyphal penetration following the capture of the prey, is followed by the formation of an infection bulb from

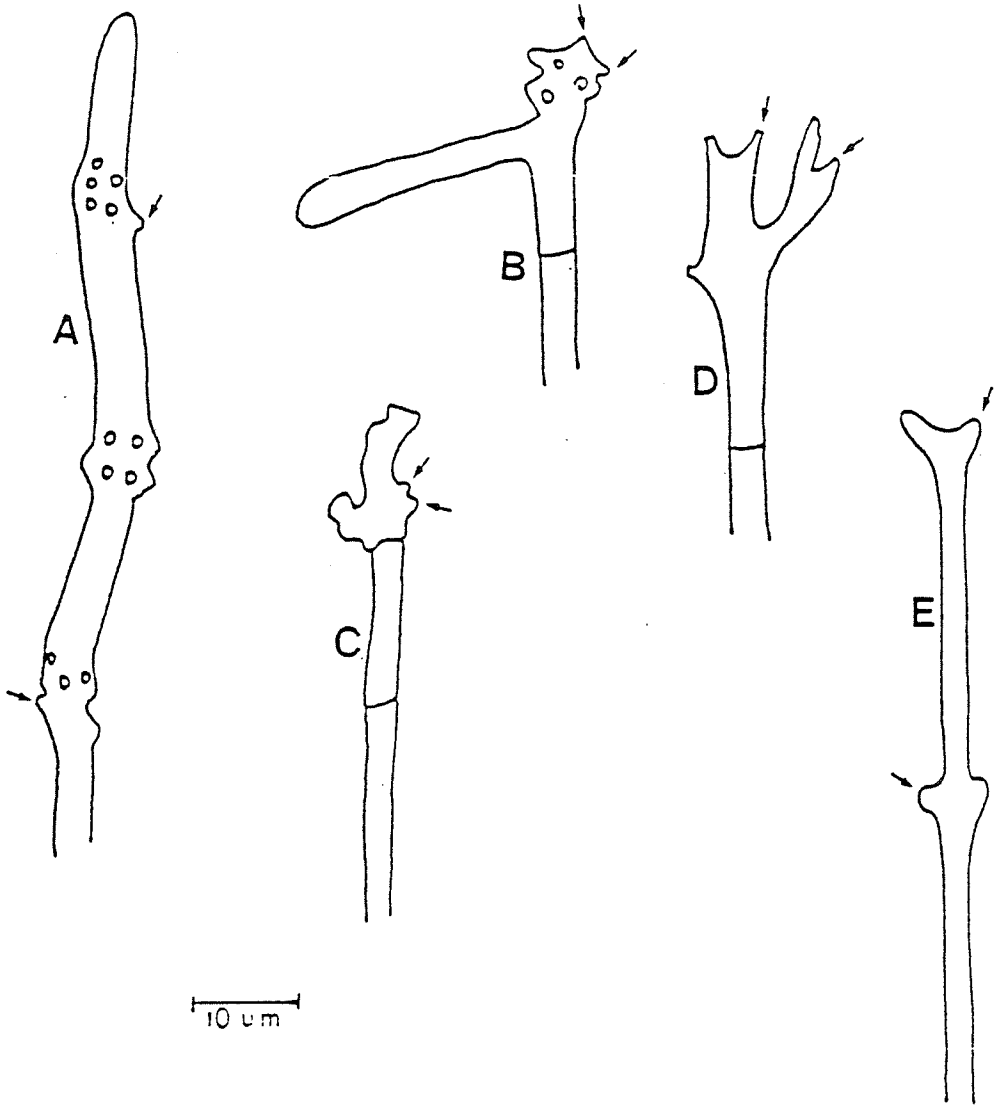

Fig. 5. Conidiophores in the genus Arthrobotrys Cda.:
A. A proliferating nodal conidiophore. Conidia on short denticles (arrows) (Arthrobotrys oligospora Fres.)
B A proliferating branched conidiophore. Conidia on short denticles (arrows) (Arthrobotrys arthrobotryoides Lindau).
C. A conidiophore with swollen apex. Conidia on short denticles (arrows) (Arthrobotrys cladodes Drechs. var. cladodes).
D. A proliferating conidiophore. Conidia borne singly at the end of short branches (arrows) (Arthrobotrys musiformis Drechs.).
E. A proliferating conidiophore. Conidia on large denticles (arrows) (Arthrobotrys dactyloides-Drechs.)
Camera lucida drawings.

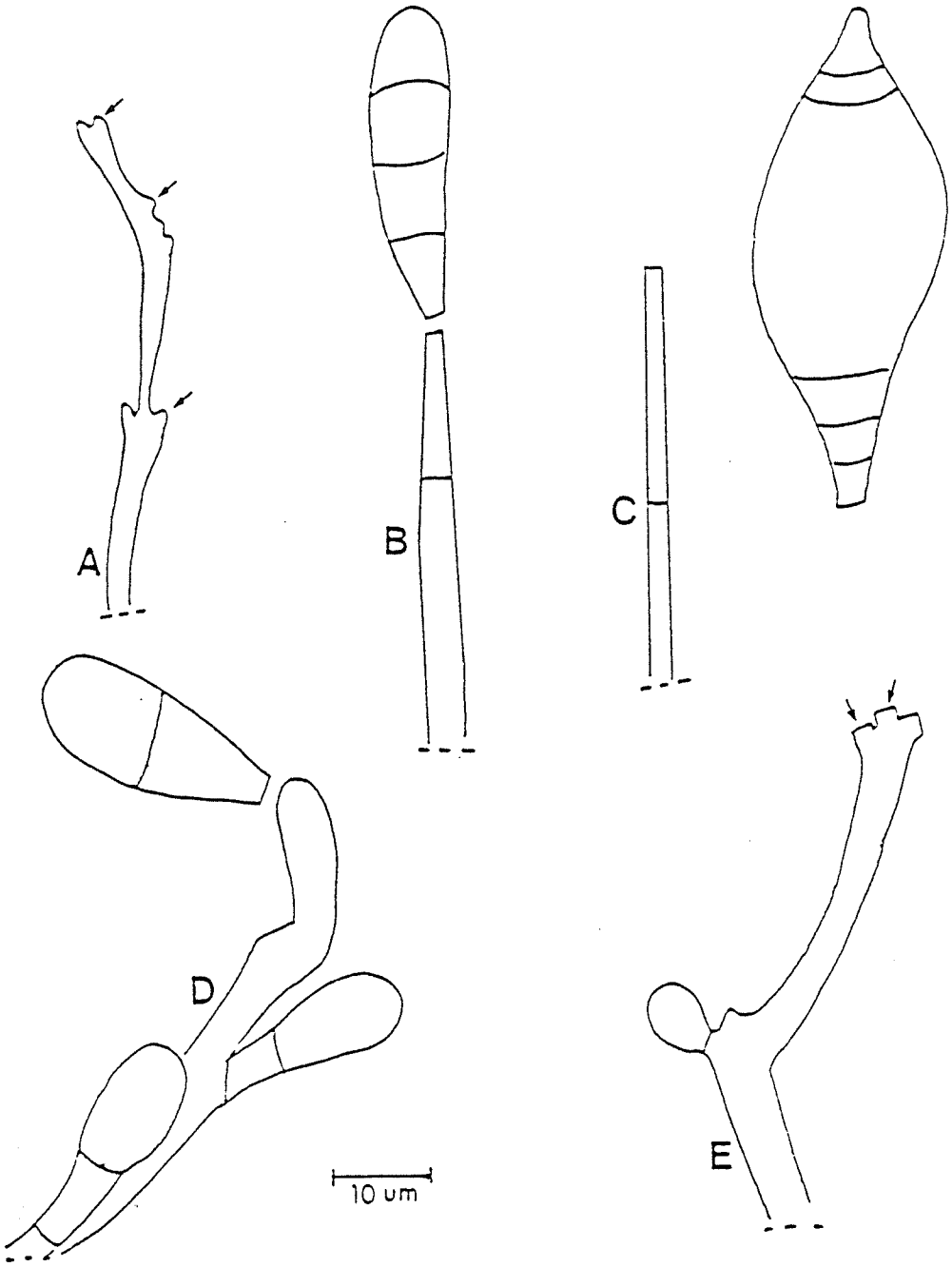

Fig. 6 Conidiophores in the genera: Dactylaria Sacc., Dactylella Grove, Monacrosporium Oudem., Duddingtonia R.C. Cooke and Geniculifera Rifai.

A. A proliferating conidiophore. Conidia on large denticles (arrows) (Dactylaria brochopaga Drechs.)

B. A determinate conidiophore. Single conidium (Dactylella lobata Dudd.)

C. A determinate conidiophore. Single conidium (Monacrosporium coelobrochum (Drechs.)Subram.

D. A proliferating conidiophore. Conidia sessile (Duddingtonia flagrans (Dudd.) R.C. Cooke).

E. A subapically proliferating conidiophore. Conidia on large tubular denticles (arrows) (Geniculifera cystosporia (Dudd.)Rifai.

Camera lucida drawings.

which trophic hyphae will grow out in both directions. Trapping mechanisms, such as net-works and constricting rings are found in the genera Arthrobotrys, Dactylaria and Dactylella of the Arthrobotrys series. Considering the sophistication of these mechanisms, Duddington pointed out the possible close relationship among these organisms, because it would be difficult to think that this method of trapping had evolved more than once. Stalked adhesive knobs are present only in the genera Dactylaria and Dactylella and are uniform in size, shape and length of the stalk. The differences among Arthrobotrys species, as pointed out by Duddington, are small and generally consist of differences in size and shape of spores. Nevertheless, in his 1956 publication, Duddington expressed the opinion that he was not in favour of the suggestion by Soprunov and Galiulina (1951) of putting all the predaceous Hyphomycetes with two celled conidia into the same genus Didimozophaga.

Duddington also pointed out that the genera Dactylaria and Dactylella often cause confusion because both have conidia with more than one cell. In Dactylaria conidia are in clusters, but some species, such as D. psychrophila do not produce all of their conidia at the same time. In Dactylella spores are solitary, but in certain species further conidia are produced on branches at lower points on the conidiophore. The predaceous genera Tridentaria Preuss , Pedilospora Hohnel and Triposporina Hohnel which have very primitive organs of capture, are not clearly related to the other predaceous Hyphomycetes.

The taxonomy of predaceous fungi has been extensively studied and revised. However, much less has been done with the endoparasitic species. Duddington (1955d) expressed the opinion that the Zoopagaceae are a quite closely interrelated family of fungi showing only the physiological

specialization of being obligate parasites. In 1973, Duddington divided the family Zoopagaceae into two families: Zoopagaceae and Cochlonemaceae in which he placed respectively the predaceous forms and the endoparasitic forms. According to Duddington (1955d) the endozoic nematophagus Hyphomycetes have in common the development of the fungus inside the prey, but are not a homogeneous group. The genus Nematoctonus grows in pure culture, has very distinctive hour-glass shaped adhesive knobs and relatively big spores. The common genera of endozoic parasites Harposporium and Acrostalagmus produce small spores from phialides and do not grow in pure culture. At that time Duddington thought that the spores of Harposporium anguillulae would adhere to the cuticle of passing nematodes and start an infection. To day we know (Aschner and Kohn 1958) that the spores of this group must be ingested by the nematodes, and the place where they germinate inside the nematode may vary depending on the species. Other genera are: Spicaria coccospora Dreshs., forming chains of conidia on phialides; Cephalosporium balanoides Drechs., with cylindrical phialides; and one species of Verticilium attacks nematodes (Goodey 1951). Subramanian (1977) proposed to move Acrostalagmus obovatus to the genus Verticillium. Dowsett et al. (1982) did a scanning electron microscopy study on Cephalosporium balanoides and proposed to move this species to the genus Verticilium as Verticillium balanoides (Drechs.) Dowsett, Reid and Hopkin. The whole genus was reviewed by Gams (1971). Gams and Jansson (1985) studied Meria coniospora and its classification.

Differences in opinions amongst taxonomists show that morphological and then developmental data do not give enough informations on this group of organisms to result in a stable taxonomic system. For e.g. members of the Arthrobotrys series appear morphologically very similar, but it is

difficult to differentiate between homologous characters that are inherited from a common ancestor and analogous characters produced instead by a long coevolution in a similar ecological habitat.

In recent years, biochemical characteristics such as electrophoretic or immunological properties of proteins, lipid and carbohydrate content have been used to distinguish between closely related strains of fungi. This approach could be used for the taxonomy of the nematophagous fungi.

Nematophagous fungi can be identified using the Cooke and Godfrey key (1964). While this key is not up to date, it is still the best one available. Haard (1968) and Jarowaja (1970) presented keys for the genus Arthrobotrys and Domsch et al.(1980) have produced a key to a few very common Arthrobotrys species. Thorn and Barron (1986) published an up to date key to the genus Nematoctonus.

Physiology

Predaceous Hyphomycetes have been studied to determine conditions of optimal growth in the hope they might be used in biological control of pathogenic nematodes.

Cooke (1963) found that most species would grow well on corn meal agar at temperatures between 15 to 25 C, while below 15 and above 25 C, growth was slow or lacking. Cooke pointed out that while net-work trappers are more efficient saprophytes, they are less efficient predators than constricting ring , adhesive knob and adhesive branch species. The latter species show more predaceous efficiency and often produce traps spontaneously.

Soprunov (1958) has a chapter on physiological and cultural properties of the predaceous Hyphomycetes in which he recorded the effect of temperature and fluctuations of pH on the fungal growth of Turkmenistan strains. He found that the strains of predaceous fungi in his collection were more thermophilic than the species isolated by Drechsler and while they grew between pH 4.0 to pH 9.0, growth was better between pH 5.5 to pH 8.5.

Tarjan (1961) studied the growth of Dactylella drechsleri Tarjan, a new predaceous fungus isolated from a citrus grove in Florida. On corn meal agar at 22 C it grew slowly, but abundantly and the most suitable pH range was from 5 to 6, though the organism would grow in conditions up to pH 8.2.

Olthof and Estey (1965) studied several predaceous Hyphomycetes in vitro and found that they could be grouped as follows: (a) faster growing species, (b) those intermediate in growth and (c) slow growing species. They also noticed that in general, on a specific medium and at 15 C, their

fast growing species preferred a pH range from 5-6 while their slow growing ones preferred a pH of 4.

Coscarelli and Pramer (1962), Faust and Pramer (1964) found that A. conoides Drechs. and Dactylella ellipsospora require the addition of biotin, thiamine and zinc, at concentrations of 5, 100, and 400 ug/L respectively to glucose-inorganic salt medium in order to obtain maximum growth. Satchuthananthavale and Cooke (1967a) studied in vitro the vitamin requirements for seven predaceous Hyphomycetes and concluded that all required thiamine for growth and all but one required biotin. In a further study, Satchuthananthavale and Cooke (1967b) found that the adhesive net-work trappers were able to utilize nitrite, nitrate, ammonium and organic nitrogen for their growth, while the constricting ring species could not utilize nitrite and had difficulty in utilizing nitrate. The net-work trappers appeared to be more competitive saprophytes and, according to Duddington (1962) and Duddington and Wyborn (1972), produce traps more rarely in pure culture and are also less easily stimulated to do so by artificial means than the constricting ring species.

Predaceous species and most endoparasitic species appear to be able to prey on a variety of nematode species. Barron (1978) investigated the host endoparasitic interaction of Rhabditis terricola Dujardin and found that out of forty endoparasitic species tested, thirty-two were capable of attacking this soil nematode.

Nordbring-Hertz and Mattiasson (1979) demonstrated the presence of a lectin in the adhesive material on the traps of A. oligospora which binds to a carbohydrate on the nematode surface, and this lectin in laboratory experiments did not appear to be strictly specific for a carbohydrate. Later research in the laboratory pointed out that the lectins of certain

fungi are specific for a carbohydrate on the nematode cuticle (Nordbring-Hertz et al 1982).

Early experiments by Couch (1937) and Comandon and De Fonbrune (1939) showed that net-work trappers produce traps when stimulated by sterile water which had contained nematodes. Pramer and Stoll (1959) stimulated trap formation in A. conoides with filtrates of Neoplectana glaseri and found that the most effective dilutions were one part in five and one part in ten. Pramer and Stoll agreed with Lamy (1948) that there was a substance given off by nematodes which would stimulate trap formation. They called this substance nemin. They found that nemin was soluble in water, ethyl alcohol and in n-butanol, but not in benzene, carbon disulfide or ethyl ether. Their nemin did not precipitate when diluted to five times the original volume with acetone and was not inactivated by exposure to a temperature of 100 C for ten minutes.

Soprunov (1958) investigated the formation of net-works in predaceous Hyphomycetes, and listed substances that would stimulate trap formation. Among those were snow collected and left at room temperature then filtered, and rain water collected preferably at the starting of a storm and again filtered before using it as a stimulant. Soprunof concluded that the stimulating substance was CO_2.

Bartnicki-Garcia and Pramer (1964) studied trap formation in A. conoides and came to the conclusion that carbon dioxide plus a substance released by the nematodes are necessary to stimulate trap formation.

Kuyama and Pramer (1962) isolated a protein, in powder form from ascarides, which had nemin activity. Winkler et al (1961) devised a nemin assay procedure to test the nemin activity of animal sera and aqueous extracts of two types of nematodes. They found that the extract of

Panagrellus redivivus had the greatest nemin activity, followed by ascarid extract.

Some other experiments (Feder et al. 1963) tested the sensitivity of various Dactylella species to a morphogenetic substance obtained from Panagrellus redivivus and these showed that Dactylella species vary in their degree of sensitivity to nemin, but they all responded to the presence of one single living nematode.

Studies have also been done on the production of constricting rings and it was found that, ring traps form easily under chemical stimulation. Couch (1937) observed Dactylella bembicodes producing rings in pure culture when he used phosphoric acid as a stimulant.

Roubaud and Deschiens (1939) demonstrated that various animal substances including human serum and dung extract caused trap formation in D. bembicodes, but plant extracts had no effect.

Lawton (1957) confirmed the observation of Lamy (1943) that horse serum stimulated trap formation. Lamy observed the effect of horse serum and earthworm extract on Dactylella bembicodes. Both stimulants have a maximum concentration and a minimum concentration, above and below which there is no response. Lamy observed also that young mycelia respond more quickly to stimulation than old mycelia.

Duddington (1962), based on the work of Feder et al. (1960) on the formation of constricting rings in pure culture by Dactylella doedycoides, suggested that the conidia of this fungus vary in their ability to produce rings in pure culture, depending upon their heterocaryotic state. Turnbull and Zachariah (1978) induced the production of giant rings in Dactylaria brochopaga by growing their cultures under conditions of poor ventilation and in darkness.

Couch (1937) found that distilled water between 33 and 75 C caused the closure of constricting rings. The rings would close also when a hot scalpel was held in the vicinity of the traps. This was a very useful discovery, because it provided an easier way of experimenting with the mode of operation of this sophisticated mechanism.

Comandon and De Fonbrune (1938) published their observations on the net-works of A. oligospora, adhesive knobs of Dactylella ellipsospora, the constricting rings of Dactylaria brochopaga, and the adhesive branches of Stylopage hadra Drechs., they also produced an eight mm motion picture of their work. From their observations, they concluded that the hyphae of a the three dimensional net-work are covered with adhesive material, younger hyphae having more adhesive than older ones. Traps are to some extent selective, as certain objects, such as glass, would not stick to them.

The above authors also observed that physical stimulation of net-works or of adhesive hyphae of Stylopage hadra caused movement of protoplasm away from the point touched. They speculated that this was in relation to secretion of adhesive material. They also reported that the sticky knobs of Dactylella ellipsospora behaved in a similar manner.

Comandon and De Fonbrune (1938) also noted that in the absence of nematodes, ring traps could be induced to close by mechanical stimulation. Rubbing the luminal side of any of the ring cells with a microneedle, induced a prompt inward swelling of the touched cell which was quickly followed by the swelling of the other two ring cells. Comandon and De Fonbrune (1939) showed that after inflation of the ring, small vacuoles increased in size and fused together to form a large vacuole.

Muller (1958) studying ring closure in Arthrobotrys dactyloides and Monacrosporium doedycoides concluded stimulation of the inner wall of the

ring cell caused an instantaneous decrease in the pressure potential of the wall and an increase in membrane permeability. This allows for a rapid water uptake and results in cell expansion.

Heintz and Pramer (1972) studied constricting ring function at the ultrastructural level in A. dactyloides before and after expansion. They reported that an open ring contained extensive membrane-bound inclusions, labyrinthyne networks and an electon-lucent region between the protoplast and the cell wall on the luminal side of the ring. After closure, these feature which they speculated were necessary in the expansion process, were no longer visible.

Rudex (1975) studying in vitro constricting ring closure in D. brochopaga suggested that stimulation of the cell causes a rearrangement of protoplasm, this rearrangement generates spaces within the cell and this condition would act as a stimulus for the imbibition of water through the stalk. Rudex although he had evidence for this passage of water, agreed that imbibition alone could not explain the rapidity of the phenomenon , but he felt it was playing a part in the response. The work of Eyring et al. (1946), had shown that unfolding of protein chains is accompanied by an increase in the absorption of water by these proteins and this will cause an increase in molecular volume of 1% . Rudex proposed that this could also play a part in the inflation of the cell.

Ultrastructural studies on constricting rings of Dactylaria brochopaga by Dowsett et al. (1977) showed that the wall of the ring, on the luminal surface, is composed of four or even five layers. This wall has a layer or layers of fibrils which extend lengthwise along the cell wall. The outer wall contains only two layers, the outer one appeared electron-opaque and continuous with the inner layer and the inner one appeared electron lucent.

Inclusions are located inside the plasma membrane in the areas of activity and would serve as reserve membrane or available surface for ring cell expansion. Dowsett and Reid (1983) did an ultrastructural study on the normal and the giant rings of Dactylaria brochopaga and observed multilaminate bodies in the cells of the rings. These multilaminate bodies could represent additional membrane reserve or surface for the expanding cells.

Barron (1981) suggested a simple theory that would accomodate all the known information: a line of weakness exists along the middle of the wall of the luminal face. This line will break at any physical disturbance. He envisaged the closure of the ring as similar to the sudden discharge of ascospores from an ascus. The membrane does not change permeability. Release of wall pressure causes wall rupture, generates a rapid intake of water that in turn causes the wall to balloon into the lumen. The sudden increase of cell volume results in an equivalent decrease in osmotic pressure and this explains why the ring does not always constrict the nematode immediately.

Giuma and Cooke (1971) speculated on the presence of a nematoxin when they observed nematodes becoming immobile and moribund on contact with germinating conidia of Nematoctonus haptocladus Drechs. and N. concurrens Drechs. Balan and Gerber (1972) studied the interaction of Panagrellus redivivus and A. dactyloides and showed that a filtrate from the fungus contained a nematocidal substance that they thought was ammonia. They also showed the presence of nematode attracting substances, one of which was CO_2. They commented that their finding was in agreement with previous work by Klingler (1963) and Peacock (1961) that showed that CO_2 is an attractant for plant parasitic nematodes. Balan et

al. (1974) found that A. conoides, A. oligospora, and Monacrosporium rutgeriensis Cooke and Pramer produced nematode attracting and nematocidal substances in the presence of nematodes. Barron and Thorn (1987) have shown inequivocally that Pleurotus ostreatus immobilizes its prey with a powerful toxin contained in stalked cells on the hyphae.

Isolation Techniques

Predaceous fungi can be isolated by plating small amounts of soil containing organic matter, decaying wood, moss or other material rich in nematodes onto media such as water agar or corn meal agar (CMA). Drechsler used CMA and although this procedure is demanding in terms of time, according to Barron (1977b), it allows for the recovery of the fullest range of nematode-destroying fungi from a sample.

Warcup (1950) suggested the preparation of plates by transferring a small amount of soil to 9 cm plastic plates, to which were added 8-10 ml of cooled medium and the soil was dispersed throughout the agar by gentle agitation. Old cultures made in this way could have their life extended by adding a thin film of sterile agar over them with subsequent appearance of later growing species of predaceous or endoparasitic nematophagous fungi (Duddington 1955a).

Soil dilutions are very selective for highly sporulating species and they would not yield many nematophagous species. Warcup (1950) published a table giving the results obtained by employing the soil dilution and the Warcup method. More species were isolated with the Warcup method and the best results with the soil dilutions were obtained from the residue, not from the suspension.

Barron (1969; 1977b) described methods and techniques for the isolation, culture and maintenance of nematode-destroying fungi. He pointed out that endoparasitic species are less aggressive than predaceous species and, when in competition with them, may not appear at all. To overcome competition, Barron suggested the Baermann funnel technique (Giuma and Cooke 1972) followed by differential centrifugation that would spin down large spores at low speed and keep small spores in

the supernatant, then the small spores can be spun down at higher speed. Generally endoparasitic fungi have small spores and persist in soil in the form of resting spores or conidia. Selective nematode baiting can be employed to isolate or to avoid endoparasitic fungi such as Harposporium species whose spores need to be ingested by the nematode in order to start the infection inside the host.

Gray (1984) did a comparison of the soil sprinkling method and the Baermann funnel technique for the isolation of endoparasitic species. The Baermann funnel technique was significantly more effective in isolating endoparasitic fungi, but did not isolate all the species contained in the sample and the results appeared to be influenced by the nematode density of the sample.

Thorn and Barron (1986) described how they isolated and cultured species of Nematoctonus and how they started fungal cultures of basidiomycetes in Petri dishes from basidiospores or small fragments of the pileus. From their study on the genus Nematoctonus in Ontario, they concluded that species isolated with the soil sprinkling method were not usually isolated with the Baermann funnel or the centrifuge technique. The Baermann funnel and the centrifuge techniques appeared to be complementary. Consequently they thought that if they had processed the samples by the sprinkling method and by Baermann funnel and centrifuge techniques, they would have recovered more species.

METHODS AND MATERIALS

Sampling

A total of 120 samples were collected during the fall of 1985, the spring, summer and fall of 1986 and the fall of 1987 from various locations in Manitoba (Fig. 7). The collection sites were city parks, gardens, provincial forests, farms, marshes, river and creek banks, and lake beaches some of which are illustrated in figures 8-11. Selection of sites was determined by the desire to explore accessible but different habitats that would include untouched sites with original vegetation, sites exploited by man, wet habitats and peculiar sites such as a northern bird sanctuary. The survey carried out in each site, even if limited to a few samples, could give an indication of its typical and common nematophagous fungal population and results from the different sites could be compared. Soil, manure, bark, wood, decaying wood and leaves, moss and wild animal droppings were collected at those sites. The study of different substrates should again yield diversified isolations and useful information. Basidiomata of small lignicolous gilled Basidiomycetes were also collected with the purpose of growing their vegetative mycelia in laboratory conditions and testing them for predatory activity.

The total collection comprised 43 soil samples from forested areas; 12 soil samples from gardens and city parks; 9 samples of manure from cow and chicken farms; two soil samples from agricultural land; 15 moss samples, including a sample collected in 1971; 30 wood samples consisting of bark and decaying wood; nine samples of wild animal droppings and; 10 basidiomata.

Fig. 7. Collecting sites in the Province of Manitoba.

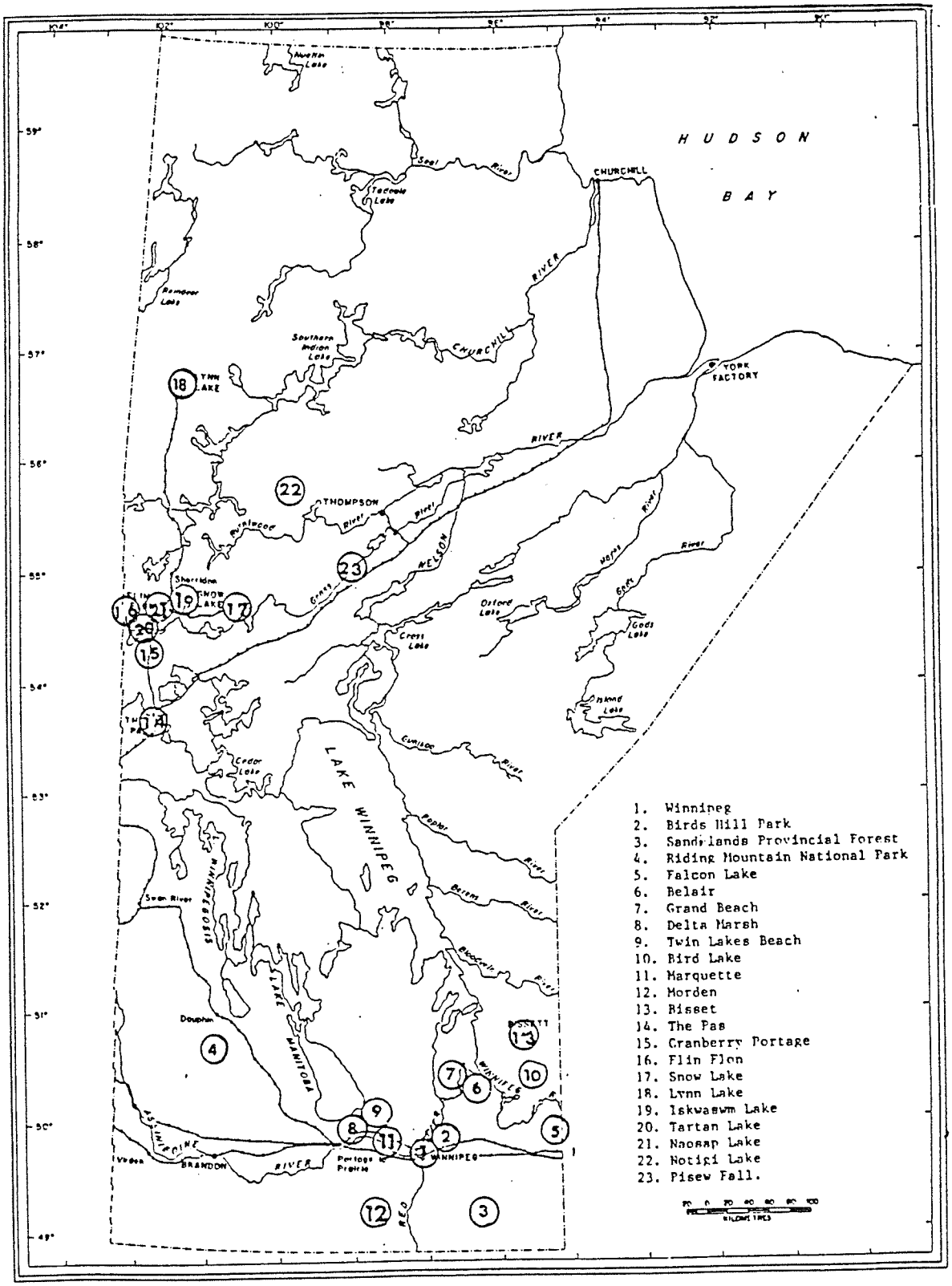
HUDSON
BAY
CHURCHILL
YORK FACTORY
THOMPSON
LAKE WINNIPEG
BRANDON
Portage la Prairie
WINNIPEG
1. Winnipeg
2. Birds Hill Park
3. Sandilands Provincial Forest
4. Riding Mountain National Park
5. Falcon Lake
6. Belair
7. Grand Beach
8. Delta Marsh
9. Twin Lakes Beach
10. Bird Lake
11. Marquette
12. Morden
13. Bisset
14. The Pas
15. Cranberry Portage
16. Flin Flon
17. Snow Lake
18. Lynn Lake
19. Iskwasum Lake
20. Tartan Lake
21. Naosap Lake
22. Notigi Lake
23. Pisew Fall.

Fig. 8. Wildlife Park, Flin Flon.

Fig. 9. Sturgeon Creek, Winnipeg.


8


9

Fig. 10. Bruce Park, Winnipeg.

Fig. 11. Collection site: base of an elm tree.


10


11

(a) Soil samples

The first 10 soil samples were collected by cutting out a block of soil 15 cm x 15 cm wide and 25 cm deep. The size of the sample was then reduced to a block 15 cm x 10 cm wide and 15 cm deep to avoid unnecessary storage of large quantities of material and because emphasis was being placed more on varieties of substrates and sites of collection than on the size of sample.

(b) Other samples

Pieces of bark, rotting wood and leaves, moss and animal dropping were easily collected with a small shovel. The quantity of each sample depended on the availability of the material and the size of the containers used for storing them. All samples except the animal droppings, were placed in ziploc freezer bags 27 cm x 32 cm. The animal droppings were placed in 9 cm plastic plates. All containers were sealed with masking tape to preserve their moisture content. Samples were numbered and dated. Description of the material, site of collection, plant cover and any other useful information was recorded. Whenever possible, the animal dropping was identified with an animal species.

(c) Gilled Basidiomycetes

Basidiomata were wrapped individually in tissue paper and carried in a basket. As soon as possible they were identified and processed. A spore print was obtained by placing each basidioma overnight on a clean 9 cm plastic plate. The next morning, spore print colour was recorded and a small sample of spores was collected in a drop of sterile water and placed

on a microscope slide 75 X 25 mm covered with a cover slide 22 X 22 mm, 0.17 mm in thickness (Fisher Scientific Co.) and observed under the microscope. Spore shape and measurements of thirty spores were recorded.

Laboratory Studies

(a) Determination of the pH of the sample

A clean 50 ml beaker was filled with sample material to the 10 ml level, then distilled water was added to bring the content of the beaker to the 30 ml level. The diluted sample was vigorously stirred with a clean glass rod and left to stand for 10 minutes. Bark, decaying wood, plant material etc. were crushed with an hammer or ground up in a blender prior to being put into the beaker.

A colorpHast indicator strip (EM Science, Cherry Hill, N.J.) was immersed in the supernatant and allowed to stand for 10 minutes, to permit full colour development on the stick. The pH of the sample was determined by comparing the stick colour to the supplied standard colour chart. The degree of acidity and alkalinity of the sample was described using the table given by Brady (1974).

(b) Soil plating techniques for the recovery of predaceous fungi

All collections were stored at 5 C until processing. Each soil samples was throughly mixed at room temperature, then 40 g of soil was removed and placed in a clean 1000 ml Erlenmeyer flask and diluted with 800 ml of molten CMA (Difco Laboratories, Detroit, Michigan.). The flask was stirred to disperse the soil particles throughout the agar and the content was plated out 20 ml at a time into 50 standard sterile 9 cm plastic plates. After processing three soil samples in this way, the procedure was

changed to avoid the time consuming work of regularly inspecting 50 plates for each soil sample. Subsequently, the sample was not mixed, a weighed aliquot of one g of sample taken at random from the bulk sample was placed into a sterile plate (Warcup 1950). The operation was repeated 20 times. Approximately 20 ml of molten CMA at 45 C were added to each of the twenty plates. The plates were well stirred. When the sample was not homogeneous in nature, i.e. it contained pieces of wood, roots, moss, leaves etc., care was taken to place representative material into the plates.

Bark, rotting wood and any other material collected in large pieces, were crushed into small pieces prior to weighing and plating them out. All plates were incubated in a darkened incubator at 25 C for six days after preparation. Plates were then removed and examined under the dissecting microscope to ascertain whether nematodes were naturally present; if not a drop of sterile suspension of nematodes was added to each plate. All plates were returned to the incubator when the presence of nematodes was assured.

(c) Plating techniques employed in the recovery of endoparasitic fungi

Eighty grams of soil were placed in a sterile Baermann funnel on four layers of cheese cloth and 200 ml of sterile water were added to cover the sample. After 24 h, the clamp on the collecting tube was opened and 25 ml of water were collected in a small sterile bottle. This bottle was left undisturbed for several hours, then 15 ml of the supernatant were discarded with the help of a sterile pipette and 15 ml of sterile water were added to the bottle. The bottle was agitated and three drops of the solution were transferred to freshly prepared water agar (WA) plates

(Gibco Diagnostics, Madison, Wisconsin); ten replicates were prepared from each bottle. These plates were sealed, labelled and incubated at 25 C.

After the above procedure was completed, the remaining sample material adhering to the cheesecloth was scraped from the cheesecloth and resuspended in the water remaining in the Baermann funnel. this solution was transferred to a clean beaker and mixed well. The mixture was then passed through 4 layers of cheese cloth and the filtrate again collected in a clean beaker. The deposit left in the cheesecloth was discarded and the filtrate was centrifuged at 3000 rpm/min for three minutes using a GLC-2B centrifuge (Dupont Instruments). The supernatant of the centrifuged sample was transferred to a clean 50 ml beaker and three drop aliquots were added to each of ten plates containing WA and nematodes. All these plates were labelled and stored at 25 C. The WA plates containing nematodes were prepared in advance by placing one drop of nematode suspension in sterile 9 cm plastic plates to which were added 20 ml of molten agar. The plant parasitic nematodes Aphelenchus avenae Bastian were not immobolized in the agar during this procedure that appeared always to produce uncontaminated plates. When dealing with free living nematodes, the drop of nematode suspension was placed on the agar, otherwise they remained stuck in the agar. At least 20 replicate plates were made and all plates were stored at 12 C in a darkened incubator. The Baermann funnel and the centrifuge technique were used only a few times on samples previously processed by the Warcup (1950) soil plating technique.

(d) Culturing and testing the vegetative mycelium of lignicolous Basidiomycetes for nematophagous ability

To obtain basidiospores, the pileus of the lignicolous basidioma was suspended for one h on two glass rods above the surface of a water agar plate which contained nematodes. Before incubation at 25 C in a darkened incubator, the plate was inspected to make sure a large number of basidiospores were present on the surface of the water agar. After a week, such plates were examined to determine whether spores had germinated and if infected nematodes were present. Inspection was repeated every 3 or 4 days. After a month, if spores did not show any sign of germination, the plates were discarded.

(e) Isolation , culture and storage of isolated fungi

When sufficient mycelium had developed, generally after one week with water agar plates and 10 - 15 days for CMA plates, the incubated plates were inspected under the dissecting microscope to determine whether trapped nematodes or sporulation typical of predaceous fungi could be seen. This inspection was repeated each week for three months.

Single spores of fungi suspected of being predaceous were isolated from the conidiophores using a dissecting microscope, and a sterile needle coated with a film of warm CMA; such spores were transferred on fresh CMA plates (Booth 1971). Isolates were numbered according to the original soil sample, and incubated at 25 C in a darkened incubator. When growth occurred stock tubes of each isolate were prepared and stored at 5 C

The growth rate of each isolate was also measured in terms of diameter of the colony. A block of culture taken with 5mm diameter cork

borer, was transferred on a sterile CMA plate or other medium, three replicate plates were made and these plates were stored in a darkened incubator at 25 C. After a week the plates were removed and their diameter measured and recorded as an average.

If growth of predaceous fungi was unsatisfactory on CMA, other media were tested e.g: potato dextrose agar (PDA) (Gibco Diagnostics, Madison, Wisconsin), 2% malt extract agar (MEA) (Gibco, Diagnostics, Madison, Wisconsin) plus 0.05% yeast extract (Difco laboratories, Detroit, Michigan) or soil extract agar (SEA) (Appendix).

A drop of nematode suspension was added to a few plates of these media while plating them out to stimulate germination of obligate parasites. In the case of Harposporium species, attempts to obtain a pure culture were made by transferring a diseased nematode to a plate of WA containing 1 mg/L penicillin-g and 1 mg/L streptomycin (Sigma Chemicals Co., St. Louis, Missouri) and to which was added free living nematodes. When nematophagous basidiomycetes did not produce conidia, a small piece of clean mycelium was transferred on CMA or PDA. These cultures were then transferred to slants, as previously described.

(f) Identification and photomicrography of isolated nematophagous fungi

Fungal cultures were regrown for identification from stock cultures onto appropiate media. When sufficient growth had occurred slide cultures were prepared from one plate (Koneman et al. 1979), while others were retained for periodic examination. When sporulation occurred slides were prepared. All slides were examined by using interference contrast optics on a Leitz Ortholux II microscope and the fungus identified to specie using

the standard taxonomic keys of Cook and Godfrey (1964), Haard (1968), Jarowaja (1970) and Van Oorschot (1985). At least thirty conidia were measured to establish the size range of the conidia of each isolate. Conidial septation was recorded and the nature of the conidiophores, conidiogenous cells and trapping devices and, when appropriate, measurements were taken. In addition the growth pattern and colour of the mature colony was recorded. Illustrations of important features were prepared using a camera lucida, or they were photographed with a Leitz microscope fitted with an automatic camera attachment and interference contrast optics using Kodak Panatomic - X film, ASA 32. The films were developed in Kodak D-76 developer and printed on Kodak Polycontrast rapid II RC paper F using Kodak D-72 developer and standard procedures.

Nematophagous basidiomycetes were identified from their basidiomata employing the following references: Groves (1979); Lincoff (1981); and Miller (1984) Their basidiomata were also photographed with a 35 mm Pentax camera using Kodacolor VR-G CA135-12 film. This film was develped and printed by Astra Photo Ltd, Winnipeg. The basidiomata were left to dry and stored in 9 cm plastic plates. The nematophagous Basidiomycetes were cultivated on laboratory media and their growth thereon, particularly in the presence of nematodes, was studied. Again characteristic structures were drawn and photographed.

(g) Slide preparation

Slide culture technique

A flamed 25 mm x 75 mm slide was placed into a sterile 9 cm plastic plate on a sterile V-shaped glass rod. A 6 mm x 2 mm inoculum block cut from a prepared culture with a sterile scalpel was placed on the slide.

The inoculum block was covered with a flamed coverslip. Five ml of sterile water were than added aseptically to each plate to create a humidity chamber and the system was incubated in the dark at room temperature. When necessary,additional sterile water was added to maintain high humidity levels in these chambers. One week after such chambers were prepared, a drop of nematode suspension was added under one corner of the cover slip. When sporulation and trapping devices were visible under the dissecting microscope, the coverslip was removed and placed mycelial side down on a second slide in a drop of Melzer's solution lacking iodine. The agar block was removed from the original slide, and again a drop of Melzer's solution lacking iodine was placed on the fungal growth and the slide covered with a 22 x 50 mm, N 1 cover slide. Two such humidity chambers were prepared for each isolate, and the slides from each were sealed by ringing the coverslip with finger nail polish to preserve the mounts until examination could be completed.

Slides

A small sample of each culture containing conidiophores, conidia, and other structures useful for identification was placed on a slide, mounted in a drop of Melzer's solution lacking iodine and covered with a cover slide .

(h) Maintenance of nematode stock cultures and nematode suspensions

Bacteria-free stock cultures of the plant-parasitic nematode Aphelenchus avenae Bastian were maintained on plates of CMA inoculated with Rhizoctonia solani Kuhn. Fresh cultures were regularly prepared by transferring a small square of agar containing both R. solani and

nematodes from these cultures on new CMA plates. After ten days these plates were placed into a 13 C incubator for storage.

Sterile nematode suspensions were prepared using the Baermann funnel technique (Goodey, 1957). Agar, bearing mycelium from three plates prepared as above, was cut in squares with a sterile scalpel, and the squares were placed into a sterile Baermann funnel lined with four layers of sterile cheese cloth and covered with sterile tap water. After 24 h, nematodes were collected in a sterile bottle with 25 ml aliquots of water. These bottles were labelled, dated and stored at 6 C in a refrigerator.

(i) Supply of free living nematodes to serve as bait for Harposporium species

Free living nematodes were obtained from plated sample as described above. A few drops of the suspension from the Baermann funnel were placed on a slide and observed at high magnification to make sure that a large proportion of nematodes did not have a stylet in the buccal cavity and were thus free living nematodes that feed on spores and bacteria. The nematode suspension, centrifuged (Barron 1977b) at 1000 rpm/min gave a pellet that was resuspended in 10 ml of sterile water. The whole procedure was repeated a second time to remove contaminants and then the bottle was labelled and stored at 6 C in a refrigerator ready to be used.

RESULTS AND DISCUSSION

Arthrobotrys arthrobotryoides (Berl.) Lindau, Krypt.-Fl.1(8): 371. 1907.

Plate I, Figs. a-c.

Colonies attaining a diameter of 53 mm in seven days at 25 C on CMA; creamy to pale pink with a mealy texture. The vegetative mycelium hyaline, septate; hyphae 3-4 um wide and forming abundant mycelial rings and fasciculate aerial strands from which conidiophores arose in large numbers. Conidiophores macronematous; simple to branched; 200-450 um long with inflated tips; and 4-5 um wide at the base; indeterminate, and denticulate. Conidiogenous cells polyblastic, integrated, and terminal. Conidia holoblastic; produced asynchronously and sympodially upon the short denticles in close whorls at the end of conidiophores and branches. Conidia hyaline; 15-28 x 8-12 um, ellipsoidal, divided by a septum into two almost equal cells. Trapping nematodes by adhesive net-works with loops having an opening of 20-30 um. Smooth, spherical chlamydospores, 12-20 um in diameter, were present in old cultures.

DISTRIBUTION AND HABITAT in Manitoba: pH range 5.5-7. A. arthrobotryoides was isolated from samples collected during spring, summer and fall at several locations in Manitoba: in Sandilands Provincial Forest, from fresh horse droppings (once) and from soil (sand and organic plant material) under pine (Pinus banksiana Lamb (once); in Birds Hill Park from peat of black spruce bog (Picea mariana (Mill.) B.S.P.) (once), from peat of cedar bog, (Thuja occidentalis L.) (once), and from soil (sand and organic material) under scotch pine (Pinus sylvestris L.) (once); at Falcon Lake, from peat of a black spruce bog (once); within or at the outskirt of Winnipeg, in city parks, from the top soil of a burned area (once), soil (clay) close to a rotten trunk of a popular tree, (Populus deltoides Bartr.) (once),

from soil (clay and organic plant material) under elm tree (once) and bark from elm tree (Ulmus americana L.) (5 times), soil (clay) under (Populus balsamifera L.), from soil, grass cover collected in a farm (once), from soil (clay, sand and organic plant material) under a mixed forest along highway 59 (once); in Flin Flon from a soil sample (clay, sand, bird droppings and decomposed feathers) and near Notigi Lake from peat under mixed boreal forest (once).

ISOLATES 6, 8, 9, 17, 18, 19, 20, 28, 38, 58, 61, 62, 63, 67, 75, 79, 89, 96, 99, 113, 114.

DISCUSSION: All isolates agreed very closely with Drechsler's (1944a) description of the species. The species appeared to be restricted to slightly acidic substrates having the relatively narrow pH range 5.5 - 7 and generally to wooded habitats. The high number of isolates obtained (twenty-one) indicated that this fungus is very common in Manitoba. It has been reported that A. arthrobotryoides can utilize pectin , cellulose and chitin (Tubaki 1958) and thus would be highly competitive in the habitats in which it was found. It has been frequently isolated in North America, including a report by Barron in Ontario (1977b), but also has been reported by Soprunov in Turkmenistan (1958) and by Jarowaja in Poland (1970). This species appeared to be easily separated from other Arthrobotrys species, including the close relative A. cladodes, by constant characteristics such as the well defined shape and size of the conidia, their position at the inflated tips of conidiophores and branches, and because of the presence of numerous chlamydospores.

Arthobotrys cladodes Drechs. var. cladodes, Mycologia 29: 463. 1937.

Plate I, Figs. d-f.

Colonies attaining a diameter of 40 mm in seven days at 25 C on CMA; white to creamy in colour; mealy in texture. Mycelium hyaline septate; hyphae 3-4 um wide; forming numerous mycelial rings and fasciculate aerial strands from which conidiophores arose in large number. Conidiophores macronematous 150-400 um long; producing one or two side branches; conidiophore apex irregularly inflated; in general, non-proliferating; and denticulate. Conidiogenous cells polyblastic, integrated, terminal. Conidia holoblastic, produced asynchronously and sympodially on short minute denticles at the conidiophore tips and at the tips of its branches. Conidia 14-18 x 6-8 um obovoid to ellipsoid, with one median septum and rounded at both ends. Trapping with adhesive net-works in which the loops have openings of 30-35 um. Chlamydospores absent.

HABITAT AND DISTRIBUTION IN Manitoba: pH range 5.5-7. Isolated from a few samples collected in summer and fall at different sites in Manitoba: in Sandilands Provincial Forest from rotten Jack Pine wood (once); at Bird Lake from moss cushion (once) and in Winnipeg from Bur Oak bark (Quercus macrocarpa Michx.) (once); and in Marquette from cow manure (once).

ISOLATES 39, 43, 84, 78.

DISCUSSION: This variety was only recovered from slightly acidic substrates and all isolates conformed to Drechsler's (1937a) description of

Arthrobotrys cladodes Drechs. var. macroides Drechs., Mycologia 36: 138. 1944. Plate I, Figs. g and h.

Colonies attaining a diameter of 50 mm in seven days on CMA; creamy to pale pink, mealy in texture. Vegetative mycelium hyaline septate; hyphae 2.0-3.5 mm wide, forming mycelial rings and fasciculate aerial strands from which numerous conidiophores arise. Conidiophores macronematous; branched once or twice; 180-300 um long and 5-7 um wide at the base; bearing a large number of conidia at their irregularly swollen tips. Conidiogenous cells polyblastic, integrated terminal. Conidia elongate, obovoidal to elongate ellipsoidal divided by one septum in two almost equal cells, measuring 20-28 x 8-9.6 um. Trapping nematodes with adhesive net-works and loops having an aperture of 24-35 um. Chlamydospores small, smooth, barrel-shaped in long chains.

DISTRIBUTION AND HABITAT in Manitoba: pH range 5.5-7.5. Isolated from samples collected in spring, summer and fall. Present in the Sandilands Provincial forest where isolated from humus under larch, Larix laricina (Duroi) K. Koch. (once); near the outskirts of Winnipeg, where it was isolated from rotting wood of a deciduous tree (twice); and in Winnipeg parks, it was isolated from soil (clay) (twice), and from bark of an American Elm (once).

ISOLATES 24, 47, 53, 54, 74, 94.

DISCUSSION: This variety was only recovered from moderately acidic to slightly basic substrates having a relatively narrow pH range and all the six isolates conformed to Drechsler's (1944a) description of A.

cladodes var. macroides with little variation therefrom. This variety was recognized by Drechsler as being distinct from the variety cladodes because of the more elongate shape of its pedicellate conidia and the fact it produced chlamydospores. Van Oorschot (1985) described the conidiophores of A. cladodes var. macroides as non proliferating. In subculturing islolates of the present study, a certain degree of proliferation was observed, this variation did not appear to have taxonomic significance in separating the isolates from A. cladodes var. cladodes, but it did cause confusion in separating them from A. superba that has been reported to have chlamydospores. Soprunov (1958) isolated this species in Turkmenistan and Jarowaja (1970) in Poland.

Arthrobotrys conoides Drechs., Mycologia 29: 473. 1937. Plate II, Figs. b, c.

Colonies in pure cultures attaining a diameter of 38 mm in seven days on CMA at 25 C; creamy to yellowish with a velvety texture. Vegetative mycelium hyaline septate; hyphae 3-4 um wide, forming numerous mycelial rings from which conidiophores arose. Conidiophores macronematous, nodal, indeterminate, generally unbranched, but in two isolates the conidiophores showed a bifurcation. Conidiophores 400-700 um long and 4-5 um wide at the base. Conidiogenous cells polyblastic, integrated and terminal. The holoblastic conidia were produced asynchronously in several whorls at regular intervals on the conidiophores. Conidia obconical; 18-36 x 8-16 um; constricted at the septum; distal cell larger and longer than the proximal cell. Trapping nematodes with adhesive net-works; the openings of the loops measured 25-35 um. Chlamydospores smooth, yellow, spherical 16-20 um in diameter or ellipsoidal 20-40 x 16-18 um.

DISTRIBUTION AND HABITAT in Manitoba: pH range 6.5-8. Isolated from samples collected in summer and fall. Present within and in the outskirts of Winnipeg, where it was isolated from soil (clay) under deciduous forest (once) and under American Elm in a city park (once), and from soil (clay), grass cover along creek bank (once); present at Delta marsh in organic muck, common reed (Phragmites australis (Cav.) Trin. ex Steud) cover (twice); and at Falcon lake in mosses and leaves under mixed forest (once).

ISOLATES 3a, 3b, 16, 57, 70, 78.

DISCUSSION: This fungus appeared to be restricted to neutral to slightly basic substrates having a relatively narrow pH range. The six isolates were in agreement with Drechsler's (1937a) description of the species. This species is similar to A. oligospora in the manner in which its conidia are distributed along the conidiophores, but it is easily separated from A. oligospora by the elongate conidia. Van Oorschot (1985) mentioned that the type strain in the CBS collection, today produces longer conidiophores and mostly larger conidia than in the original description of Drechsler. Only the conidia of two isolates of the present study were slightly larger than those described by Drechsler (19-42 x 8-15) otherwise they were around his average size (121 x 30). The presence of A. conoides has been recorded in Canada (Barron 1977b) and was the most commonly recorded species in Australia (McCulloch 1977).

Arthrobotrys dactyloides Drechs., Mycologia 29: 486. 1937. Plate III, Figs. g-i; Plate IV, Fig. a

Colonies slow growing, attaining a diameter of 8 mm in seven days at 25 C on CMA; white, velvety in texture. Vegetative mycelium hyaline; septate; hyphae 2.4-3.5 um wide. Conidiophores macronematous; indeterminate; denticulate; 200-250 um long and 4.5 um wide at the base, arising from prostrate hyphal element. Conidiogenous cells polyblastic, integrated and terminal. Conidia holoblastic; elongate-ellipsoidal and slightly curved 1-septate; 36-44 x 4-10 um; produced on large denticles in a asynchronous fashion, in a somewhat sympodial fashion. Microconidia present in old culture. Trapping nematodes by means of constricting rings having an opening of 13.8- 14.2 um.

DISTRIBUTION AND HABITAT in Manitoba: pH range 6-7. Isolated in Winnipeg in spring from soil (3 times) in the same city park, but in different niches: soil from a flower bed, soil close to an old stump and soil under Bur Oak.

ISOLATES 18, 31, 32.

DISCUSSION: This fungus was recovered from slightly acidic to neutral substrate. The conidium measurements obtained from these isolates suggest the spores were slightly shorter, but less variable in length, than those observed by Drechsler (1937a) (32-48 x 7-9.5 um.), otherwise the Manitoba isolates closely agreed. This species has been previously recorded in Ontario (Barron 1977b), Quebec (Estey and Olthof 1965), and Nova Scotia (Alger 1980).

Arthrobotrys musiformis Drechs., Mycologia 29: 481. 1937. Plate II, Figs. g-j; Plate III, Figs. a, b.

≡ Candelabrella musiformis (Drech.) Rifai and R. C. Cooke, Trans. Brit. mycol. Soc. 49: 163. 1966.

Colonies attaining a diameter of 46 mm in seven days on CMA at 25 C; creamy-pink, mealy in texture. Mycelium hyaline; septate; aerial and prostrate; hyphae 2-2.5 um wide; producing a profusion of conidiophores having a candelabra-like branching system; each conidiophore branch 8-9 um long and producing a single, terminal, holoblastic conidium. Conidiophores 200-350 um long and 6 um wide at the base; proliferating subapically to produce more conidia in loose capitate heads at higher levels on the conidiophores. Conidiogenous cells polyblastic, integrated, terminal. Conidia holoblastic; elongate; ellipsoid; occasionally curved; 23-37 x 7-10 um; 1-septate; distal cell comprising two-thirds of the total length of the spore. Trapping nematodes by adhesive branches, that are quite often curved, more rarely in the typical loop shape. Few chlamydospores typical of the genus where observed.

DISTRIBUTION AND HABITAT in Manitoba: pH range 6.5-7. Isolated from samples collected in spring in a Winnipeg city park from soil (clay), under Basswood (Tilia americana L.) (once), Manitoba Maple (Acer negundo L.) (once) and from Bur Oak bark (once).

ISOLATES 34, 35, 36.

DISCUSSION: This fungus was recorded from essentially neutral substrata, and all three isolates obtained produced the typical branching system described by Drechsler (1937a) for A. musiformis. The size of the conidia did not reach the top of the range he recorded (22-44 x 7.5-12.7 um), but they were close to his average size (33.9 x 10.4). The observation that conidia often started infection by simply germinating and invading slow or lethargic nematodes, could indicate that conidia produce a nematode-attracting and nematicidal substance. These would attract and immobilize nematodes in the vicinity of the conidia, thus making it possible for the germ tubes of germinating conidia to contact and invade the nematodes. The presence of nematode attractant has been suggested to occur in an extract of A. musiformis (Monson and Ranieri 1972); nematode-attractants and nematicides were obtained from the mycelia of other predaceous Hyphomycetes which had developed in the presence of nematodes (Balan et al. 1974). A. musiformis has been previously recorded in Ontario (Barron 1977b; Nova Scotia (Alger 1980) and Quebec (Estey and Olthof 1965).

Arthrobotrys oligospora Fres., Beitr. zur. mykol. t. III f. 1 (in Sacc. IV, p. 18, 1886). Plate II, Figs. d-f.

Colonies attaining a diameter of 58 mm in seven days at 25 C on CMA; white to yellowish; mealy in texture. Mycelium hyaline; septate; prostrate and aerial; hyphae 3-4 um wide; forming mycelial rings from which conidiophores arose in large numbers. Conidiophores macronematous; indeterminate; nodal; 200-700 um long; 6-7 um wide at the base; bearing several whorls of conidia spaced at regular intervals along their length. Conidiogenous cells polyblastic, integrated and terminal. Conidia holoblastic; produced asynchronously; broad obovate; 17-24 (33) x 10- 12 (14) um; unequally two celled, the distal cell being the largest. Trapping nematodes by adhesive net-works with loops of internal aperture 35-40 um. Chlamydospores smooth; spherical; 16-20 um in diameter; ellipsoidal up to 54 x 20 um were observed in large numbers in old cultures.

DISTRIBUTION AND HABITAT in Manitoba: pH range 6-8. Isolated from samples collected in spring summer and fall. Present in Winnipeg in farm soil (clay) cover grass (once), in cow manure (once); in city park in rotten wood from a tree stump (once), American Elm bark (once), soil (clay) under American Elm, Cottonwood and Bur Oak (4 times); in Marquette in chicken manure (once); in Sandilands Provincial forest in rotting wood, Trembling Aspen (Populus tremuloides Michx.) (once) and in cow manure (once).

ISOLATES 4, 14, 25, 29, 32, 54, 57, 60, 62, 92, 100.

DISCUSSION: The species was only obtained from substrates having a relatively narrow pH range centered at neutrality. All the isolates obtained during this study conformed to Drechsler's (1937a) description of the species. The manner in which conidia were produced along the conidiophores, and their shape and size of conidia left no doubt as to the identity of these isolates. One vigorous isolate produced abundant net-works in pure culture.

A. oligospora has been listed in all recorded surveys of nematophagous fungi, and often, during such surveys it is the most frequently isolated species (Estey and Olthof 1965; Jarowaja 1970; Fowler 1970; Alger 1980). Fowler (1970) found A. oligospora to be the predominant species in samples with high organic content and pH nearly neutral and this correlates with the findings of the present study.

Arthrobotrys superba Cda., Pracht-Fl. 1839. Plate I, Figs. i and j; Plate II, Fig. a.

Colonies attaining a diameter of 46 mm in seven days on CMA at 25; white to pink, mealy in texture. Mycelium hyaline; septate; aerial and prostrate; hyphae 2-3 um wide. Coniodiophores macronematous; indeterminate; denticulate; 160-200 um long having inflated tips often proliferating repeatedly up to reach 600 um in length. Conidiogenous cells polyblastic, integrated and terminal. Conidia; holoblastic; produced asynchronously; narrow 1-to rarely 2-septate; with parallel sides and measuring 17-24-28 x 6-10-11 um. They were produced on short small denticles and in several whorls along the conidiophores. In one isolate, several swollen conidiogenous heads coalesced and bore a large number of conidia. Trapping by adhesive net-works with loop apertures 18-35 um. Chains of barrell-shaped chlamydospores 7 - 14 um long in old cultures.

DISTRIBUTION AND HABITAT in Manitoba: pH range 6-7. Isolated from samples collected in the fall. Recorded at Birds Hill Park, where isolated from peat of white spruce bog, (Picea glauca (Moench) Voss (once), at Cranberry Portage from peat of black spruce bog in the boreal forest (once), at Falcon Lake from peat of black spruce bog (once); at Morris, isolated from a twig of a fruit tree found on the ground on a farm (once) and in Sandilands Provincial Forest from moose droppings (once).

ISOLATES 10, 66, 119, 83, 121.

DISCUSSION: This species appeared to be restricted to slightly acidic substrates within the neutrality. The isolates were placed in the species

A. superba because the conidia were larger than those reported for cladodes var. cladodes and cladodes var. macroides (Drechsler 1937a, 1944a) and the conidiophores proliferated repeatedly. Conidium size in this species appears to vary, especially in lenght from one isolate to the other. In the present study, conidia of one isolate were 20-28 x 8-11 while the conidia of the other four isolates were shorter. Drechsler (1937b) reported for his isolate conidia 12-23 (28) x 6.5-9.5 (10) and no chlamydospores. Taxonomic studies on the genus Arthrobotrys (Haard 1968; Van Oorshot 1985) reported respectively for this species conidia 13.5-26.5 x 5.6-11.2 um. and (10.5)-13-22-(25) x 5-8-(11). The latter study reported the presence of chlamydospore. This fungus has been recorded in Ontario (Barron 1977b) and Nova Scotia (Alger 1980).

Arthrobotrys taxonomic species #1. Plate III, Figs. c-f.

Colonies attaining a diameter 40 mm on CMA at 25 C in seven days; creamy to pink in colour, mealy in texture. Mycelium hyaline; septate 2.5 mm wide; aerial and prostrate; producing large numbers of conidiophores macronematous; indeterminate; denticulate; 250 mm long and 5 um wide at the base; proliferating subapically to produce loose heads of conidia. Conidiogenous cells polyblastic, integrated, and terminal. Conidia holoblastic; produced asynchronously and sympodially upon denticles; they were obovoidal; constricted at the septum; 22-35 x 12-15 um; 1-septate produced on denticles. On occasion a denticle reached 8 um in length. Sporulation was very abundant. Trapping nematodes by adhesive branches, but very often infection initiated from conidia located in proximity of nematodes. In very old cultures, formation of simple net-works was observed.

DISTRIBUTION AND HABITAT in Manitoba: ph 7. This species was isolated in the fall at Delta Marsh from an organic sample under common reed.

ISOLATE 115.

DISCUSSION: The predation mechanism of this organism was similar to one of our isolates of A. musiformis, but the lack of a definite candelabrum branching system and the shape of the spores did not allow the placement of this organism in this species. An isolate from France (Virat 1977) of A. javanica Rifai and R. C. Cooke appeared to share certain features with our isolate, such as shape and size of conidia, and their

arrangement in loose heads on a more or less geniculate conidiophore. Unfortunately, we were unable to examine the type strain and thus draw a conclusion.

Dactylaria brochopaga Drechs., Mycologia 29: 517. 1937. Plate IV, Figs. b-d.

Colonies in pure cultures attaining a diameter of 10 mm in seven days on CMA at 25 C, white, velvety in texture, dense. Mycelium hyaline; septate; prostrate; producing a large number of conidiophores; macronematous; indeterminate; denticulate; 150-250 um long; 5-6 um wide at the base producing several conidia in one or two loose heads. Conidiogenous cells polyblastic, integrated, and terminal. Conidia holoblastic; produced asynchronously and sympodially on short stout denticles; curved and elongate-ellipsoidal; 28-44 x 5-9 um; 2-4 septate, but commonly 3-septate. Trapping nematodes with constricting rings with openings of 10-11 um.

DISTRIBUTION AND HABITAT in Manitoba: pH range 5.5-7. This fungus was isolated from samples collected in spring, summer and fall. It was recorded in Winnipeg along a river bank from soil (clay), grass cover (once) ; in city parks, from soil (clay), close to an Manitoba Elm tree (once) and close to a Manitoba Maple (once); on the outskirts of Winnipeg in a wooded area, isolated from Manitoba Elm bark (once), from bark of an Eastern Cottonwood tree (once); in Riding Mountain Park from mosses (once); and in Sandilands Provincial forest from rotten wood (once).

ISOLATES 12, 29, 35, 33, 76, 78, 113, 126.

DISCUSSION: Isolation of this fungus was confined to substrates having a relatively narrow pH range (5.5- 7) from moderately acid to neutral and their morphological features were in close agreement with

Drechsler's (1937a) description of the species. This species has been recorded in Quebec (Estey and Olthof 1965), in Ontario (Barron 1977b), in Nova Scotia (Alger 1980) and by other researchers in many parts of the world.

Dactylaria sclerohypha Drechs., Mycologia 42: 57. 1950. Plate IV, Figs. e-h.

Colonies attaining a diameter of 18 mm in seven days on CMA at 25 C; white; medium dense; velvety in texture. Mycelium hyaline; septate; hyphae 1.5-3 um wide ; producing slender conidiophores; macronematous; indeterminate; 200-350 um long and 5-7 um wide which generally bear one or two loose heads of conidia. Conidiogenous cells polyblastic, integrated, and terminal. Conidia holoblastic and produced singly and asynchronously on branch-like denticles and individually near the apex or below; spindle shaped with a truncate base; measured 30-50 x 6-10 um; 3-to 5 but chiefly 4-septate. Adhesive knobs almost spherical; 5-7 x 6-7.3 um; developing on short stalks 4- 8 um long and 2 um wide. Chains of chlamydospores were produced in old culture along the hyphae and inside the consumed nematodes.

DISTRIBUTION AND HABITAT in Manitoba: pH range 5.5-7. This fungus was isolated from three samples collected in the fall. It was recorded in Flin Flon, from soil collected in the Wildlife Park (once); in Winnipeg from American Elm bark collected in a city park (once) and at Morris from cow manure (once).

ISOLATES 38, 63, 72.

DISCUSSION: These isolates conformed rather closely to Drechsler's (1950a) description of the species. They were restricted to substrates having a relatively narrow pH range (5.5 - 7) from moderately acid to neutral.

Dactylella lobata Dudd., Trans. Brit. mycol. Soc. 34: 489. 1951.

Plate V, Figs. a-c.

Colonies attaining a diameter of 15 mm in seven days on CMA at 25 C; white, velvety in texture; dense. Mycelium hyaline; septate; hyphae 2-4 um wide producing many conidiophores; macronematous;determinate; 150 um long and 7 um wide at the base which tape to 4 um at the tip; each bears a single holoblastic conidium. Occasionally short lateral subapical branches were produced, which formed a single terminal conidium. Conidiogenous cells, monoblastic integrated, terminal. Conidia fusiform; 1-6 septate; 25-40 x 6-8 um. Trapping nematodes with lobes, 10 x 8 um, covered with a yellow sticky material and which appeared to proliferate to form chains of lobes.

DISTRIBUTION AND HABITAT in Manitoba: pH 7. Isolated from bark collected in the fall in a mixed forest at Riding Mountain National Park (once).

ISOLATE 130.

DISCUSSION: Conidia of this isolate were smaller than those observed by Duddington (1951c) in pure culture (32-54 x 8-10) or with nematodes (32-54 x 8-12 um), otherwise the organism was in close agreement with his description of the species. Sporulation was very abundant in pure culture. This organism has been placed in the genus Dactylella instead of the genus Monacrosporium because of the division of the conidium in almost equal cells. The shape of its trapping mechanism is unusual and also the adhesive material that covers it, has a typical yellow coloration. D. lobata was recorded in Ireland (Gray and Duff 1982) from a sample of deciduous leaf litter.

Duddingtonia flagrans (Dudd.) R. C. Cooke, Trans. Br. mycol. Soc. 53 (2): 316. 1969. Pl at e V, Figs. d-g.

≡ Trichothecium flagrans Dudd., Trans. Br. mycol. Soc. 32: 284. 1949.

Colonies attaining a diameter of 65 mm in seven days on CMA; white to pale pink. Mycelium hyaline septate, producing thick fasciculate mycelial strands from which conidiophores arose in larger number. Conidiophores macronematous, simple, indeterminate, initally bearing a single conidium, then one conidium was produced at the side of the first and more conidia were produced below. Conidiophores proliferated to a certain distance and produced another loose head of conidia in the same manner as before. Conidiogenous cells polyblastic, integrated and terminal. Conidia holoblastic; ovoid to cylindrical; quite varied in shape; with truncate base; 28-54 x 7-15 um.; generally one septate, rarely 2-septate. Certain cylindrical conidia appeared to separate at the septum. Sporulation abundant and even in young cultures very many exospores; warty; intercalary and apical ; spherical up to 30 in diameter; and ellipsoidal up to 60 x 30 um. Trapping by adhesive net-works.

ISOLATE 78.

DISTRIBUTION AND HABITAT in Manitoba: pH 6.5. Isolated from rotting elm wood collected in the fall in an old deciduous forest at the outskirts of Winnipeg (once).

DISCUSSION: This isolate was a vigorous organism that sporulated profusely and produced traps in pure cultures. Cooke (1969a) and Virat (1977) recorded respectively the isolation of a T. flagrans whose conidia

(25-50 x 10-15; 42-60 x 12- 18) exceeded the average measurements reported by Duddington (1949) (27-37 (45) x 14-16 (17.5)). Another similar organism, isolate 17, was recovered from the same habitat and same area during the present study. This isolate sporulated in scattered fashion. Conidiophores 200 um long and conidia 21-28 x 6.5-14 um; less variable in shape. No researcher has yet recorded isolates of Duddingtonia flagrans with such small conidia. All the other morphological characteristics of isolate 17 and 78 were identical including conidiogenesis and the large production of warty exospores. When the two isolates grew together on the same plate, they kept their individual characteristics. Perhaps, isolate 17 represents a distinct strain which we are unable to verify at this point.

Geniculifera effusa (Jarowaja) van Oorschot, Stud. in Mycology 26: 96. 1985. Plate VI, Figs. e-i; Plate VII, Figs. a and b.

≡ Dactylaria effusa Jarowaja, Bull. Acad. Pol. Sci., Cl. 5. Ser. Sci. biol. 16: 773. 1968.

= Arthrobotrys constringens Dowsett, J.A., J. Reid and R.S. Kalkat, Mycologia 76: 559. 1984

Colonies in pure cultures attaining a diameter of 15 um in seven days on CMA at 25 C; white; velvety in texture. Mycelium hyaline septate producing constricting rings in pure culture and a large number of conidiophores macronematous; 200-300 um long; 5 um wide at the base and; tapering to 3 um at the tip. The conidiophores had rounded tips and produced initially only a single conidium. Conidiogenous cell integrate, terminal. Conidia; holobastic; ovoid; 24-34 x 15-24 um, several aseptate or with 1-3 septa. In aging colonies, the conidiophores proliferated to one side of the first conidium to produce at a certain distance a second conidium and even a third or more by repeating the process. The conidiophores became geniculate. Conidia germinated to produce secondary smaller conidia. Constricting rings had openings around 10.5 um.

DISTRIBUTION AND HABITAT in Manitoba: pH range 6.5-7. Inhabitant of wet areas around lake Manitoba. Isolated from samples collected in the fall, from organic muck from Delta Marsh (once) and from a sand and gravel soil sample collected on the Twin Lakes Beach (once).

ISOLATES 103, 115.

DISCUSSION: The present Manitoba isolates were initially thought to be of the species Dactylella doedycoides Drechs. as the apex of the conidiophore was rounded, and only a single conidium that corresponded in its shape, size and septation to Drechsler's (1940b) description was found when young cultures were examined. In older cultures, however, proliferating conidiophores were found. The proliferation of the conidiophores with the production of further conidia did not allow the placement of the organism in the genus Monacrosporium. In spite of the proliferating conidiophores (Plate VI, Fig, f), all other morphological characters resembled those of D. doedycoides and the two species could therefore be considered related. Only two organisms with similar production of conidia have been isolated previously (Jarowaja 1968 and Dowsett et al. 1984a). The authentic material of G. effusa is not available, but the illustrations and descriptions of the species indicate a close similarity with the present isolates and the previous one (Dowsett et al. 1984a) from Manitoba.

Geniculifera taxonomic species # 1. Plate VI, Figs. b-d.

Colonies attaining a diameter of 36 mm in seven days on CMA at 25 C; mycelium white, velvety in texture. Mycelium hyaline; septate; hyphae 3-4 um wide; producing conidiophores macronematous; indeterminate; denticulate; becoming geniculate due to the repeated subapical proliferation up to 400 um in length and 6 um wide at the base. Conidiogenous cells polyblastic, integrate and terminal. Conidia holoblastic; obovoid; 21-28 x 10-14 um; 1-septate, with the septum produced in the third portion of the conidium. Septal constriction lacking. Conidia seceeded living cylindrical truncate denticles on the conidiophores. This voracious trapper caught nematodes by adhesive net-works with loop openings of 30-35 um.; traps present in pure culture. Few smooth spherical chlamydospores 14- 18 um in diameter were present in old cultures.

DISTRIBUTION AND HABITAT: pH 7. Isolated from old cow manure (once) collected in the fall at Morris and from bark from balsam fir (Abies balsamica (L.) Mill.) (once) collected in the fall at Riding Mountain National Forest.

ISOLATES 72, 126.

DISCUSSION: These isolates were very similar to Geniculifera cystosporia (Dudd) Rifai, but their conidia were smaller (21-28 x 10-14 um) than the measurements reported by Duddington in the presence of nematodes (1951d) 25-35 x 18-24 um or in pure culture on CMA 24-30 x 16-23 um. The shape of the conidia, the large cylindrical denticles on

which conidia were produced and the repeated subapical proliferations of the conidiophores were in complete agreement with his description of the species. G. cystosporia has not been reported to produce chlamydospores by Duddington (1951d) or by Rifai and R.C. Cooke (1966). The two isolates in discussion produced few chlamydospores smooth, spherical, yellow in old cultures. G. cystospora has not been recorded in surveys in Canada, but is common in England (Duddington 1951d; R.C. Cooke 1966) and Ireland (Gray 1984). The conidia of the present isolates are also similar to the conidia of G. perpasta R.C. Cooke, a species described to trap by adhesive hyphae or branches (Rifai and R.C. Cooke 1966). While the production of chlamydospores is possible in any Hyphomycetes (Gray 1987), the smaller size of the conidia, especially in width, raises the question if the present isolate is a distinct strain from Geniculifara cystosporia.

Monacrosporium cionopagum (Drechs.) Subram., J. Indian bot. Soc. 42: 293. (1963) 1964. Plate VII, Figs. c-h..

≡ Dactylella cionopaga Drechs., Mycologia 42: 22. 1950.

Colonies attaining a diameter of 14 mm in a week on CMA at 25 C, whitish; velvety in texture; dense. Mycelium hyaline septate; hyphae 2-4 um wide, giving rise here and there to adhesive branches in pure culture and to many conidiophores macronematous; determinate; 200-300 um long; 5-7 um wide at the base; tapering to 4 um at the tip and bearing a single holoblastic conidium. Conidiogenous cells monoblastic, integrate and terminal. Spindle shaped conidia; holoblastic; quite variable in form and septation; 2-6 septate; 44-54 x 10-18 um. The adhesive branches varied in length from 1-5 cells or even more, and occasionally formed loops.

DISTRIBUTION AND HABITAT in Manitoba: pH range 5.5-7. Isolated from samples collected in spring and fall: from soil, scotch pine cover, collected at Birds Lake Park (once), from soil, mixed forest cover, collected near English Lake (once).

DISCUSSION: These isolates are in agreement with Drechsler's (1950a) description of the species. Dactylella cionopaga has been recorded in several surveys of nematophagous fungi carried out in different part of the world: England (Duddington 1951b), Ireland (Gray and Duff 1982),and New Zealand (Fowler 1970) .

Monacrosporium coelobrochum (Drechs.) Subram., J. Indian bot. Soc. 42: 293. (1963) 1964. Plate VIII, Figs. a-e.

≡ Dactylella coelobrocha Drechs., Mycologia 39: 5. 1947.

Colonies attaining a diameter of 15 mm in seven days on CMA at 25 C; withish; dense; velvety in texture. Mycelium hyaline septate; hyphae 2 um wide; producing numerous conidiophores; macronematous; determinate; 240-250 um long; 6 um wide at the base; and tapering to 4 um at the tip; bearing a single large broad fusiform conidium holoblastic; 37-60 x 14-23 um, 3-5 septate. Conidiogenous cell monoblastic, integrate and terminal. Trapping nematodes with constricting rings with an opening of 10 um. Few constricting rings were produced in pure culture.

DISTRIBUTION AND HABITAT in Manitoba: pH 6. Isolated from peat collected in the fall in a black spruce bog at Birds Hill Park.(once).

ISOLATE 8.

DISCUSSION: The above described fungus conformed to Drechsler's (1947) description of the species.

Monacrosporium drechsleri (Tarjan) Cooke and Dickinson, Trans. Brit. mycol. Soc. 48: 623. 1965. Plate VIII, Figs. f-h; Plate IX, Figs. a and b.

≡ Dactylella Drechsleri Tarjan, Mycopath. Mycol. App. 14: 143. 1961.

Colonies attaining a diameter of 12 mm in seven days on CMA at 25; white; dense; velvety in texture. Mycelium hyaline; septate; hyphae; 1.6-2 um wide; producing conidiophores macronematous; determinate; 130 um long; 6 um wide at the base; tapering to 4 um at the tip; bearing a single; holoblastic; fusiform conidium 30-44 x 10-14 um, average 32 x 11 um and 3-4 septate, quite commomly 3-septate. Occasionally a second conidium was produced from a branch below the conidiophore tip. Conidiogenous cells monoblastic, integrated, and terminal. Adhesive knobs were produced in pure culture and more abundantly in the presence of nematodes; almost spherical; 10 x 8-9 um; on stalks 6-8 um long and 3 um wide.

DISTRIBUTION AND HABITAT in Manitoba: pH range 5.5-6.5. Inhabitant of forested areas, isolated in summer and fall from rotting wood popular (once), elm (once) and from mosses (twice).

ISOLATES 29, 30, 76, 78.

DISCUSSION: These isolates were similar in shape to Dactylella ellipsospora Drechs., but the range in size of their conidia was much smaller than reported by Drechsler (1937b) 24-65 x 7.5-19. Conidia were more commonly 3-septate rather than the 4-septate; germinated into adhesive knobs and furthermore the knob stalks did not vary very much in length. Instead, they conformed very closely to Tarjan's (1961) description

of Dactylella Drechsleri. Tarjan (1961) observed the best growth of this organism between pH 5 to pH 6 which is very close to the relatively narrow pH range of the substrates in which it was found.

Monacrosporium gephyropagum (Drechs.) Subram., J. Indian bot. Soc. 42: 293. (1963) 1964. Plate X, Figs. a-d..

=Dactylella gephyropaga Drechs., Mycologia 29: 508. 1937.

Colonies attaining a diameter of 15 mm in seven days on CMA at 25 C; whitish; velvety in texture. Mycelium hyaline septate producing adhesive branches here and there and numerous mycelial fasciculate strands from which conidiophores arose in large numbers. Conidiophores macronematous; determinate; 200-400 um long; 7 um wide at the base; 2.5 um at the tip; producing a single conidium holoblastic; turbinate; 36-50 x 16-18 um; 2-4 septate. Conidiogenous cells monoblastic, integrated and terminal. The adhesive branches very abundant in the presence of nematodes; produced at regular intervals on the hyphae; and reaching a constant similar height of two cells. These branches tended to grow bridges between themselves and to form regular scalariform net-works in two dimension and of varying lengths.

DISTRIBUTION AND HABITAT in Manitoba: pH 7. Isolated in the fall at the outskirts of Winnipeg from a sample of bark of old deciduous forest (once).

ISOLATE 113.

DISCUSSION: The above isolate closely matched Drechsler's (1937a) account of this taxon, because it formed regular scalariform net-works. The conidia were generally slightly longer. This species has been isolated in Ontario (Barron 1977b), in Quebec (Estey and Olthof 1965) and in Australia (McCulloch 1977).

Monacrosporium heterosporum (Drechs.) Subram., J. Indian bot. Soc. 42: 293. (1963) 1964. Plate X, Figs. e and f; Plate XI, Figs a and b.

≡ Dactylella heterospora Drechs., Mycologia 35: 339 1943.

The conidia of this organism germinated on CMA but would stop growing after a few days even in the presence of nematodes. They germinated and grew well on MEA plus yeast or on CMA plus bacteria transferred accidentally from an original plate. Colonies in pure culture attaining a diameter of 10 mm in seven days at 25 C; white yellowish; velvety in texture; dense; producing a large number of conidiophores macronematous; determinate; up to 400 um long; 8 um wide at the base; and 2.5 um at the tip. Conidiogenous cells monoblastic, integrated and terminal. Conidia holoblastic; solitary; elongate; prolate-ellipsoid; 27-38 x 10-16 um. Small secondary conidia are often produced upon germination of the macroconidia. Trapping nematodes with constricting rings with an opening of 13-15 um. Constricting rings, numerous also in pure culture. Chlamydospores smooth, yellow, produced in long intercalary chains.

DISTRIBUTION AND HABITAT in Manitoba: pH 5.5. Isolated from mosses collected in the boreal forest at Cranberry Portage.

ISOLATE 121.

DISCUSSION: Drechsler (1943a) described this species and was able to grow it on CMA, but Duddington (1951a) could not grow his isolate in pure culture. The fact that the present isolate did not grow in pure culture, unless the medium contained yeast, points to the existence of strains unable to synthesize a vitamin or some other growth factor. The conidia of

the present isolate were not as variable in length as those of the Drechsler's isolate but in all the other morphological characteristics they were identical. Spores or chlamydospores of this isolate must have long viability because the sample, from which this species was isolated, had been collected in 1978. Monacrosporium heterosporum has been isolated in Nova Scotia (Alger 1980).

Harposporium anguillulae Lohde, Tagebl. Versamml. dtsch. Naturf. Aerzte Breslau 47: 206. 1874. Plate XI, Figs. c and d.

Conidiophores semi-macronematous; short unbranched; broke out of the nematode integument and produced spherical phialides; 3-4 x 4-5 um with a tubular apex. Conidia enteroblastic; elongate; 10-18 um x 1-2 um; pointed at both end;s held in clusters. Chlamydospores, 5-10 x 5-6 um, yellowish, formed from old hyphal cells in chains inside the consumed nematode body.

DISTRIBUTION AND HABITAT in Manitoba: pH range 5.5-6.5. Isolated in Winnipeg and its outskirts from bark of Ulmus species collected in parks (twice) and in Flin Flon from soil collectected in the Wildlife Park (once).

DISCUSSION: This species was confined to moderately or slightly acidic substrates. All isolates were in agreement with the description of the species (Karling 1938). This species was not isolated in pure culture, but was kept in active state for several months by adding a thin layer of warm water agar to plates that were drying out. Harposporium anguillulae has been often recorded in surveys of nematophagous fungi (Duddington 1951b; McCulloch 1977; Barron 1980).

Harposporium helicoides Drechs., Phytopatology 31: 794. 1941. Plate XI, Figs. e and f; Plate XII, Figs. a and b.

Conidiophores semi-macronematous; aerial; protruding out of the nematode body up to 90 um in length; bearing spherical polyphialides 4 x 4 um with 3 or 4 projecting processes. Conidia enteroblastic; helicoid; 18-22 x 1.6-1.8 um, terminating in a round, drop like base.

DISTRIBUTION AND HABITAT in Manitoba: pH 5.5. Isolated from mosses (once) with the Baermann funnel and centrifuge techniques collected in the fall at Riding Mountain National Park.

ISOLATE 126.

DISCUSSION: The organism in question conformed to Drechsler's (1941b) description. The spherical phialides with more than one projecting process separated it from H. oxycoracum Drech. This species has been reported in Ontario (Barron 1977b) and in many countries including Australia (McCulloch 1977).

Verticillium obovatum (Drechs.) Subram., Kavaka 5: 98. 1977. Plate XII, Figs. c and d.

≡ Acrostalagmus obovatus Drechs., Phytopath. 31: 784. 1941.

Conidiophores semi-macronematous erupted from the nematode integument and trailed on the substrat;, they were up to 260 um in length and bore simple flask shaped phialides or groups of 2-3 phialides; 7-12 um long; and tapering to a slender neck. Conidia enteroblastic; almost spherical; 2.5 x 3 um; produced in large clusters. Infection initiated after adhesion of one or more conidia to the nematode cuticle. Assimilative hyphae; septate; 2-3 um wide.

DISTRIBUTION AND HABITAT: PH 5.5. Isolated with the Baermann funnel technique from the soil sample collected in the Fall at the Wildlife Park in Flin Flon (once).

DISCUSSION: This organism was in close agreement with the Drechsler's (1941b) description of the species. This species was placed in the genus Verticillium as proposed by Subramanian (1977). Verticillium obovatum has been recorded in Ontario (Barron 1977b), Nova Scotia (Alger 1980) and in many other places including England (Duddington 1951b), Ireland (Gray and Duff 1982) and Australia (McCulloch 1977).

Stylopage grandis Dudd., Mycologia 47: 245. 1955. Plate XII, Figs. e-g.

Mycelium hyaline, aseptate, scarce, consisting of a main hypha and a few lateral branches produced at right angles to the main hypha. The capture of nematodes was by means of yellow adhesive material, clearly visible under the microscope. Nematodes were generally held in the mouth region and no infection bulb was produced after fungal penetration. After a short period of time devoted to predation, the fungus produced delicate erect conidiophores macronematous; indeterminate; up to 250 um in length; 4 um wide at the base; and 2 um at the tip bearing initially a single conidium; then the conidiophores proliferated at the side of the first conidium to produce a second conidium and even a third was produced in this manner. Conidiogenous cell polyblastic, integrated and terminal. Conidia aseptate; holoblastic; obovoid; 32-55 x 16-17 um.

DISTRIBUTION AND HABITAT in Manitoba: pH 6.5. Isolated from moss and rotten wood collected in an old deciduous forest in the fall in the outskirts of Winnipeg (once).

DISCUSSION: The fungus examined matched Duddington 's (1955c) description of the species. Conidia that fell on the surface or were transferred on CMA, PDA , MEA plus yeast and water agar, with or without nematodes and antibiotics, did not germinate, nor would small pieces of mycelium transferred on to these media start a new colony. Old colonies were revived with a thin film of water agar. This fungus appeared to be a poor competitor, because as soon as an other predaceous species invaded the substratum, it stopped all activity. The unsuccesful attempts to isolate this fungus in pure culture could be due to specificity of the

organism for a certain nematode species, required in abundance, to stimulate germination. Stylopage grandis was recorded from Delhi soils and observed to capture nematodes of the genera Rhabditis and Chephalobus (Sashchidananda 1967).

Nematoctonus amatus Thorn and Barron, Mycotaxon 25: 351. 1986. Plate XIII, Figs. a and b.

Colonies white; cottony; attaining a diameter of 9 mm in seven days on CMA at 25 C. Assimilative and fertile mycelium hyaline, septate with clamp connections. The assimilative hyphae 2-2.4 um wide, developed inside the nematodes infected by adhesive knobs on external hyphae or by conidia. The assimilative hyphae grew out of the nematode cuticle and became fertile producing conidia from simple tapering pegs. Conidia holoblastic, tapered at the base and generally ended in a hook. They measured 14-23 x 4-4.5 um and germinated to produce an adhesive hour-glass knob at the end of a short germ tube or directly above the hook. Adhesive knobs were also formed intercalarily on the hyphae. The hour-glass cells were 8-10 x 2-3 um covered by a ball of adhesive material 9 x 7 um.

DISTRIBUTION AND HABITAT in Manitoba: pH 7. Isolated from old cow manure (once) collected at Marquette.

ISOLATE 39

DISCUSSION: The above description matches the description of the species by Thorn and Barron (1986). This species has been reported only by Thorn and Barron in Ontario and found to have a teleomorphic state Hohenbuhelia mastrucata (Fr.: Fr.) Singer.

Nematoctonus concurrens Drechs., Mycologia 41: 382. 1949. Plate XIII, Figs. c-f; and Plate XIV, Fig. a.

Colonies white; cottony; attaining a diameter of 9 mm seven days on CMA at 25 C. Assimilative and fertile hyphae septate; 2.3-4 um wide; possessing clamp connections. The fertile hyphae produced conidia holoblastic; cylindrical; 12-20 x 5-6 um on tapering small pegs, 2-7 um long and 2 um wide, and adhesive knobs on short branches. The hour-glass cells measured 7-9 x 3.2-3.6 um and were surrounded by an adhesive mucoid droplet 10 x 9 um. On occasion, the adhesive knob proliferated to produce a second and a third knob.

DISTRIBUTION AND HABITAT in Manitoba: pH 8. Isolated from cow manure collected in Winnipeg (once).

ISOLATE 15.

DISCUSSION: This isolate conformed to Drechsler's (1949) description of the species. N. concurrens was reported by Barron (1978) in Ontario.

Nematoctonus pachysporus Drechs., J. Wash. Acad. Sc. 33: 185. 1943.
Plate XIV,

Figs. b-d.

Colonies white, cottony attaining a diameter of 12 mm in seven days on CMA. Assimilative and fertile hyphae hyaline; septate 1.5-2.5 um wide, showing clamp connections. Conidia holoblastic; elongate-ellipsoidal; measuring 13-20 x 5-6 um; produced on short pegs germinated to form a tapering germ tube ending in an hour-glass secretory cell. This cell measured 3.5-4.5 x 1.2-1.8 um and was surrounded by an adhesive droplet. The germ tube often continued to produce a second and even a third adhesive knob in a sympodial fashion. This isolate produced large aleuriospores, broadly elliptical, yellowish and warty that measured 10-30 x 5-8 um.

DISTRIBUTION and HABITAT in Manitoba: pH 7. Isolated from bark of Quercus macrocarpa in a Winnipeg city park.

ISOLATE 36.

DISCUSSION: The presence of the typical aleuriospores combined with the presence of all the other morphological characteristics of the species described by Drechsler (1943b), confirmed the identy of the above isolate. This species has been reported in Ontario (Barron 1977b) and Australia (McCulloch 1977).

Nematoctonus robustus Jones. Trans. Brit. mycol. Soc. 47: 57. 1964.

Plate XIV, Figs. e and f; Plate XV, Fig. a.

Colonies white, cottony attaining a diameter of 9 mm in seven days on CMA at 25 C. Assimilative and fertile hyphae hyaline; septate; 1.8 -2 um wide; possessing clamp connections. Fertile hyphae produced conidia; holoblastic; strongly curved or straight; 12-16 x 4 um supported on processes 2-5 um long, and adhesive intercalary and terminal hour-glass knobs. The adhesive cell measured 3 x 4.5 um and was covered by a large mucus drop 10 x 8 um; the supporting stalk was 3 x 4.5 um.

DISTRIBUTION AND HABITAT in Manitoba: pH 6.5. Isolated on the outskirts of Winnipeg from mosses and rotting wood of an old deciduous forest (once) using the Baermann funnel and the centrifuge technique.

ISOLATE 78a.

DISCUSSION: This isolate had in general a robust appearance, produced intercalary and terminally adhesive hour-glass knobs and strongly curved conidia, typical of the species as described by Jones (1964). Spores were not observed to germinate. N. robustus was recorded several times in New Zealand (Fowler 1970). Three species of Hohenbuhelia yielded anamorphs referable to N. robustus.

Nematoctonus tylosporus Drechs., Phytopath. 31: 779. 1941. Plate XV, Figs. b-d.

Colonies white, cottony attaining a diameter of 15 mm in seven days on CMA at 25 C. Assimilative and fertile hyphae hyaline; septate; 2-3 um wide with clamp connections. Fertile hyphae extending from the nematode body above the substratum, producing conidia hoblastic; fusiform; 14-22 x 2.2-4 um on processes of variable length 5-12 um long. Conidia germinating into adhesive knobs typical of the genus; 3-4 x 1 um. Chlamydospores produced among the conidia; 8-10 x 2-4 um.

DISTRIBUTION AND HABITAT in Manitoba: pH 6.5. Isolated from moss and rotten wood from an old deciduous forest (once) using the Baermann funnel and centrifuge technique.

ISOLATE 78b.

DISCUSSION: This isolate conformed closely to the Drechsler's (1941b) description of the species. This species was recorded in similar habitats in Nova Scotia (Alger 1980) and in England (Duddington 1951b).

Panus rudis Fr. Plate XV, Figs. f and g; Plate XVI, Figs. a-c.

Basidioma, hairy, tough, tan, pink pileus, 4 cm wide with a small excentric stalk (Figs. 12 and 13). Basidiospores 6 x 4 um; white in mass. Colony white cottony in pure culture originating from basidiospores. Hyphae hyaline; septate; 4 um wide; with clamp connections. No anamorph was produced during the time of the study. The basidiospores of this organism on water agar plus nematodes germinated and produced quite abundant mycelium. Nematodes appeared to weaken and finally were invaded generally at three sites by fungal hyphae that formed around the victim almost resembling a net-work. The tip of the hyphae extending toward the nematode body appeared swollen and in some way modified. The stalked secretory cells producing nematoxin described by Barron and Thorn (1987) were absent, though the nematodes appeared to become less and less active and on occasion, they were observed to be moribund but not yet invaded by the fungus.

DISTRIBUTION AND HABITAT in Manitoba: The basidioma of this fungus was collected in the fall in the Sandilands Provincial Forest from a small dead branch of a deciduous tree.

ISOLATE 125.

DISCUSSION: Barron and Thorn (1987) tested the ability of the mycelium of several lignicolous basidiomycetes to consume nematodes and found a few including another species of Panus, that would do so, but they did not describe specifically how this organism would get to the prey. This species has been tested for the first time during the present study. In the

presence of nematodes, we suspected the release of a nematoxin from the fungus, specialization of hyphal tips for penetration, and the formation of a type of net-work where the weakened nematodes would tend to remain because they were too weak to move out. These areas of more dense hyphae would allow a rapid fungal invasion in the victim.

Pleurotus elongatipes Pk. Plate XVI, Fig. d.

Basidioma having a large whitish pileus and an excentric stalk (Fig 14). Basidiospores 5-7 m round smooth; white in mass. Colonies white and cottony in pure culture originating from basidiospores. The mycelium hyaline and septate; 2-2.3 um wide; showed clamp connections and in the presence of nematodes produced secretory stalked cells for the release of nematoxin. These secretory cells were spherical and measured 2 um in diameter and the supporting stalk was 2 um long. They were at short distances one from the other and were generally more numerous in areas where nematodes had already been invaded by the fungus. Nematodes were generally invaded through body orifices. The fungus was able to live on water agar and nematodes. No anamorph state was observed during the present study.

DISTRIBUTION AND HABITAT in Manitoba: Isolated from living elm tree in the fall in a deciduous forest on the outskirts of Winnipeg.

ISOLATE 140.

DISCUSSION: This Basidiomycete was classified as P. elongatipes for the general appearance of the basidioma, because its basidiospores were in the size range of the similar species P. ulmarius (Fr.) Kumm. This fungus immobilized, killed and consumed nematodes exactly in the way described by Barron and Thorn (1987) for Pleurotus ostreatus. Fungal hyphae appeared to lack specialization for the penetration of the nematode cuticle. Thorn and Barron (1984) found a similar organism negative for predatory activity, thus this organism should be retested again to make sure these results are correct.

Pluteus aurantiorugosus (Trog.) Sacc. Plate XVII, Figs. a and b

Basidioma with orange red pileus 2.5 -5.5 cm wide and whitish stalk (Fig 13). Basidiospores were elliptical; smooth 6-7 x 4-5 um; spores in mass pink. The colony originating from basidiospores was whitish and cottony. Mycelium hyaline; septate; 1.6-2 um wide; with clamp connections and in the presence of nematodes produced secretory cells, 2 um in diameter; with supporting stalk 2 um long for the release of nematoxin; very similar in appearance and size to those produced by the genus Pleurotus. Immobilized nematodes were penetrated generally through body orifices.

DISTRIBUTION AND HABITAT in Manitoba: The basidioma was isolated from rotten dead elm wood collected in the fall in a deciduous forest on the outskirts of Winnipeg.

ISOLATE 141.

DISCUSSION: This was the first time that the mycelium of Pluteus aurantiorugosus was tested for nematophagous activity. The way of reaching the prey is exactly similar to the way observed in the genus Pleurotus (Barron and Thorn 1987). During the present study, Pluteus cervinus (Schaeff. ex Fr) Kumm. a species in the same genus was found negative for nematophagous activity. The basidiomata of both species should then be collected again and retested to verify these results.

Fig. 12. Panus rudis Fr. (basidioma).

Fig. 13. Panus rudis Fr. (basidioma).


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PENTAX
13

Fig. 14. Pleurotus elongatipes Pk. (basidioma).

Fig. 15. Pluteus aurantiorugosus (Trog.) Sacc. (basidioma).


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PLATE I

Arthrobotrys arthrobotryoides (Berl.) Lindau

Fig. a. A branched conidiophore (x 370).

Fig. b. An unbranched conidiophore (x 370).

Fig. c. Conida (x 960).

Arthrobotrys cladodes Drechs. var. cladodes

Fig. d. A conidiophore (x 370).

Fig. e. A conidiophore (x370).

Fig. f. Conidia (x 370).

Arthrobotrys cladodes Drechs. var. macroides Drechs.

Fig. g. Conidia (x370).

Fig. h. A conidium (x400).

Arthrobotrys superba Cda.

Fig. i. A conidiophore and conidia (x 370).

Fig. J. A proliferating conidiophore and conidia (x 370).

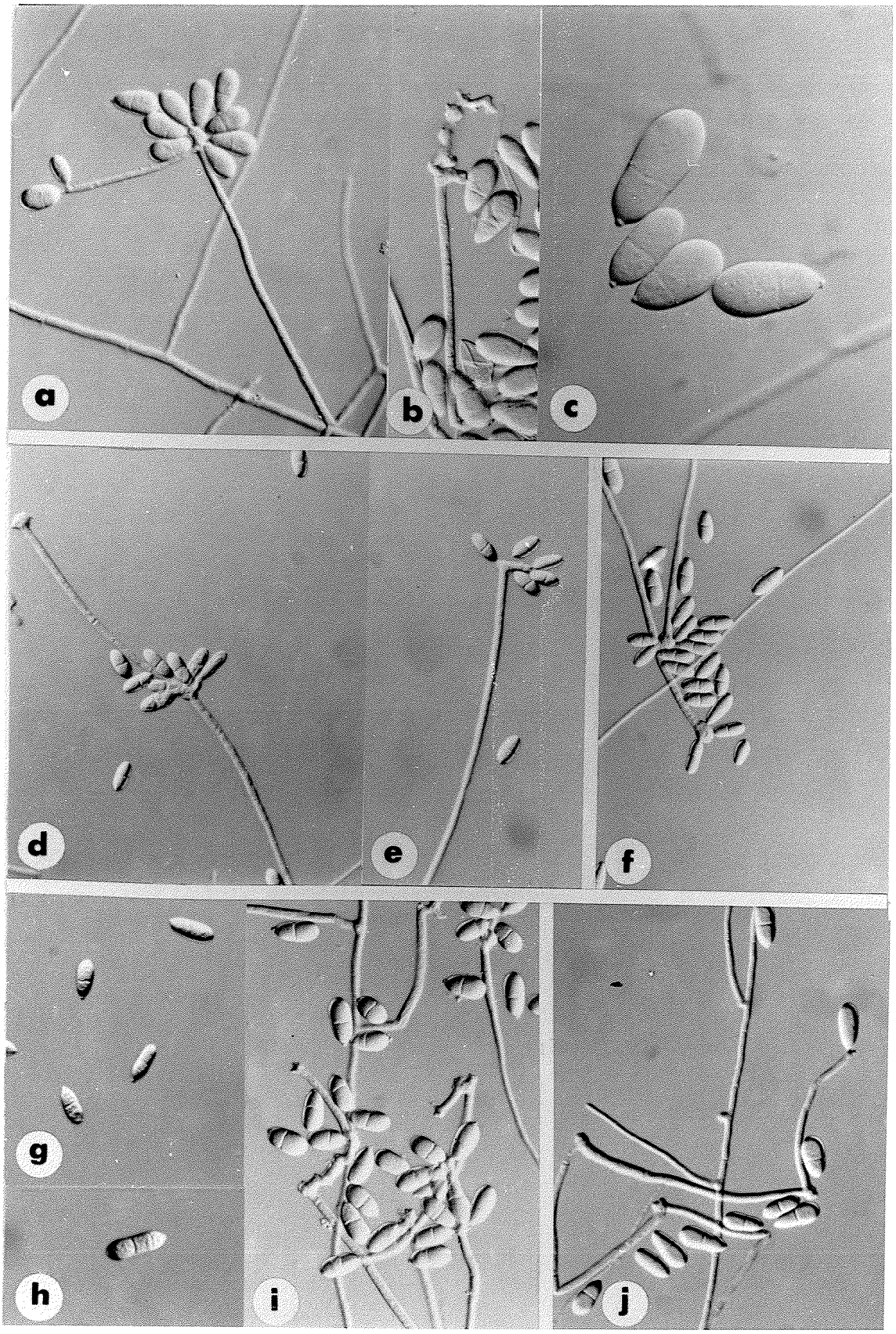
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PLATE II

Arthrobotrys superba Cda.

Fig. a. The initial stage in the development of adhesive net-works (x 370).

Arthrobotrys conoides Drechs.

Fig. b. Nodal conidiophores (x 400).

Fig. c. Conidia (x 400).

Arthrobotrys oligospora Fres.

Fig. d. A nodal conidiophore (x 400).

Fig. e. A conidiophore and conidia (x 400).

Fig. f. Conidia (x 400).

Arthrobotrys musiformis Drechs.

Fig. g. A conidiophore with conidia (x 360).

Fig. h. A conidiophore tip (candelabrum-like branching system) (x 960).

Fig. i. A conidium (x 960).

Fig. j. An infected nematode (x 960).

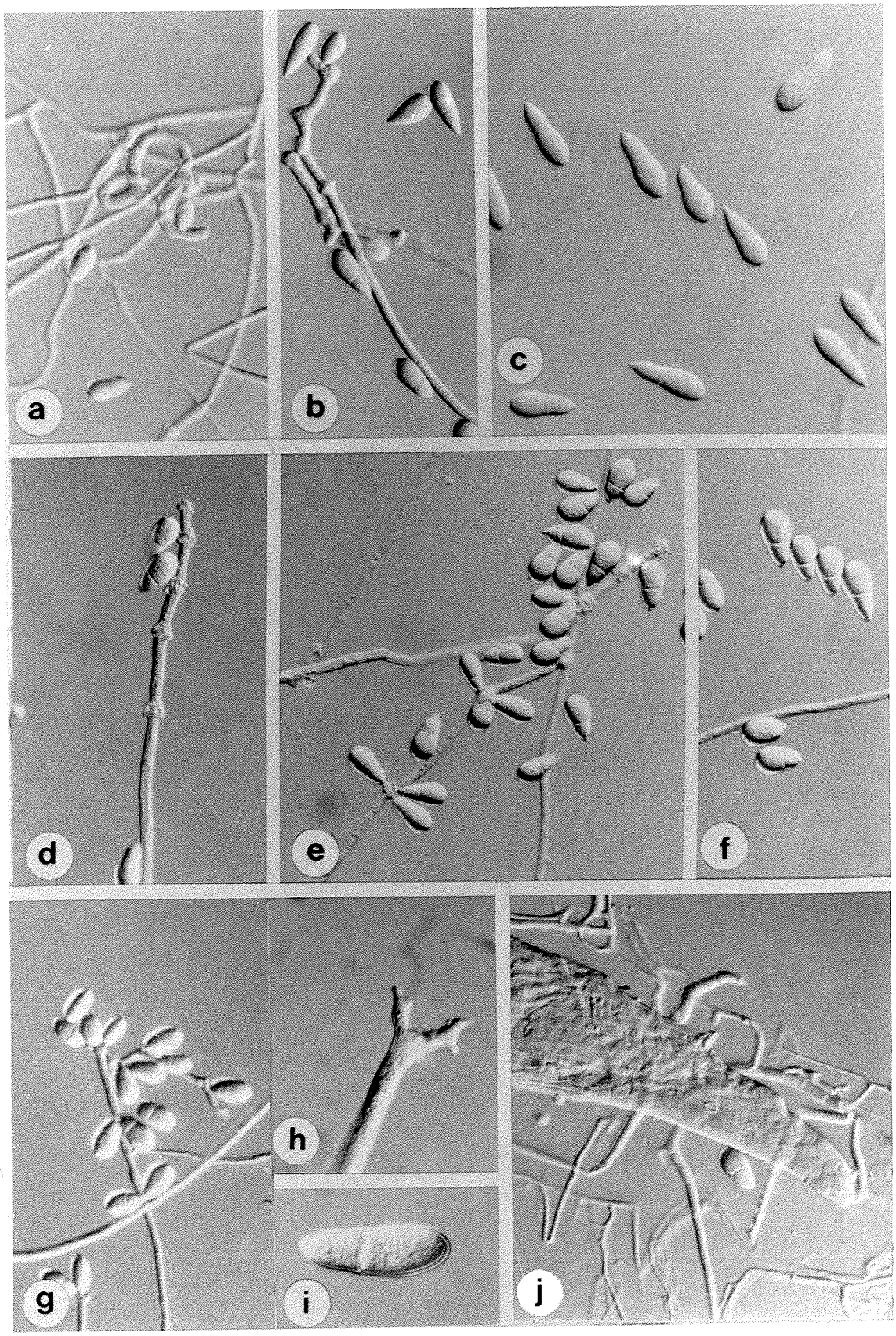
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PLATE III

Arthrobotrys musiformis Drechs.

Fig. a. An adhesive branch (x 240).

Fig. b. Chlamydospores (arrow) (x370).

Arthrobotrys taxonomic species # 1

Fig. c. A proliferating conidiophore (x 400).

Fig. d. A proliferating conidiophore (x 400).

Fig. e. An infected nematode and adhesive branch (x 370).

Fig. f. Conidia (x 370).

Arthrobotrys dactyloides Drechs.

Fig. g. Conidia (x 370).

Fig. h. A conidiophore (x 370).

Fig. i. Macro and microconidia (arrow) (x 360).

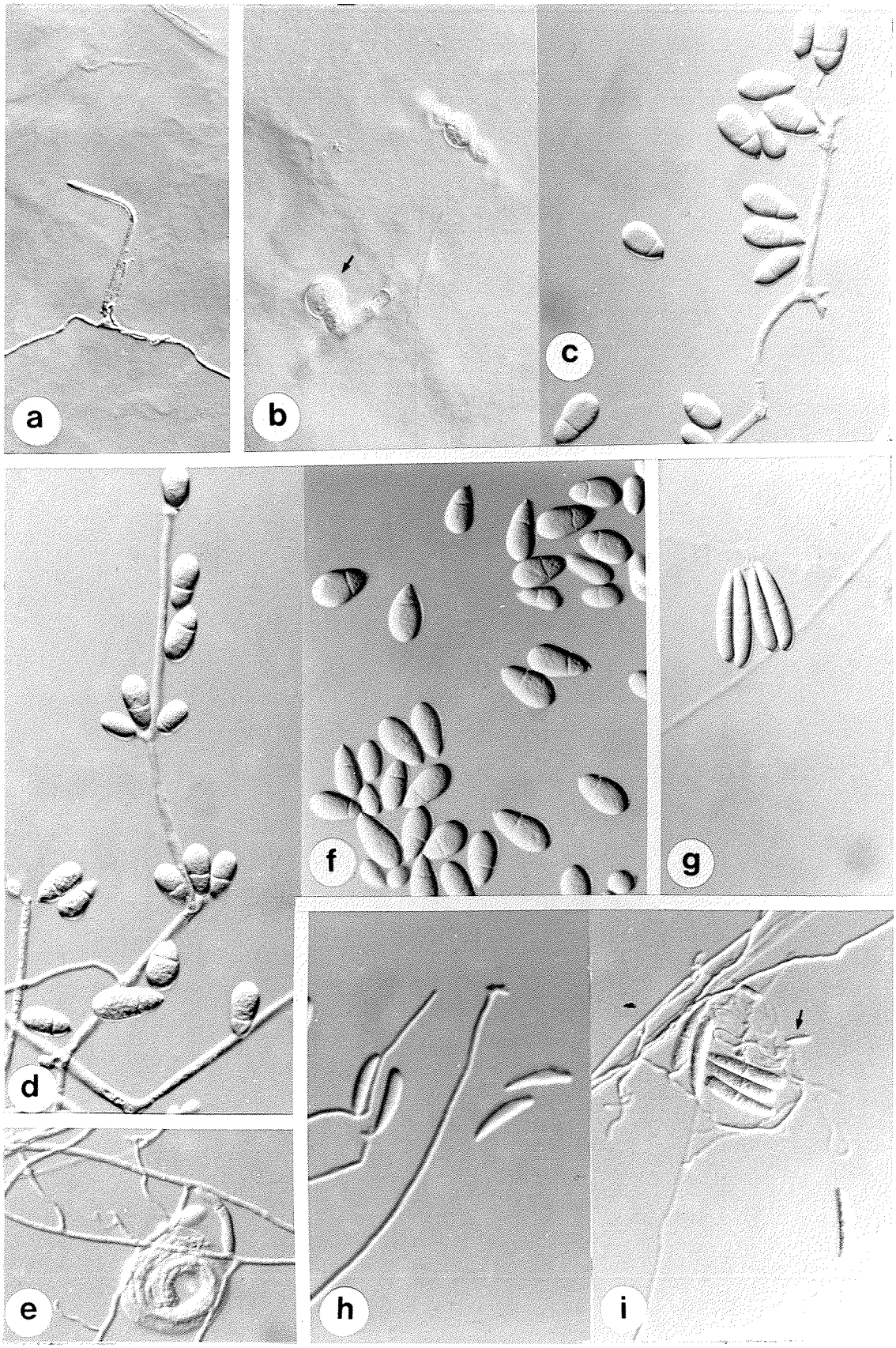
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PLATE IV

Arthrobotrys dactyloides Drechs.

Fig. a. Constricting rings (x 370).

Dactylaria brochopaga Drechs.

Fig. b. A conidiophore (x 370).

Fig. c. Conidia (x 370).

Fig. d. A constricting ring (x 370).

Dactylaria sclerohypha Drechs.

Fig. e. A conidiophore (x 370).

Fig. f. Conidia (x 370).

Fig. g. Adhesive knobs on hyphae and conidia (x 370).

Fig. h. Chlamydospores (x 370).

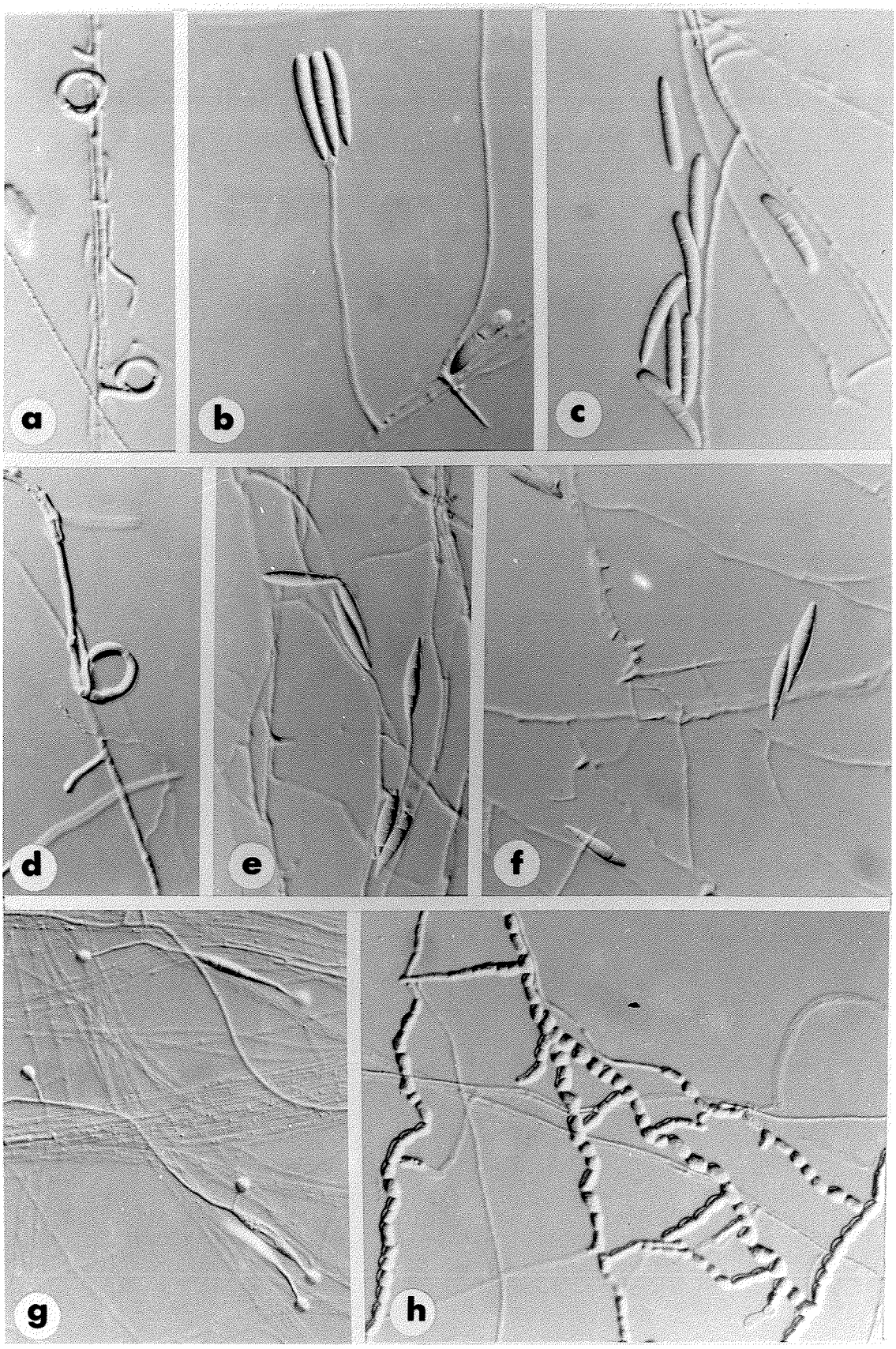
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PLATE V

Dactylella lobata Dudd.

Fig. a. A conidium (x 370).

Fig. b. An infected nematode (note granular appearence) and infected nematode eggs (x240).

Fig. c. Adhesive lobes (arrow) (x 370).

Duddingtonia flagrans (Dudd.) R.C. Cooke

Fig. d. A conidiophore (x 370).

Fig. e. Conidia of isolate 78 (x 370).

Fig. f. Conidia of isolate 78 (x 370).

Fig. g. Conidia of isolate 17 (x 370).

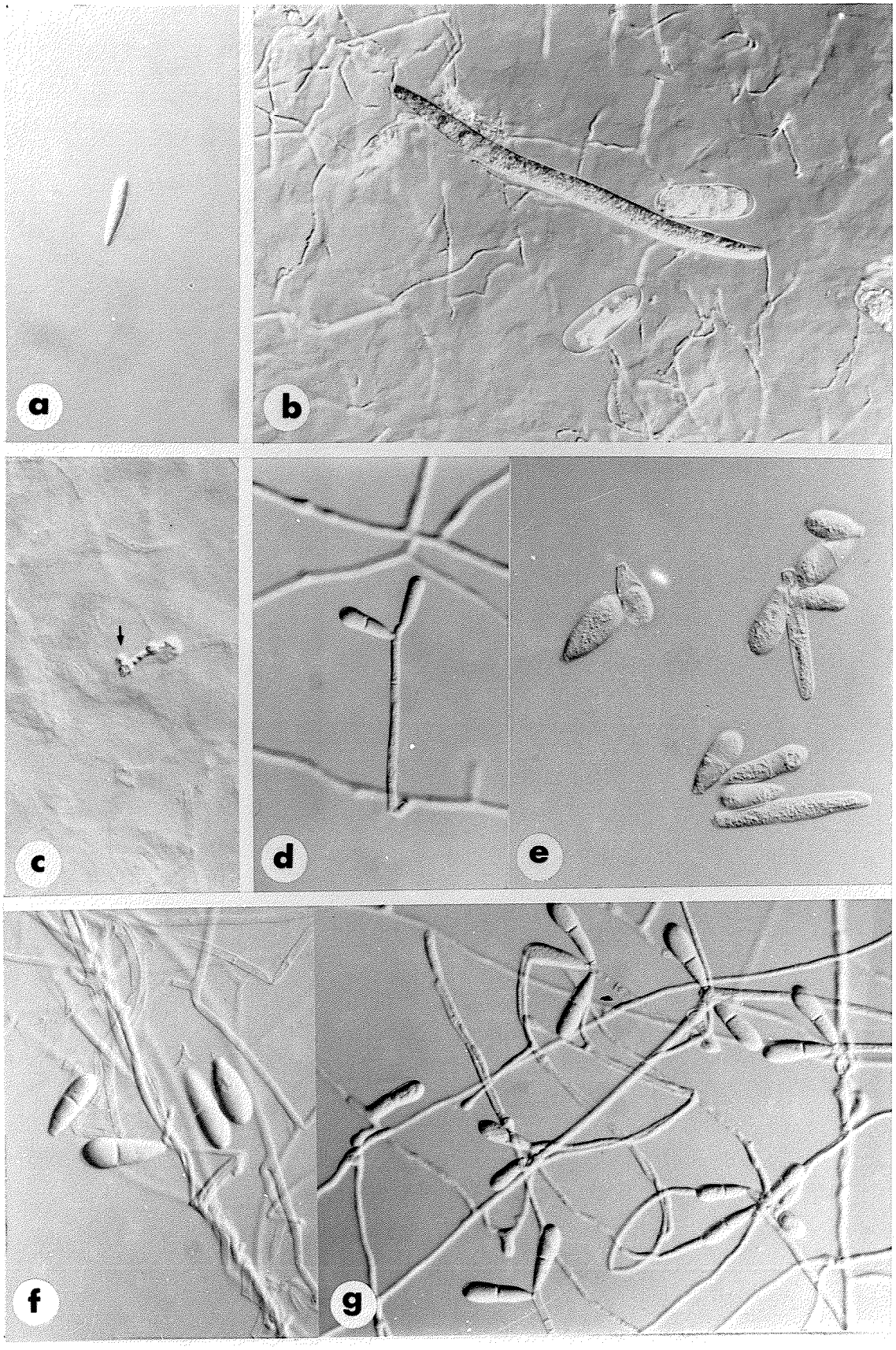
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PLATE VI

Duddingtonia flagrans (Dudd.) R. C. Cooke

Fig. a. Chlamydospores, warty exospores (arrows) (x 370).

Geniculifera taxonomic species # 1

Fig. b. A conidiophore and conidia (x 370).

Fig. c. Adhesive net-works (x 370).

Fig. d. Chlamydospores (arrow) (x 370).

Geniculifera effusa (Jarowaja) van Oorschot

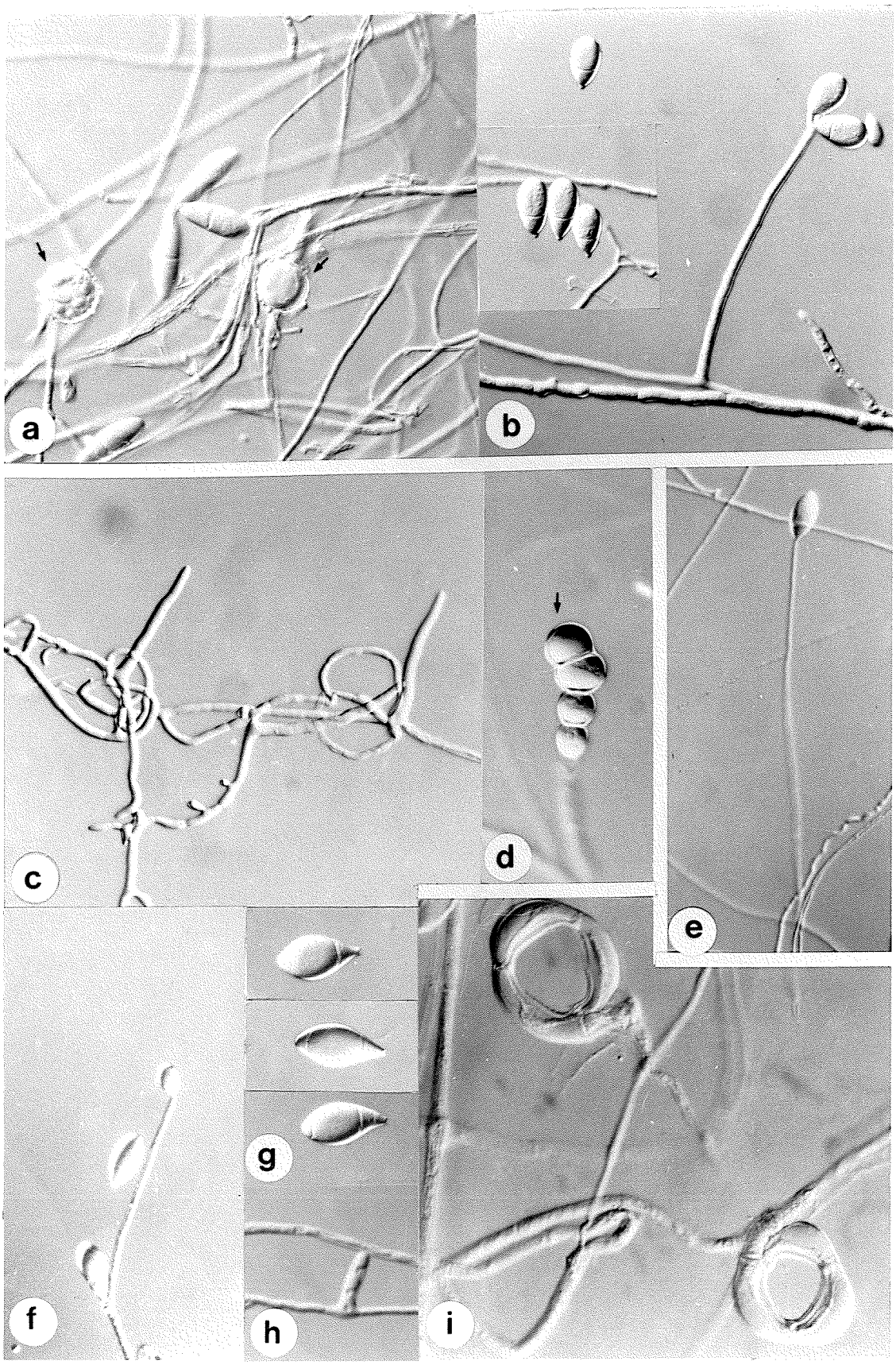
Fig. e. A conidiophore and a single conidium (x 240).

Fig. f. A geniculate conidiophore with three conidia (x 240).

Fig. g. Conidia (x 370).

Fig. h. A hyphal bridge (x 370).

Fig. i. Constricting rings (x 960).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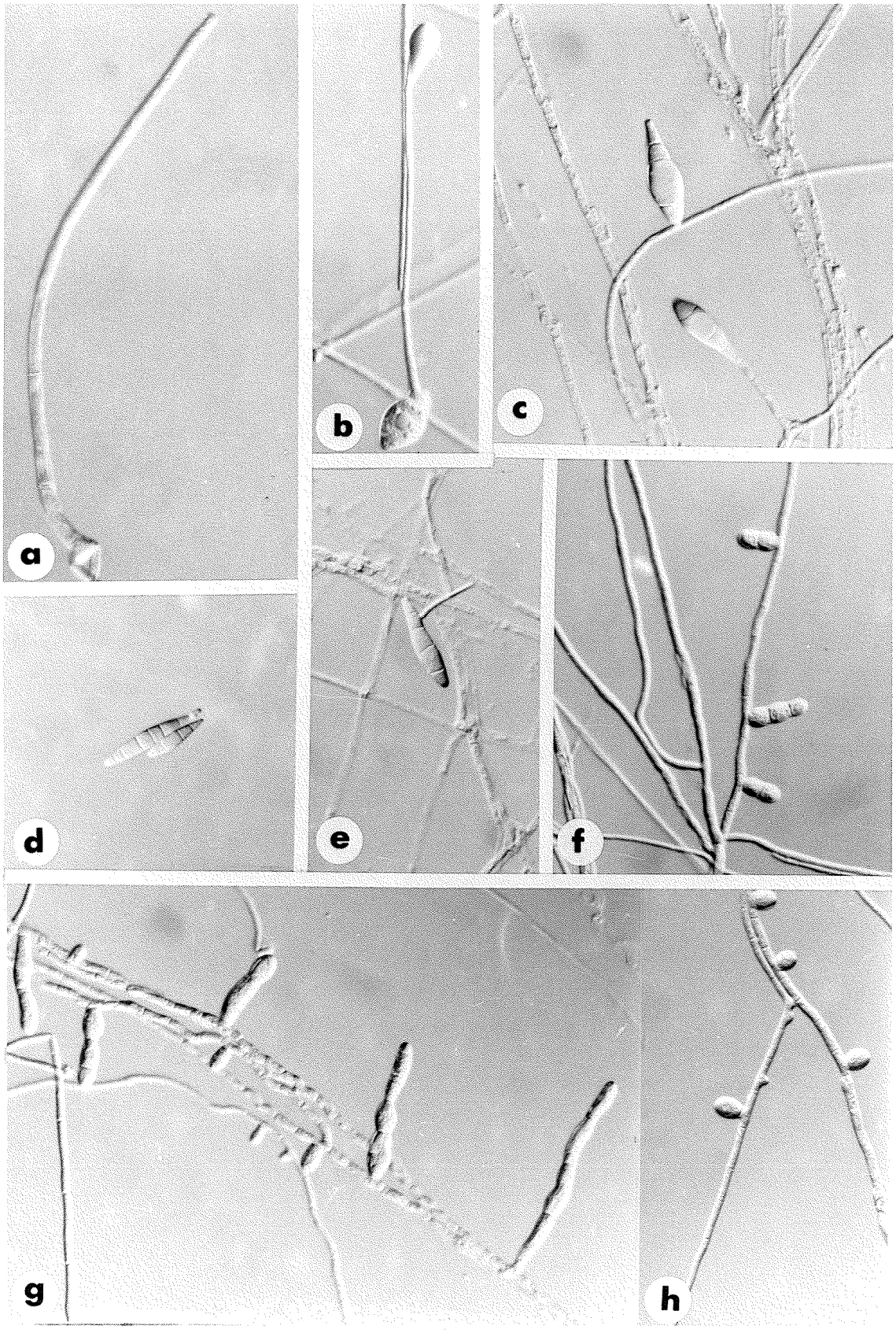
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PLATE VIII

Monacrosporium coelobrocum (Drechs.) Subram.

Fig. a. A conidiophore (x 370).

Fig. b. Conidia (x 370).

Fig. c. A conidium (x 370).

Fig. d. Conidia (x 370).

Fig. e. A constricting ring (x 370).

Monacrosporium drechsleri (Tarjan) R.C. Cooke and Dickinson

Fig. f. A conidiophore (x 240).

Fig. g. Adhesive knobs (x 370).

Fig. h. An adhesive knob on a conidium (x 960).

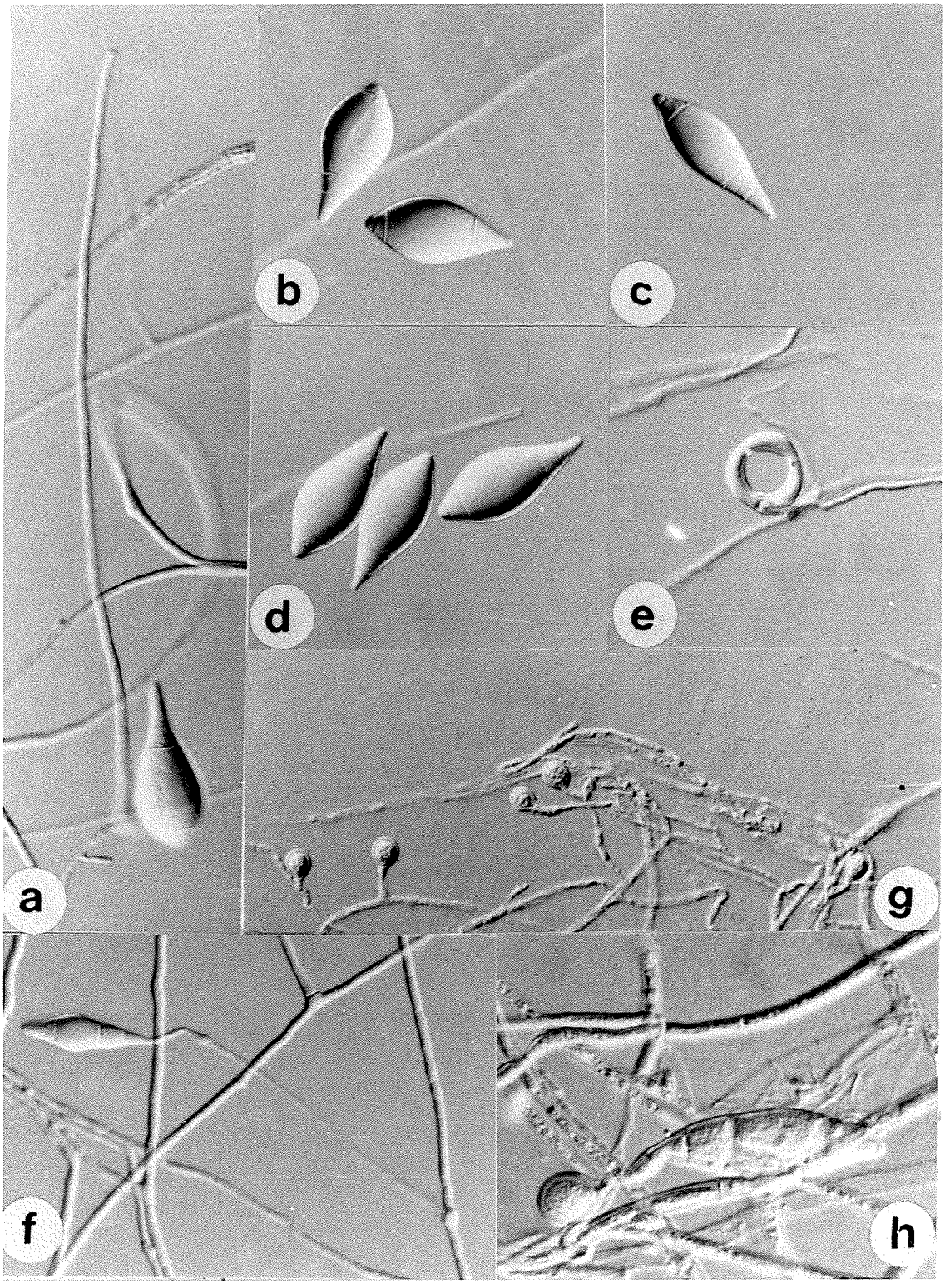
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PLATE IX

Monacrosporium drechsleri (Tarjan) R.C. Cooke and Dickinson

Fig. a. A nematode trapped by several knobs (arrows) (x 960).

Fig. b. A conidium (arrow) and adhesive knobs (arrows) (x 960).

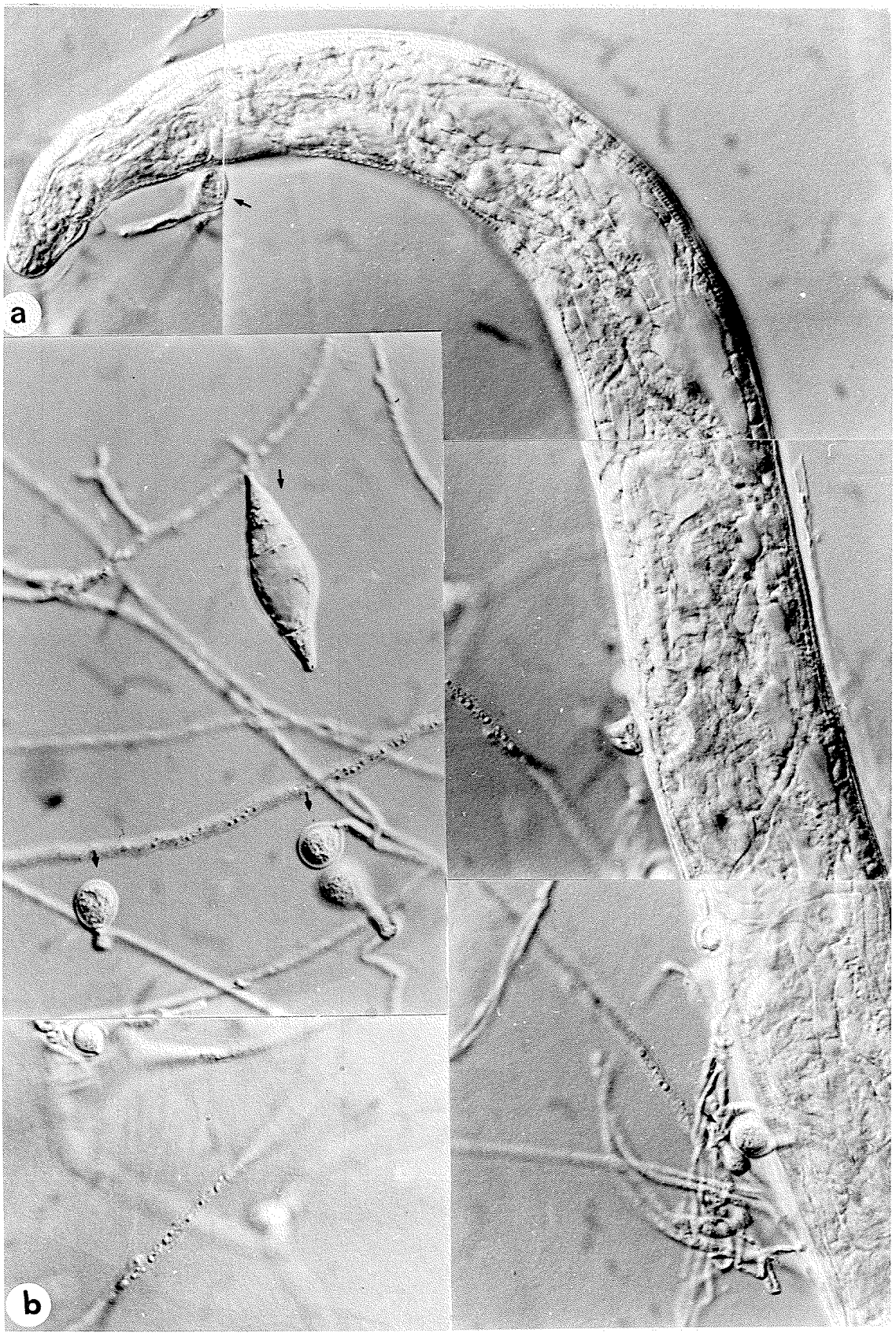
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PLATE X

Monacrosporium gephyropagum (Drechs.) Subram.

Fig. a. Conidiophores and conidia (x 370).

Fig. b. Adhesive branches (x 370).

Fig. c. Adhesive scalariform net-works (x 370).

Fig. d. A trapped nematode (x 240).

Monacrosporium heterosporum (Drechs.) Subram.

Fig. e. A conidiophore (x 370).

Fig. f. Conidia (x 370).

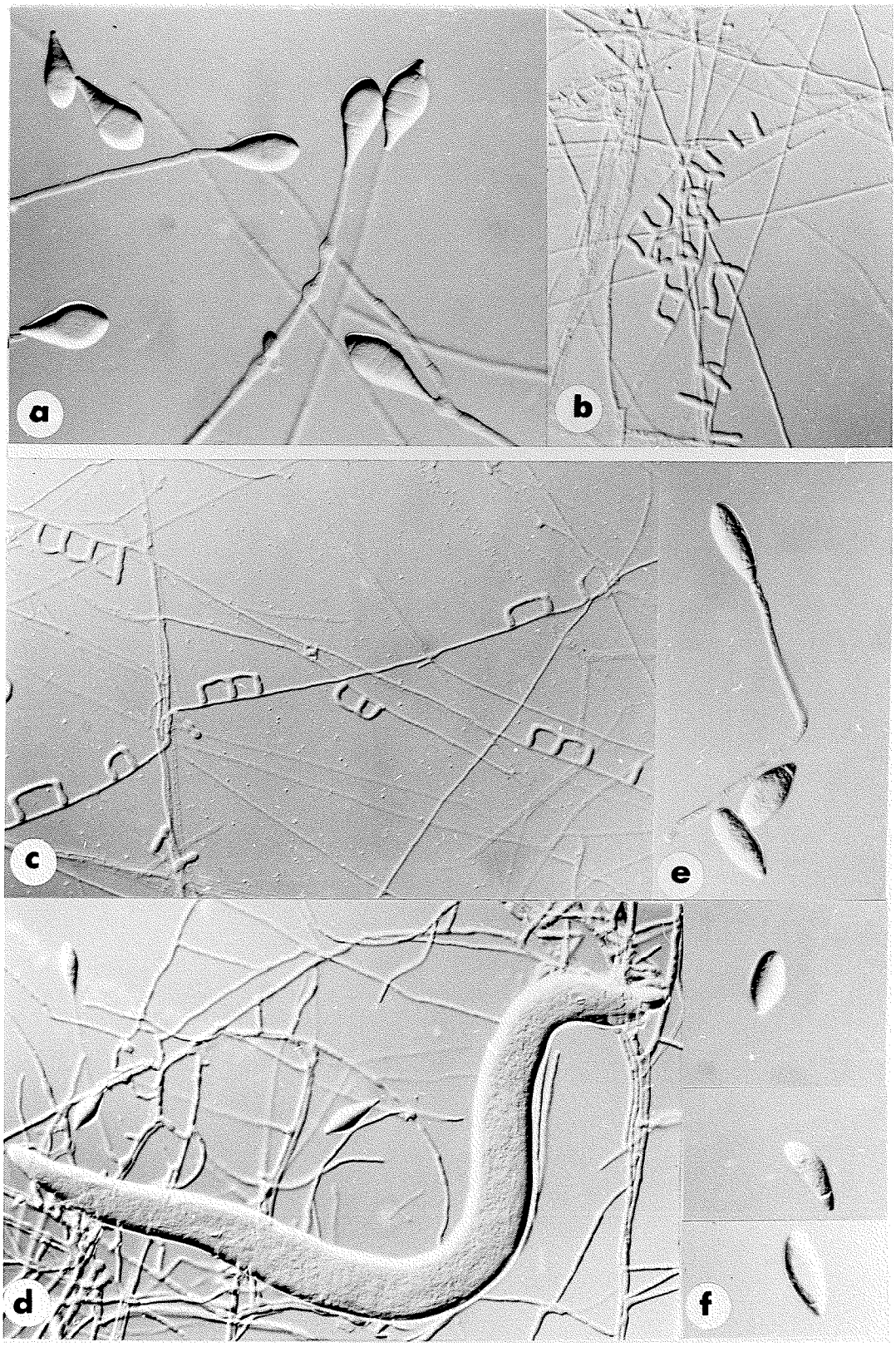
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PLATE XI

Monacrosporium heterosporum (Drechs.) Subram.

Fig. a. Conidia (x 370).

Fig. b. A nematode caught in a constricting ring (arrow) (x 370).

Harposporium anguillulae Lohde

Fig. c. A consumed nematode showing internal chlamydospores (x 960).

Fig. d. Crescent shaped conidia (arrows) (x 960).

Harposporium helicoides Drechs.

Fig. e. An infected nematode with conidiophores protruding from its body (arrows) (x 565).

Fig. f. A conidiophore (arrow) (x 960).

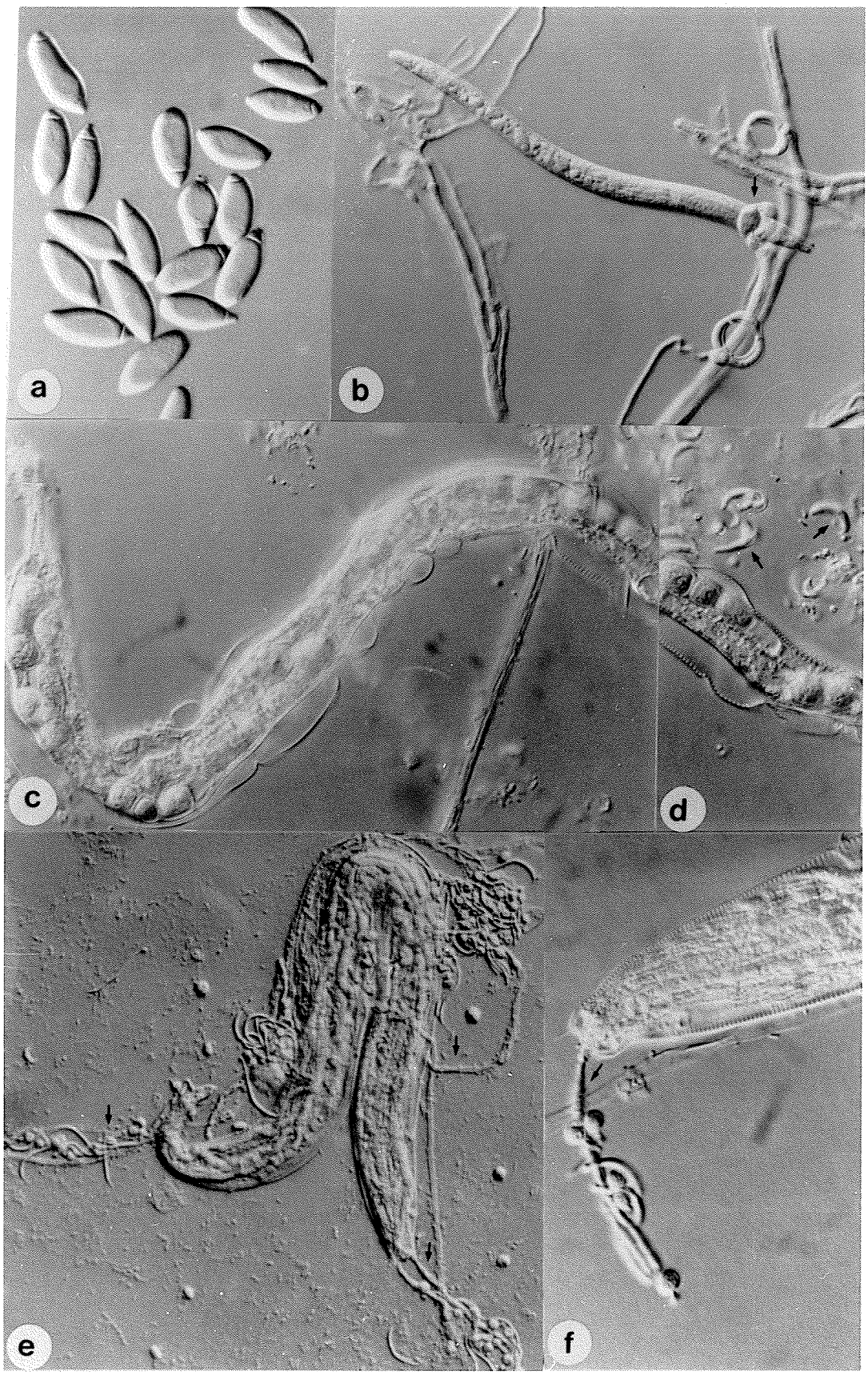
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PLATE XII

Harposporium helicoides Drechs.

Fig. a. A conidiophore with spherical phialides (arrow) (x960).

Fig. b. A conidium with bulbous end (arrow) (x 560).

Verticillium obovatum (Drechs.) Subram.

Fig. c. A conidiophore with flask shaped phialides and spherical conidia (arrows) (x960).

Fig. d. An infected nematode with conidiophores protruding from its body (x370).

Stylopage grandis Duddington

Fig. e. A conidiophore tip with two conidia (x370).

Fig. f. A nematode trapped by a drop of adhesive material (arrow) and a drop of adhesive material on hyphae (arrow) (x 370).

Fig. g. A prey of Stylopage grandis (x 370).

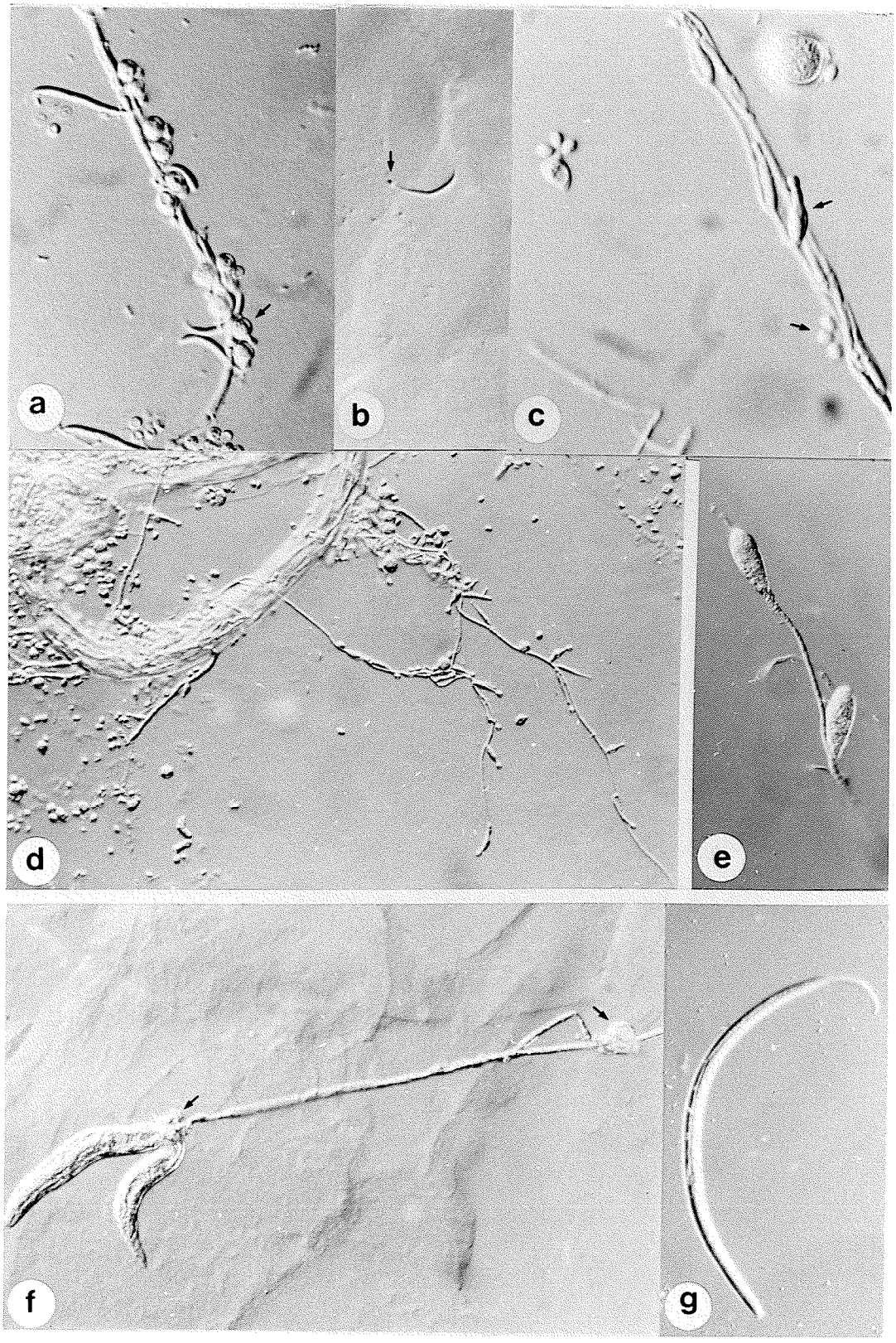
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PLATE XIII

Nematoctonus amatus Thorn and Barron

Fig. a. Fertile hyphae with conidia, and conidia germinating into an hour-glass adhesive knob (arrows) (x 370).

Fig. b. Adhesive hour-glass knobs on the hyphae (arrows) (x 565).

Nematoctonus concurrens Drechs.

Fig. c. Conidia (x 370).

Fig. d. Hyphae with clamp connections (arrow) (x 565).

Fig. e. An adhesive hour-glass knob on the hypha (x 960).

Fig. f. Proliferation of the adhesive hour-glass knob to produce a second and a third adhesive knob (arrow) (x 960).

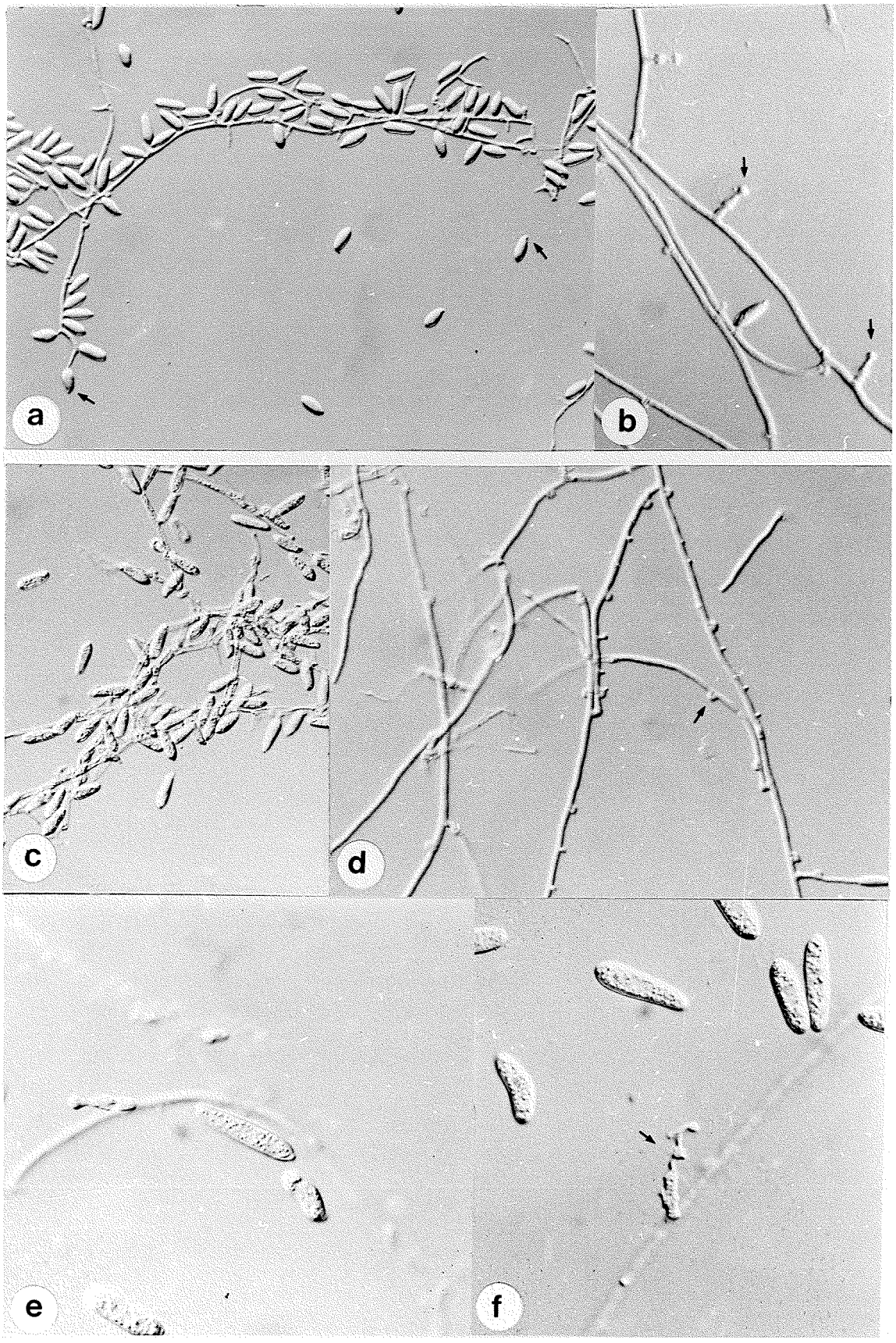
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PLATE XIV

Nematoctonus concurrens Drechs.

Fig. a A trapped nematode (x 960)

Nematoctonus pachysporus Drechs.

Fig. b. Conidia (x 370).

Fig. c. A conidium germinating into an hour-glass knob (arrow) (x 370).

Fig. d. A chlamydospore (arrow) (x 370).

Nematoctonus robustus Jones

Fig. e. Conidia (x 370).

Fig. f. Intercalary hour-glass knobs covered with a drop of adhesive material (arrows) (x 960).

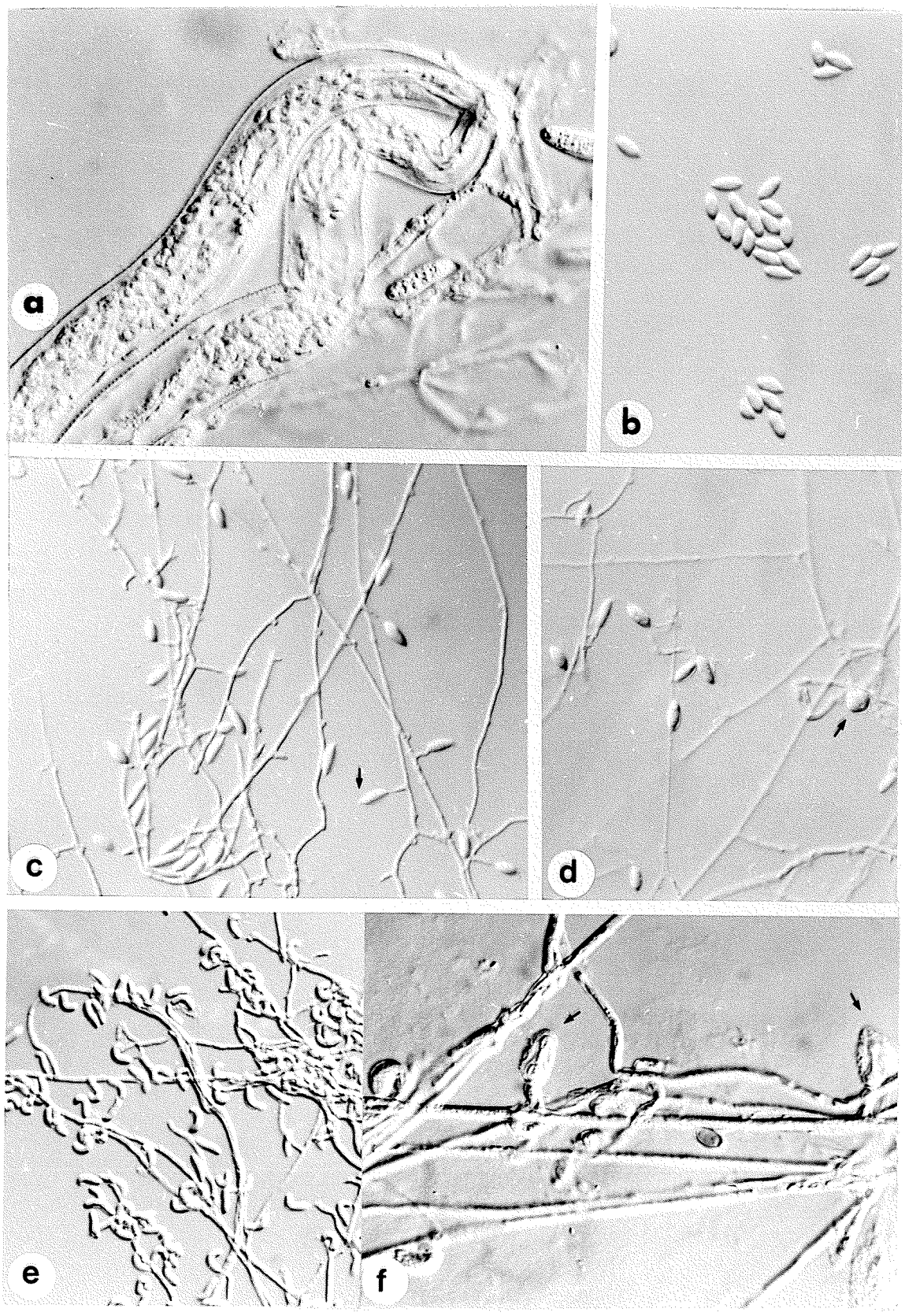
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PLATE XV

Nematoctonus robustus Jones

Fig. a. An apical hour-glass knob (arrow) (x 960).

Nematoctonus tylosporus Drechs.

Fig. b. Fertile hyphae with conidia (x 370).

Fig. c. An infected nematode with fertile hyphae protruding from its body (x 370).

Fig. d. A nematode caught by conidia which had germinated into hour-glass knobs (arrow). A conidium with an hour-glass knob (arrow) (x 370).

Fig. e. Conidia (x 960).

Panus rudis Fr.

Fig. f. An infected nematode (x 960).

Fig. g. Basidiospores (x 960).

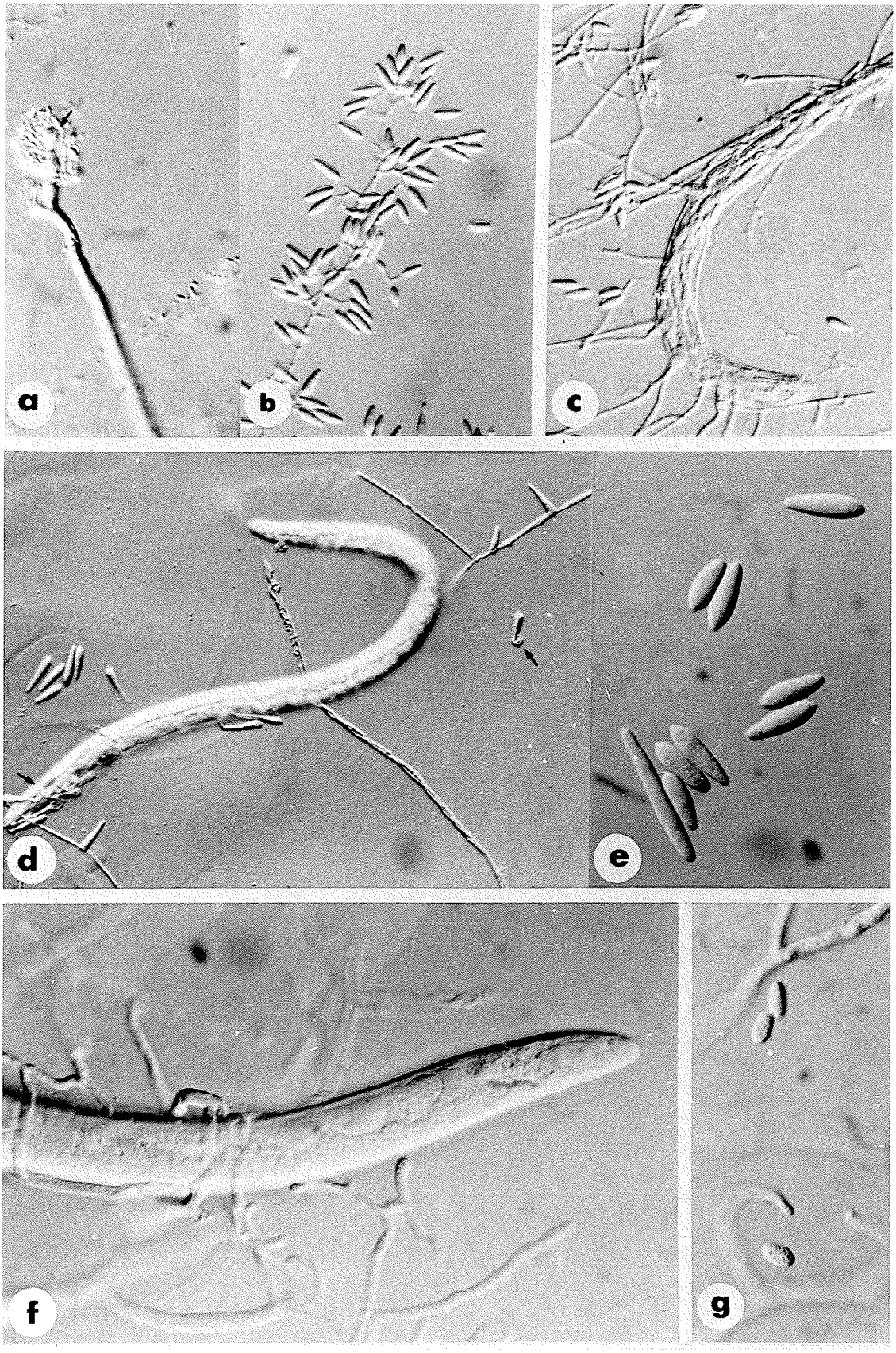
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PLATE XVI

Panus rudis Fr.

Fig. a. An infected nematode showing internal oil drops (arrows) (x240).

Fig. b. Hyphae around infected nematode (x 370).

Fig. c. Modified hyphae in the presence of nematodes (x 370).

Pleurotus elongatipes Pk.

Fig. d. An infected nematode and secretory stalked cells for the release of nematoxin (arrows) (x 565).

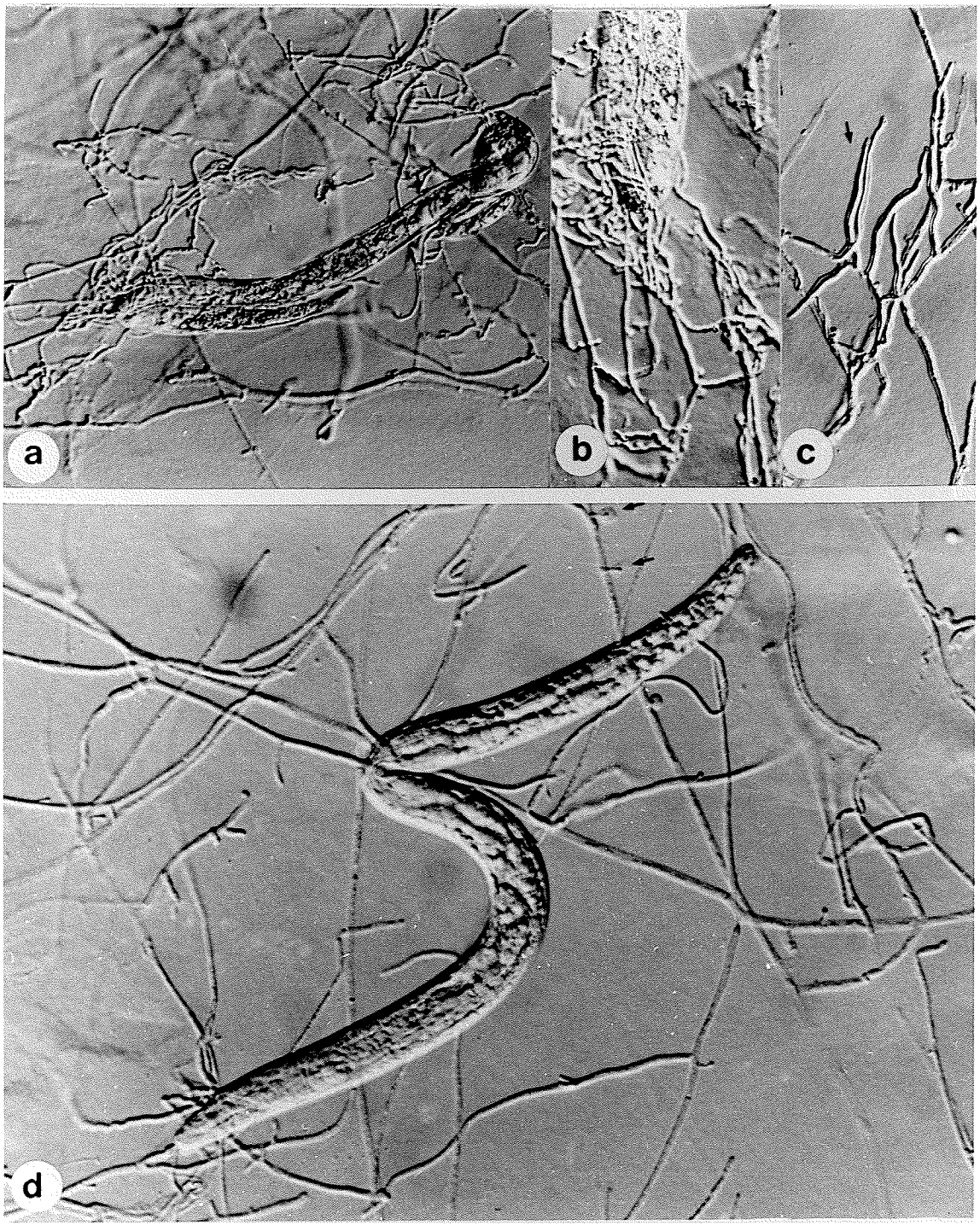
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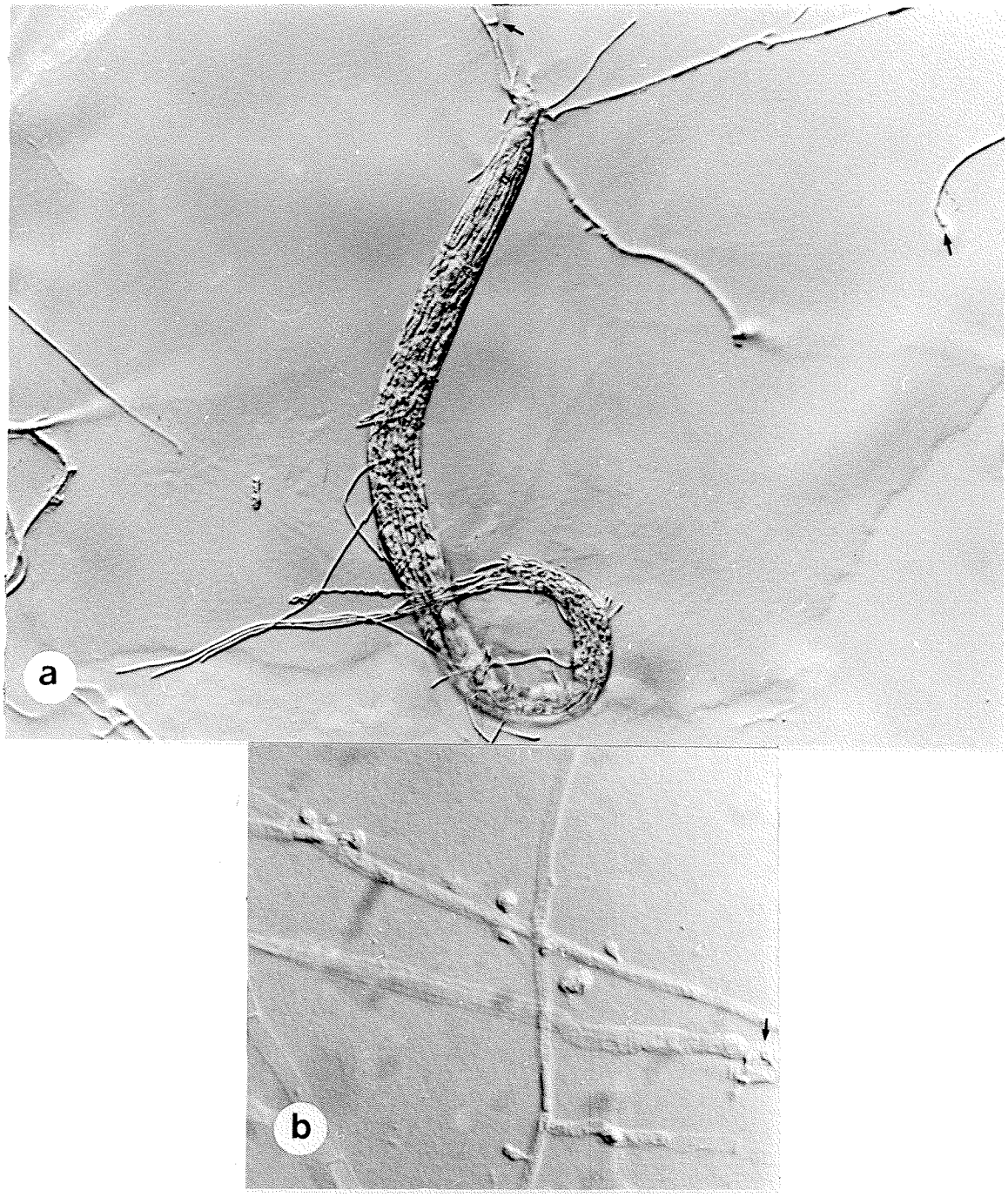
PLATE XVII

Pluteus aurantiorugosus (Trog) Sacc.

Fig. a. An infected nematode and secretory stalked cells on hyphae for the release of nematoxin (arrows) (x 565).

Fig. b. Secretory stalked cells for the release of nematoxin. Collapsed cell that has discharged the nematoxin (arrow) (x960).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General discussion and conclusion

This investigation on the occurrence of nematophagous fungi in Manitoba has shown that they are abundant and widespread. From 120 samples collected, in 23 different areas in Manitoba, 106 isolations were made. The most common isolate was A. arthrobotryoides followed by A. oligospora. The various isolates belong to 31 different species and are divided among the Zygomycotina, Deuteromycotina and Basidiomycotina. Sixteen species are first reports for Manitoba, namely:

Arthrobotrys dactyloides Drechs.

Arthrobotrys taxonomic specie # 1

Dactylella lobata Dudd.

Duddingtonia flagrans (Dudd.) R.C. Cooke.

Geniculifera taxonomic specie # 1

Monacrosporium coelobrocum (Drechs.) Subram.

M. gephyropagum (Drechs.) Subram.

M. heterosporum (Drechs.) Subram.

H. helicoides Drechs.

Verticillium obovatum (Drechs.) Subram.

Stylopage grandis Dudd.

Nematoctonus amatus Thorn and Barron.

N. concurrens Drechs.

N. pachysporus Drechs.

N robustus Jones.

N. tylosporus Drechs.

Furthermore, the three predaceous Agaricales Panus rudis Fr., Pleurotus elongatipes Pk.. and Pluteus aurantiorugosus (Trog.) Sacc. have been tested and proved positive for nematophagous activity.

The predaceous Hyphomycetes of Manitoba have been placed in the genera Arthobotrys Corda, Dactylaria Sacc., Dactylella Grove , Duddingtonia R.C. Cooke, Geniculifera Rifai and Monacrosporium Oudemans. The classification has been based on the review by van Oorschot (1985) of Arthrobotrys and allied genera., but the genus Dactylaria has been retained, because D. scerophypha, one isolate in the present study, has fusiform conidia and traps with adhesive knobs, thus it is closer to Dactylella and Monacrosporium species than to Arthrobotrys. Dactylella lobata, with a conidium divided into more or less equal cells and an unique trapping device in the form of a lobe, has been placed in the genus Dactylella. The species of Dactylella having fusoid conidia with a large central cell have been placed in the genus Monacrosporium. The isolations of a Geniculifera species and of Duddingtonia flagrans provided the opportunity to study typical conidiophores of these genera and to conclude that species with similar conidiophores can be separated from Arthrobotrys and referred to their own genera. Based on Subramanian (1977), the isolate originally assigned to Acrostalagmus obovatus, has been now classified as Verticillium obovatum.

The present survey in Manitoba recovered more predaceous (23) than endoparasitic (5) types. This result was expected since all samples except three were processed by the Warcup method. A survey of nematophagous fungi carried out in Quebec (Estey and Olthof 1965) employing the sprinkling method yielded eleven species of predators and two endoparasites from 175 samples of various kind of organic material. The

outcome of a survey in Nova Scotia (Alger 1980) was quite different. Alger found thirty-one species of nematophagous fungi from 120 samples of organic substrates using the sprinkling and the Baermann funnel techniques. Eleven species were predators and nineteen were endoparasites. Barron (1980) recovered forty species of endoparasites from 500 samples collected in mixed wood, agricultural soils and gardens in Ontario. He used three techniques: Baermann funnel, differential centrifugation and sprinkling. The Baermann funnel yielded 32 species of endoparasites; differential centrifugation, 19 and soil sprinkling, 21. Barron concluded that the main advantage of the Baermann funnel was the recovery of Chytridiomycetes and Oomycetes.

During the present study in Manitoba the Baermann funnel and centrifuge techniques contributed to the recovery of species of endoparasites not detected by the Warcup method. Isolation techniques markely influence the isolation of the different species of nematophagous fungi, but another very important factor is the source of organic material. Soil and particularly mosses and wood, collected in the southern part of the Province, have been a very good source of nematophagous fungi. Samples from which no isolations were made had a combination of low pH and lack of moisture or they had very little organic content.

Of the 13 soil samples collected in northern Manitoba, only three samples yielded nematophagous fungi. The pH of these samples ranged from 4 to 7.5, and isolations were made only from samples with pH between 5 and 6. Samples collected in southern Manitoba had pH between 4.5 and 8.5 and isolation were made from samples with a pH between 5 and 8.

Gray (1985a) studied the effect of organic matter, soil moisture, pH, and nematode density on the distribution of nematophagous fungi in

Ireland. He found that pH and moisture had more influence on the presence of predatory fungi than any of the other factors. Most of his predaceous fungi were recovered from substrates with an average pH of 5.5. The presence of certain endoparasites on the other hand was influenced by higher nematode density. Looking at the different species found in Manitoba and the pH of the samples from which they were isolated (Table 1), we observe that the two very similar species A. oligospora and A. conoides were found in substrates having a narrow pH range from slightly acid to slightly basic. The species in the genera Dactylaria and Monacrosporium appeared to prefer a pH range from moderately acid to neutral and this would seem to be the case for most Arthrobotrys species isolated with the exception of the two species mentioned previously. Harposporium species (four isolates) were found in substrates moderately to slightly acidic, while the five species of the genus Nematoctonus (each species represented by one isolate) were found in substrates slightly acidic to slightly basic.

Differences in soils and natural vegetation between the southern and the northern part of the Province (Weir 1983) may well explain the trend toward fewer isolations of nematophagous fungi from the northern samples.

Superficial soils in Winnipeg and surrounding areas, where sampling was carried out, belong to the Chernozemic order (See Fig. 16). Under grass and forbs, soils belong to the black Chernozem group, in areas of transition between grass land and forest, they belong to the dark gray Chernozem group. In poorly drained areas or places subjected to spring flooding, these soils developed into soils of the Gleysolic order in the Humic Gleysol group. Natural vegetation of the areas (See Fig. 17)

TABLE 1. Nematophagous species isolated and pH of samples.

Species	pH range
Arthrobotrys arthrobotryoides	5.5 - 7
A. cladodes var. *cladodes*	5.5 - 7
A. cladodes var. *macroides*	5.5 -7
A. conoides	6.5 - 8
A. dactyloides	6 - 7
A. musiformis	6 - 7
A. oligospora	6 - 8
A. superba	6 - 7
A. species	7
Dactylaria brochopaga	5.5 - 7
D. sclerohypha	5.5 - 7
Dactylella lobata	7
Duddingtonia flagrans	6.5 - 7
Geniculifera cystosporia	6.5 - 7
Monacrosporium cionopagum	5.5 - 7
M. coelobrochum	6
M. drechsleri	6
M. gephyropagum	7
M. heterosporum	5.5
Harposporium anguillulae	5.5 - 6.5
H. helicoides	5.5
Verticillium obovatus	5.5
Stylopage grandis	6.5
Nematoctonus amatus	7
N. concurrens	8
N. pachysporus	7
N. robustus	6.5
N. tylosporus	6.5

Fig. 16. Superficial soils at the collecting sites (after Weir 1983).

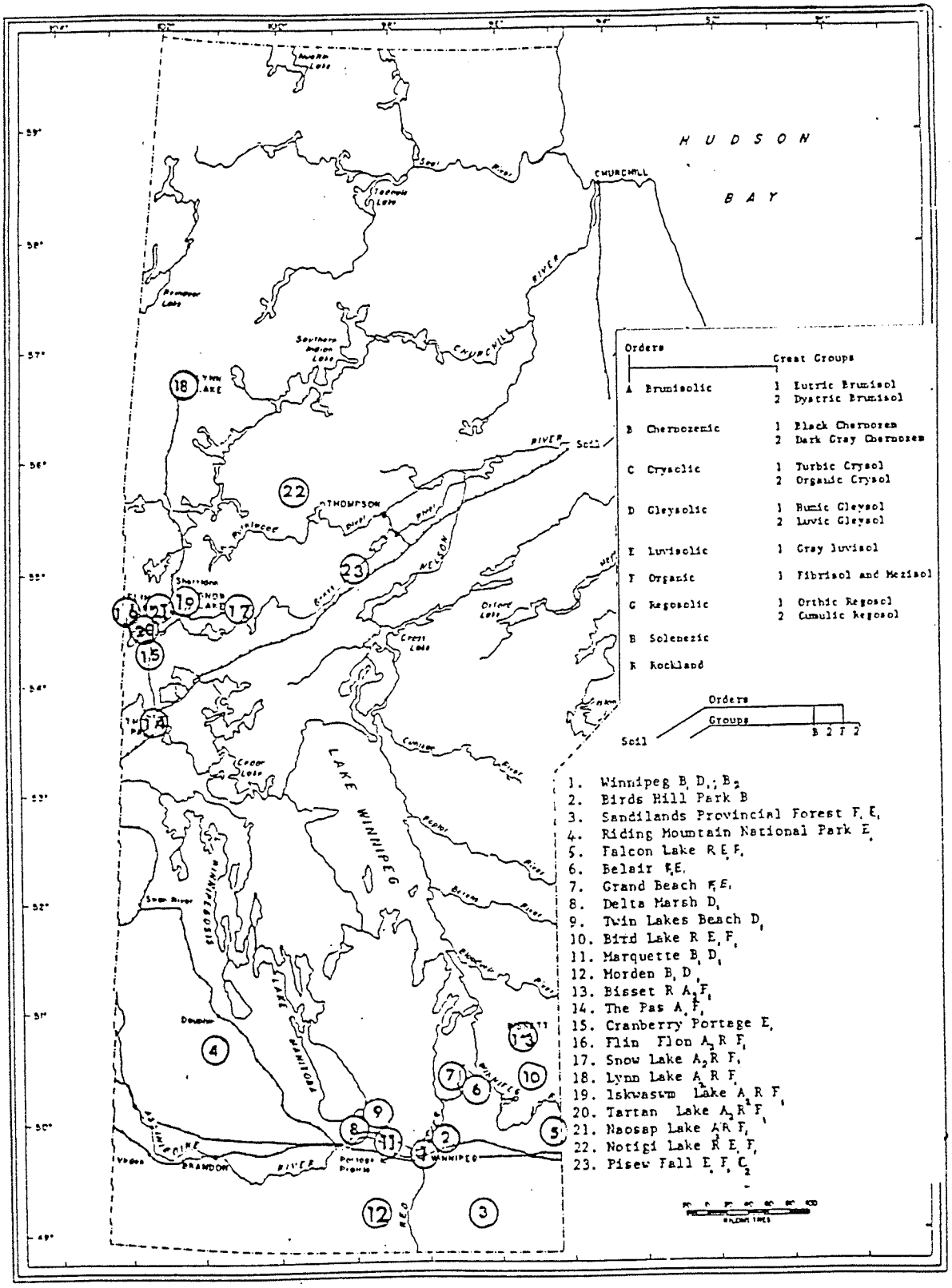
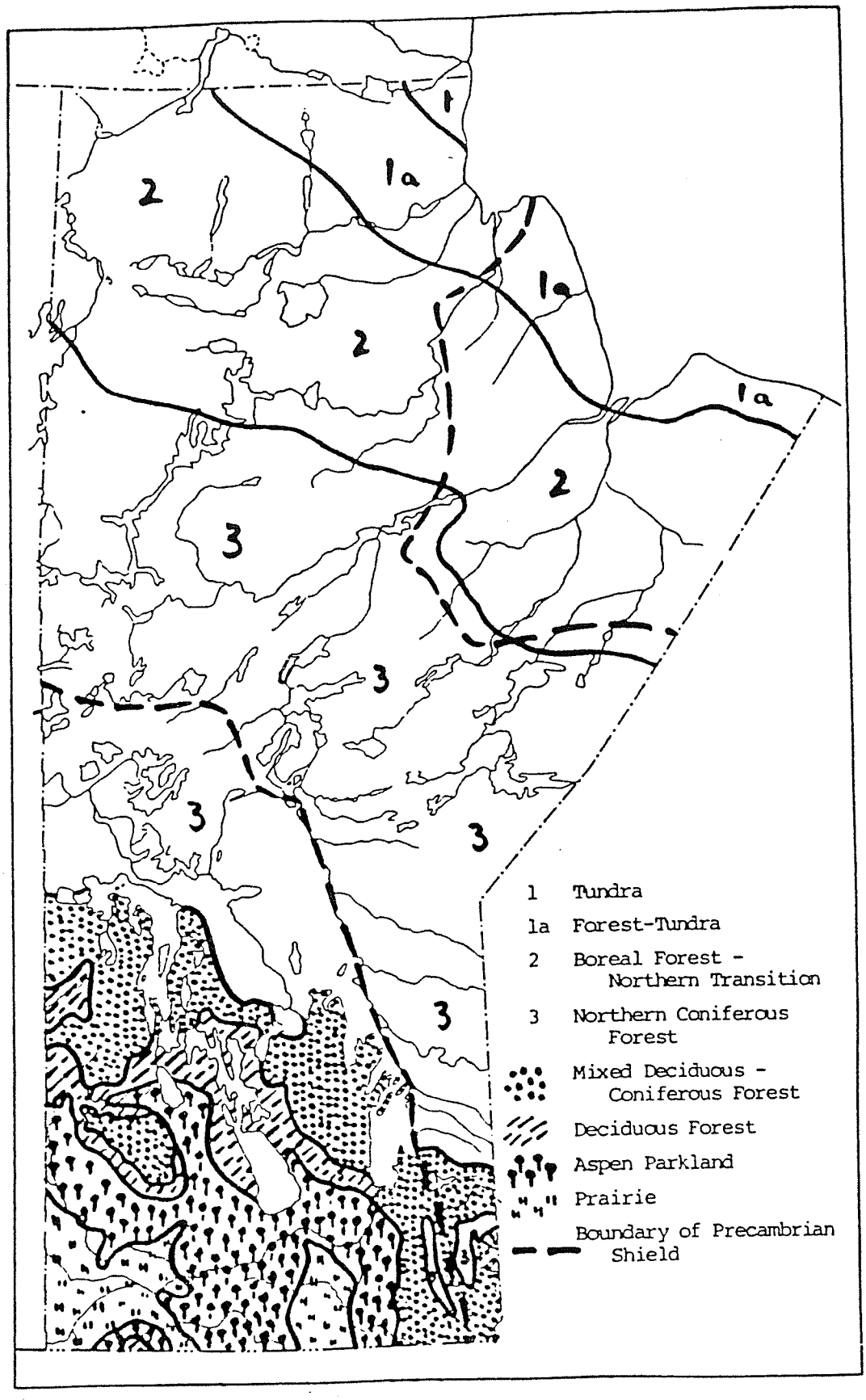

HUDSON
BAY
CHURCHILL
RIVER
THOMPSON
NELSON
LAKE WINNIPEG
BRANDON
RIVER
Orders
Great Groups
A Brunisolic
1 Eutric Brunisol
2 Dystric Brunisol
B Chernozemic
1 Black Chernozem
2 Dark Gray Chernozem
C Cryosolic
1 Turbic Cryosol
2 Organic Cryosol
D Gleysolic
1 Humic Gleysol
2 Luvic Gleysol
E Luvisolic
1 Gray luvisol
F Organic
1 Fibrisol and Mesisol
G Regosolic
1 Orthic Regosol
2 Cumulic Regosol
H Solonetzic
R Rockland
Orders
Groups
Soil
B 2 F 2
1. Winnipeg B, D, ; B2
2. Birds Hill Park B
3. Sandilands Provincial Forest F, E,
4. Riding Mountain National Park E,
5. Falcon Lake R E, F,
6. Belair F, E,
7. Grand Beach F, E,
8. Delta Marsh D,
9. Twin Lakes Beach D,
10. Bird Lake R E, F,
11. Marquette B, D,
12. Morden B, D,
13. Bisset R A, F,
14. The Pas A, F,
15. Cranberry Portage E,
16. Flin Flon A, R F,
17. Snow Lake A, R F,
18. Lynn Lake A, R F,
19. Iskwasum Lake A, R F,
20. Tartan Lake A, R F,
21. Naosap Lake A, R F,
22. Notigi Lake R E, F,
23. Pisew Fall E, F, C2

Fig. 17. Major plant communities in Manitoba (after Ritchie, Larson and Weir).


1
1a
2
3
1 Tundra
1a Forest-Tundra
2 Boreal Forest - Northern Transition
3 Northern Coniferous Forest
Mixed Deciduous - Coniferous Forest
Deciduous Forest
Aspen Parkland
Prairie
Boundary of Precambrian Shield

consists of grass, forbs, mixed forest and broadleaf forest which includes species such as aspen , willow (Salix spp.), elm, ash (Sorbus americana Marsh), oak , maple, and basswood. In city parks there are weeping birches (Betula alba L.), Scotch pines, and Siberian elms (Ulmus pumila L.).

This area offers a multitude of microhabitats such as soils, bark, and mosses associated with various types of vegetation and could be further explored for isolation of nematophagous fungi.

A few samples with pH 5.2 to 6 were collected in the Sandilands Provincial Forest. A. arthrobotryoides appeared to be the common inhabitant followed by A. cladodes var. macroides. Wild animal droppings collected in the area gave similar results and, most interesting, was a rotten wood sample that yielded A. oligospora, Dactylaria brochopaga and Dactylella drechsleri. Superficial soils in the Sandilands area described (Weir 1983) as being of the Luvisolic and Organic orders. Samples were collected where superficial soils consisted of sand covered by a thin layer of organic matter, mostly pine needles. Vegetation is described as Northern Coniferous Forest (Fig. 17),

Samples collected at Grand Beach and Belair were very similar to the samples collected at Sandilands Provincial Forest, they were of pH 5.5 and did not contain any nematophagous fungi. A soil sample with pH 5.5 collected near Bisset under mixed forest, yielded only a single isolate of Dactylella cionopaga. Soils of this area were described (Weir 1983) in the orders Rockland, Brunisolic and Organic and in the Dystric Brunisol, Fibrisol and Mezisol Organic group.

Several soil samples were also collected near Falcon Lake with a pH varying from 4.5 (bog sample) to 6 (under mixed forest). Isolations made from samples with pH range 5.5 to 6 consisted of A. arthrobotryoides.

Superficial soils in this area were described (Weir 1983) in the orders Rockland, Luvisolic and Organic, and in the group of the Gray Luvisol and of the Organic Fibrisol and Mezisol. The natural vegetation is classified (Weir 1983) as Northern Coniferous Forest, consisting mainly black spruce, white spruce and jack pine.

A few samples of pH 6.5-7 were collected in wet areas such as Delta Marsh and Twin Beach where soils are in the Gleysolic order and in the Humic Gleysol group. Dactylaria scaphoides and the rare species Geniculifera effusa appeared to be confined in this habitat.

In northern Manitoba, three soil samples with pH 7.5 were collected at the Pas in a garden, under mixed forest and under coniferous forest. None yielded nematophagous fungi. Superficial soils of the area are described (Weir 1983) in the order Brunisolic Organic in the Eutric Brunisol group and in the Organic Fibrisol and Mezisol group. The Eutric Brunisol soils are generally neutral to alkaline since they have developed on calcareous parental material. Natural vegetation in the Pas is intermediate between the northern and the southern vegetation of the province. Elm and maple trees are still found and there are several grain and cattle farms. Sampling in the area was too limited to be able to draw a conclusion, but it is possible that several species of nematophagous fungi which are known to prefer acidic soils (Gray 1985) were absent.

A sample from a bog at Cranberry Portage yielded an isolate of A arthrobotryoides and an isolate of Dactylella heterospora.

Several samples were collected in the north-western part of the Province, at Flin Flon, Tartan Lake, Noasap Lake, Iskwaswm Lake and Snow Lake. The pH of these samples were between 4 and 6. Superfical soils are described (Weir 1983) of the order Brunisolic, Rockland and organic and in

the Dystric Brunisol group and in the Fibrisol Mezisol Organic group. Only the samples collected at Flin Flon in the Wild Life Park and at Notigi Lake contained nematophagous fungi. The sample collected in the Wild Life Park, a man-made bird sanctuary, was particularly interesting because it contained four different species of nematophagous fungi. The presence of the nematophagous species may be linked in some way to the birds. The birds bring conidia to the area and their droppings make a superficial soil rich in organic matter, especially nitrogen that would facilitate the establisment of a large and varied microcopic life including predators and parassites of the microscopic animals The two samples collected at Pisew Falls consisted of dry peat moss with pH 5.5 and 6 and did not yield any nematophagous fungi. Soils here are described (Weir 1983) in the order Luvisolic, Organic and Crysolic and placed in the Gray Luvisol group, Organic Fibrisol and Mezisol and in the Organic Crysol group. Organic Crysol are soils where permafrost remains close to the surface.

The only sample collected at Lynn Lake had pH 4 and did not contain nematophagous fungi. The superficial soils here are probably of the order Brunisolic, Rockland and Crysolic. Natural vegetation in this northern part of the Province is limited to the Northern Coniferous Forest with small patches of mixed forest (Weir 1983).

Unfortunately sampling in the northern part of the province was limited to a few samples, nevertheless there is an indication of a less varied and less abundant population of nematophagous fungi in this areas. The presence in the southern part of the Province of the fertile Chernozemic soils, the abundance of soils that are moderately acidic, moderately basic or neutral, and the larger variety of planted and natural vegetation,

constituted important factors in the development of a larger and more varied nematophagous population.

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APPENDIX

CULTURE MEDIA

Corn meal agar (CMA)
18 g CMA
1000 ml distilled water.

Add the distilled water to the agar in a 1800 ml flask and autoclave for 20 min.

Potato dextrose agar (PDA)
20 g PDA
1000 ml distilled water.

Add the distilled water to the agar in a 1800 ml flask and autoclave for 20 min.

Malt extract agar (MEA) plus yeast
20 g malt extract
0.5 g yeast
1000 ml water.

Add the distilled water to the ingredients in a 1800 ml flask and autoclave for 20 min.

Sample extract agar (SEA)
100 g sample
1000 ml distilled water
20 g agar.

Blend 100 g sample plus 300 ml distilled water. Filter. Add to the filtrate distilled water to adjust the volume to 1000 ml. Add to this solution 20 g agar in a 1800 ml flask and autoclave for 20 min.

Water agar (WA)
20 g agar
1000 ml distilled water.

Add to the agar the distilled water in a 1800 ml flask and autoclave for 20 min.

MOUNTING MEDIUM

Melzer's reagent (without iodine)
100 g chloral hydrate
5.0 g potassium iodide
100 ml distilled water.