FUNGI ISOLATED FROM STAINED WOOD ASSOCIATED WITH BARK BEETLE GALLERIES IN TIMBER TREES IN NEW ZEALAND, NORWAY AND WESTERN CANADA

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Gudrídur Gyda Eyjólfsdóttir

A thesis submitted to the
Faculty of Graduate Studies
in partial fulfilment of the requirements
for the degree of
Doctor of Philosophy.

Department of Botany
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ABSTRACT

Fungi isolated from stained wood, mostly coniferous and recently attacked by bark beetles, in New Zealand, Norway, Western Canada, and the U. S. A. were grown in culture under prescribed conditions to determine their specific characteristics and taxonomic relationships.

The study resulted in the preparation of detailed descriptions of 36 taxa which represent species of the genera Acremonium, Aphanocladium, Beauveria, Chalara, Dipodascus, Engyodontium, Gliocladium, Graphium, Hyalodendron, Hyalopesotum, Hyalorhinocladiella, Leptodontidium, Mariannaea, Monocillium, Phaeoisaria, Phialographium, Phialophora, Pithomyces, Rhinocladiella, Verticillium, Volutella, and taxonomic genus 1. Of these, nine are proposed as new, and are to be found in Acremonium, Beauveria, Gliocladium, Graphium, Hyalopesotum (synanamorph Hyalorhinocladiella), Monocillium, Phialographium (synanamorph Phialophora), and one for which the new genus will be erected. In addition, to accommodate one of these species, the genus Erostella was re-established, and its type, E. minima, and the only other previously described species, E. fraxinopennsylvanica, were included for comparison with E. novae-zelandiae sp. nov. prop.

Wood-staining fungi, especially members of the Ophiostomatales and their anamorphs, many of which cause blueing of the sapwood of economically important timber trees, have been the subject of numerous studies. However, other fungi which occur in association with the wood-staining organisms in and around bark beetle galleries have largely been ignored, especially if they are non-staining. This investigation sought at least

partially to redress this neglect.

This study is a taxonomic investigation of various fungi from the bark beetle galleries. Its aim was to identify the more poorly known entities and thus add information as to the nature of the bark beetle-host tree-microorganism ecosystem.

ACKNOWLEDGEMENTS

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Further thanks are due to the members of my committee, Dr. James Dowsett, Dr. David Punter, and Dr. John Mills for the interest they have shown in my work, their advice, access to their personal libraries, and for reading this thesis. Also to both the external examiner, Dr. D. Brewer and to Dr. C. Bernier for agreeing to read this submission.

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TABLE OF CONTENTS

LIST OF FIGURES

INTRODUCTION

When bark beetles attack their host trees and begin to construct their galleries, they vector numerous different microorganisms (Whitney 1982). These microorganisms rely on the beetles to overcome the mechanical and chemical defence systems present in the bark of the host trees. The beetles introduce them into the host's sapwood, a substratum otherwise not accessible to microorganisms except when they gain access through cracks in the bark. The presence of fungi may prevent the defensive mechanisms of the tree against insect attack from functioning properly by killing the adjacent host tissue and, when inoculated in this way, some fungi may also even kill the entire host. This would be advantageous for the beetles, because living host tissue often produces resins and callus tissue which hinder their reproduction (Whitney 1982).

Amongst such microorganisms are to be found several different groups of fungi. Of which the wood-staining fungi are the best known. Their mycelium penetrates the wood and discolours it either by producing pigments which diffuse into the wood surrounding the mycelium, or the hyphae are pigmented, and as they grow they thus discolour the wood which they colonize. Pigmented spores can also cause staining but, on the other hand, the fungus may remain non-staining until the food reserves are depleted and the mycelium enters a resting state; during the latter process the hyphae of many fungi become pigmented and thus cause staining (Whitney 1982).

These stains are most often dark, ranging from gray to black although usually referred to as blue; but green, red, yellow or brown

stains also occur. Käärik (1974) summarized the records of a variety of wood-staining fungi, while Whitney (1982) described the nature of the microorganisms that are vectored by the bark beetles. The association of the beetles and the microorganisms they vector with the host tree must be a product of a long co-evolution because they often rely on the presence of each other, i. e. exist in mutualistic symbiosis, at various stages in their life-cycles.

Dowding (1984) described the early colonists of standing trees or freshly cut logs, and noted that most of those fungi can invade weakened living tissue but do not cause decay of the wood. He pointed out that members of the Ophiostomatales grow primarily in the ray cells and produce their more complex fruiting structures under the bark, often in areas where the bark has been broken, or in the beetle galleries, usually at the end of rays and on the phloem. The simpler synanamorphs are produced on the mycelium throughout the colonized wood, while the macronematous conidiophores with their spore masses which are an important food source for many insects, mites and nematodes, are to be found primarily in the beetle galleries. However according to Dowding (1984), the bark beetles generally do not rely on species of Ceratocystis Ellis & Halst. sensu lato for food, but rather to suppress the tree defence mechanisms by killing the colonized host tissue. Batra (1967) lists a few bark beetle species which have symbiotic ambrosia fungi and are thus mycophagous. Other species such as those of the genera Cladosporium Link, Aureobasidium Viala & Boyer, Botrytis Micheli ex Pers. and Penicillium Link colonize the cut surfaces of logs, and are

mostly established by airborne spores (Dowding 1984).

Over the last eighty years, numerous studies of wood-staining fungi have been undertaken because their growth in the host's wood reduces its commercial value. Thus it is in countries where forestry is of economic importance that the staining organisms have been studied most thoroughly. The most important group of such fungi are members of the Ophiostomatales, in particular species of Ceratocystis sensu lato, and Ceratocystiopsis Upadhyay & Kendrick and their anamorphs.

Studies of wood-staining fungi in New Zealand, including species other than of the Ophiostomatales, were reported by Hutchison & Reid (1988a, b). In Norway, Robak (1932) studied fungi staining ground wood pulp, and Solheim (1986) investigated species of the Ophiostomatales which were associated with the bark beetle Ips typographus L. in Picea abies (L.) Karst. In Canada these fungi have been studied by Wright & Cain (1961), Griffin (1968), and Olchowecki & Reid (1974). Other fungi have also been reported, though less commonly, from bark beetle galleries in Canada (e. g. Tsuneda 1987; Tsuneda et al. 1986; Whitney & Funk 1977). Other studies have been published, but those listed above are considered to be most pertinent to this investigation.

While many of the fungi vectored by bark beetles do not cause disease of the host tree, some are well known tree pathogens which cause death. Others are less virulent, but if present in association with a intense attack by the beetles, they may kill enough tissue to girdle the tree (Whitney 1982) and thus contribute to the death of the host.

Some beetles have become dependent on certain symbiotic fungi.

They protect the fungus in specialized structures, mycangia, and inoculate the tunnels with the fungus. Here the fungus grows and forms a thin lining on the tunnel surface, and the beetles and their larvae then feed on the fungus. Batra (1967) studied the ambrosia fungi and Francke-Grosmann (1967) reported on the phenomenon of ectosymbiosis, i. e. when the beetle stores the symbiotic organism in external organs, the mycangia.

Other groups of fungi may be pathogenic to the beetles or their offspring. One of the best known of the entomogenous Hyphomycetes is Beauveria bassiana (Bals.-Criv.) Vuill. whose host range includes bark beetles; Verticillium lecanii (A. Zimmerm.) Viégas and Fusarium solani (Mart.) Sacc. are also considered pathogens of bark beetles (Barson 1976; Claydon & Grove 1984). Although some fungi have been tested for their ability to serve as biological control agents of bark beetles in nature, entomogenous fungi usually do not appear to seriously affect the beetle population as a whole, even if they proved effective pathogens in laboratory experiments (Barson 1976).

Some fungi such as Gliocladium roseum Bainier, Aphanocladium album (Preuss) W. Gams and certain species of the genus Verticillium Nees are known for their ability to parasitize other fungi. Hawksworth (1981) surveyed the mycophilic fungi and listed three species as parasitic or inhibitory to Ceratocystis species. The presence of a mycoparasite could suppress the actions of other, more harmful fungi.

The primary colonizers of standing or freshly felled trees are rather specialized organisms, capable of invading host tissue while it

is still alive although usually in a stressed condition. These fungi which are special to this habitat are poor competitors and do not grow in already colonized substrata. When the galleries are no longer used by the insects, these primary colonizers are usually overgrown and outcompeted by secondary invaders which take advantage of the changed conditions (Dowding 1984). These later invaders may have been present in the galleries but unable to compete successfully with the better adapted primary colonizers, or they may have been introduced into the galleries at a later date.

In general, fungi vectored by insects have reproductive processes specifically adapted for such dispersal, one being sticky spores which adhere to the insects. Since there is always a danger of the conidia drying out before they reach the new host, larger masses in a mucilaginous matrix generally increase the chances of successful dispersal. The slimy conidial masses also serve as a food source for various organisms found in the galleries. Fungi which are associated with bark beetles seem to express a high degree of pleomorphy, so there must be different selection forces affecting them, and diversity or plasticity thus maintained. Dowding (1984) described the differences in survival during transport which exists between the ascospores and conidia of Ceratocystis species.

This study deals with the specific characteristics and the taxonomic relationships of some of the lesser known fungi isolated from stained wood and which are associated with bark beetle galleries in timber trees in New Zealand, Norway and Western Canada. Its aim was to

identify and prepare descriptions of these fungi and, based on previous records in the literature, try to predict their possible function in the bark beetle - host tree ecosystem. Also to add to the basic information about species composition of the mycoflora of bark beetle galleries.

Since this study covers over 20 genera of Hyphomycetes, and in a few species also the ascomycetous teleomorph, it was decided to review the literature individually for each genus, immediately preceding the treated species assigned to the individual genera. Special attention was given to previous associations with: (1) coniferous wood, (2) bark- or wood-inhabiting insects, (3) forests, i. e. litter and soils, as well as to previous records of the species in the country of origin. The presumptive new taxa were not formally described herein but listed either with a specific epithet as sp. nov. prop., or as taxonomic sp. 1 of the appropriate genus.

MATERIALS AND METHODS

The fungi were isolated from wood samples obtained from standing or recently cut trees in areas of bark beetle activity. The trees sampled were all commercially important species on the North Island of New Zealand, in Eastern Norway, or in Western Canada (the provinces of British Columbia and Alberta). Lastly, a single isolate from a bark beetle trapped in Oregon, U. S. A. was also included in this study. The wood samples which still had adherent bark were placed in paper bags, enclosed in plastic and stored at <5°C until they could be examined and the fungi isolated. At that time the bark was removed and fungi growing both on its inner surface and on the exposed wood surface were isolated aseptically by transferring spores onto a small piece of agar held by an inoculating needle and then to Petri plates with corn-meal agar (CMA) (Gibco Diagnostics, Madison, Wisconsin) or 2% malt extract agar (MEA) (Johnson & Booth 1983) containing the antibiotics penicillin-g (≃30mg/L) (Sigma Chemical Co., St. Louis, Missouri) and streptomycin sulphate (≃133mg/L) (Sigma Chemical Co., St. Louis, Missouri)). From these plates the fungi were subcultured onto the same media without the antibiotics and, if necessary, purified by isolation of single spores or hyphal tips. Stock cultures (2% MEA slants in culture tubes) were prepared from the presumed pure colonies and stored at 4°C.

Malt extract agar can be prepared in various formulations. During the course of this study a modification (herein designated as MEA.YE) of that of Johnson & Booth (1983) was prepared by adding 0.75 g yeast extract, 0.07 g $CaCl_2(2H_2O)$, and 0.13 g $MgCl_2(6H_2O)$ and mixing all the

ingredients with the distilled water prior to sterilization. Other media were employed for particular species. (1) Oat meal agar (OA) was prepared by boiling 30 g cracked oats in 1 L of distilled water for 1 hour, straining it through cheese cloth, adding 20 g of agar to the filtrate and distilled water to make 1 L. This was sterilized in a large flask to keep the medium from boiling over. (2) Cellulose medium, was the unmodified version (Park 1973), with the exception that microcrystalline cellulose (Baker TLC Reagent) was used instead of "ball milled standard grade cellulose". All the ingredients were combined, the distilled water added, and the medium sterilized. (3) Rabbit food agar (RFA) was prepared by boiling 25 g of rabbit food pellets for 1 hour and then strained through cheese cloth. To the filtrate 20 g of agar was added and made up to 1 L with distilled water and the medium sterilized. Acidified MEA plates with a gradient of pH values were prepared by mixing cooled, sterilized MEA in a series of Petri plates with an increasing number of drops of 85% lactic acid (Certified A.C.S., Fisher Scientific). Growth of the isolates was then tested on a range of different pH values.

After initial examination of the isolates (on 2% MEA or CMA), those which appeared similar were grouped together as presumed representatives of a single species. Each species was then studied in detail on the culture medium recommended for it in previous taxonomic treatments. When 2% MEA was recommended or when a species grew well and produced its reproductive structures thereon, MEA.YE was used as the standard medium in this study. However, for those species which did not grow well on

MEA.YE an alternative medium was selected. For comparison and preparation of culture descriptions, sets of plates were incubated at 20°C both in darkness (although briefly exposed to light during examination and recording of growth rates) and in a controlled environment chamber programmed for an alternating 12 hours of light and 12 hours of darkness each 24 hour period. The chamber was illuminated with equal numbers of 40 watt Sylvania F20T12 Black Light Blue fluorescent (Sylvania Electric (Canada) Ltd.), and 20 watt Vita Lite fluorescent (Duro-Test Horticultural Engineering, U.S.A.) lamps. Growth rate (colony diameter of 3 colonies) was recorded after 12, 14 or 21 days for most species; for faster-growing and very slow-growing species other time intervals were selected. Variation between colonies of the same isolate and between different isolates of the same species was included in the range of growth rates reported. The colony colour was determined with the aid of Munsell Soil Color Charts (Munsell Color, Macbeth Division of the Kollmorgen Instrument Corp., Baltimore, Maryland).

The representative reproductive structures were carefully removed from the colonies and mounted in 85% lactic acid/water solution (1:15 by volume) which was kept in a syringe fitted with a millipore filtering unit (0.45 μm pores) thus filtering the solution prior to use. Slide cultures were used only on rare occasions as it became apparent that the more complex conidiogenous structures were rarely formed under such conditions. Using interference contrast microscopy (Leitz Ortholux II), the contrast obtained with this dilution of stock lactic acid was

sharper than in either undiluted lactic acid or in distilled water mounts. This dilution had been tested on Fusarium solani macroconidia and appeared to prevent both the swelling of conidia which occurred in water and the shrinkage seen in undiluted lactic acid mounts. Slides made with this solution and sealed with nail polish were temporary, but usually lasted up to two weeks before drying out. Measurements of the important morphological features were made using an oil immersion objective.

When isolates assigned to a species differed, the variation was either reported in the description and the differences outlined in the discussion, or the description was based on the majority of isolates and those which differed from it were reported separately, as exceptions, in the discussion.

The illustrations were drawn with the aid of an eyepiece drawing tube attached to the interference contrast microscope, chiefly at an original magnification of 2200x. Initial drawings were then traced and inked on to a Dietzgen polyester drafting film (Dietzgen, St. Paul, MN) and subsequently reduced. Photographs were taken of the important taxonomic features using interference contrast microscopy and Kodak Panatomic X film. These photographs are not presented here as the drawings were considered better suited to show the nature of these organisms.

The species reported on herein represent but a portion of the total number of isolates examined in this study; time constraints dictated that less unique species had to be omitted from full detailed

consideration. Admittedly judgements as to what to include may have been faulty, but something must be left for those who follow!

TERMINOLOGY USED IN THE DESCRIPTIONS

A. The colony growth rate is given as the diameter of the colonies after incubation for the number of days specified.

B. Colours were determined using the Munsell Color System's abridged version for soil colours, a system recommended by Hawksworth et al. (1983). As each name includes several colour chips the numerical designation for the colour is also provided in the interest of precision.

C. Colonies were described from their centres to their margins after incubation of 14 - 18 days, except for the fastest growing species which was described after 7 days and the slowest growing species which was described after four weeks. However, colony appearance and colour was initially determined after 6 - 8 days incubation. Further morphological and colour changes which occurred as colonies aged, were followed by examining the colonies at weekly intervals for approximately three months. Thus, descriptions referring to a colony as "when young ..." were prepared after one week of growth, and any changes which occurred in colonies older than three weeks, are denoted by "on aging ...". However, when the colony characteristics did not change over time, only its appearance during the third week of growth is reported. Using this approach one can follow the changes in colouration of the colonies as they age.

D. The texture of colonies and the nature of conidiophores origination is described according to Gams (1971, p. 6). Colonies, or parts thereof, are considered: (1) phalacrogenous when the

conidiophores arise from the submerged or surface hyphae; (2) nematogenous when they arise from single aerial hyphae; (3) plectonematogenous when they arise from hyphal strands (when the strands are thin, finely plectonematogenous is used); (4) synnematogenous when the conidiophores arise from erect strands. Colonies which consist of abundant aerial mycelium and do not form strands are considered floccose, while in lanose colonies the hyphae are separated into small tuft-like structures, also described as finely tufted. Flat colonies, or colony margins without aerial hyphae are described as appressed.

E. The conidiophores, in many of the species treated herein vary greatly in their complexity. Following Ellis (1971) the term micronematous is used for conidiogenous cells which arise directly from hyphae identical to the vegetative hyphae; semi-macronematous for conidiogenous cells which are borne on short lateral branches (the stem of the conidiophore) but are not significantly different from the vegetative hyphae; macronematous (mononematous if not otherwise specified) refers to the longer, or more complex conidiophores, with a differentiated stem. Macronematous, synnematous refers to synnemata, and macronematous, sporodochial to sporodochia.

F. The branching of the conidiophores is described as a series of branches, the first series arising from the stem, the last series bearing the apical conidiogenous cells.

G. Adelophialide is a phialidic peg, not separated from the hyphal cell by a septum. Such structures which proliferate sympodially or percurrently are referred to as pegs, and produce the conidia in the

same manner as the larger conidiogenous cells.

H. The shapes of conidiogenous cells and conidia have been adapted from Hawksworth et al. (1983, Fig. XVI, 1-47) and Snell & Dick (1971, plates xxvii, xxix, and xxx). Navicular cells are broadest above the base; cylindrical is used rather broadly for conidia with straight sides. Asymmetrical conidia are those where one side is somewhat curved, but the conidium is neither curved enough to be considered allantoid nor broad enough to be considered reniform. The base of a conidium can be pointed (for fusiform conidia), or truncate when the whole base is flat. If (in)distinctly pedicellate, truncate, then the base tapers, often abruptly, to a tiny pedicel which itself is flat (truncate).

TAXONOMY

Acremonium Link, Mag. Ges. naturf. Fr. Berlin. 3:15. 1809

=Cephalosporium Corda, Icon. fung. 3:11. 1839

=Gliomastix Guéguen, Bull. Soc. mycol. Fr. 21:230. 1905

For further synonomy see Gams (1971).

Type species: Acremonium alternatum Link.

Teleomorphic genera: Calonectria de Not., Coniochaeta (Sacc.) Cooke, Emericellopsis van Beyma, Epichloë (Fr.) Tul., Hapsidospora Malloch & Cain, Levispora Routien, Mycoarachis Malloch & Cain, Nectria (Fr.) Fr., Neocosmospora E.F.Sm., Nigrosabulum Malloch & Cain, and Peckiella (Sacc.) Sacc. (=Hypomyces fide Rogerson 1971).

The genus Acremonium is characterized by species which produce hyaline, slow-growing, fine hyphae. From these simple or basitonously branched phialophores develop that give rise to subulate phialides. The phialoconidia they produce are hyaline or pigmented, 1-celled or rarely 1-septate, and aggregate in slimy drops or form dry chains. Usually phialides produced by species of the genus develop indistinct collarettes, and the phialides are neither inflated at their bases, nor thick-walled in the lower half; further, if adelophialides are present, these develop only on the submerged mycelium.

Acremonium has been divided into five sections (Gams 1971; Morgan-Jones & Gams 1982): 1. Section Acremonium (=Simplex W. Gams; type species A. strictum W. Gams) consists of species that have slender,

thin-walled phialides which are smooth in outline below the apex, and these are produced on simple phialophores; 2. Section Gliomastix (Guéguen) W. Gams comprises species whose colonies consist of tough, chondroid hyphae, and the species of this section sometimes produce darkly pigmented phialophores or conidia; 3. Section Nectrioidea W. Gams. Here are arranged species having complex, basitonously branched phialophores which are broadest at the base, and bear phialides that are often wavy in outline below the apex and have well developed periclinal thickenings and collarettes; 4. Section Albo-lanosa Morgan-Jones & W. Gams. The species of this section develop non-fasciculate, abundant, cottony aerial hyphae, from which solitary phialides arise. The colonies are white to yellowish, and the species are anamorphs of members of the Clavicipitaceae. 5. Section Chaetomioides Morgan-Jones & W. Gams. The species herein develop white, yellowish, or olivaceous colonies that are comparatively faster growing and are cottony to funiculose in surface topography. The phialides are short-subulate to slightly lageniform, and bear chains or heads of dacroid conidia each of which have a truncate base. The species are anamorphs of members of the Chaetomiaceae and Thielavia terrestris (Apinis) Malloch & Cain, and synanamorphs of Humicola Traaen, Trichocladium Harz, and Botryotrichum Sacc. & Marchal.

Each section is generally believed to have a defined set of central characters, but Samuels (1976b) felt certain species were intermediate between the sections Acremonium and Nectrioidea; this obscured the distinction between these sections. Gams (1978) clarified the reasons

for including members of the section Gliomastix in the genus Acremonium, a decision which had been questioned by many. He furthermore erected a separate genus, Sagenomella W. Gams, for species with thin-walled hyphae and pigmented, catenate conidia with connectives on both ends. Some of these species were originally part of the section Gliomastix, but the nature of their conidial chains (connected) differed from that of other members of Acremonium and it was felt more appropriate to accommodate them in a separate genus. Morgan-Jones & Gams (1982) established the section Albo-lanosa for those species resembling representatives of the genus Verticillium Nees sect. Prostrata W. Gams, but whose phialides are always solitary and never arranged in verticils. In so defining this section they stressed that some phialides in verticils were always present in each Verticillium species; if such are lacking, the species should be placed in Acremonium.

Except for their faster growth, the microconidial states of many species assigned to Fusarium Link and Cylindrocarpon Wollenweb. possess characters similar to species of Acremonium sect. Nectrioidea; these have not been included in Acremonium. The micronematous synanamorphs of Humicola, Trichocladium, and Botryotrichum are now a part of the section Chaetomioides.

Members of the genus Acremonium are quite diverse and known from a wide variety of substrata. Many are saprophytic and are found in soil or on decaying plant remains; others are saprophytes or parasites on other fungi. A few species are plant pathogens, e.g. Nectria fuckeliana C. Booth (microconidial state) and A. tsugae W. Gams, both having been

isolated from conifers, and N. rishbethii C. Booth which was isolated from insect galleries. Several Acremonium species are endophytes of grasses, a few are human pathogens, but only one species is listed as an insect pathogen (Gams 1971).

The genus Acremonium has over 100 species; Hawksworth et al. (1983) estimated their number at 103, with those described since bringing the number to about 120. In addition to those formally described, species of several ascomycetes have Acremonium anamorphs which have not been named (Cannon & Hawksworth 1984; Samuels 1976b; Samuels et al. 1984). Others have named such anamorphs (Morgan-Jones & Gams 1982; Samuels 1973; Stolk & Orr 1974; Ueda & Udagawa 1983), giving them the status of a species, and a degree of independence from their teleomorphs.

Acremonium berkeleyanum (P. Karst.) W. Gams, Neth. J. Pl. Path. 88:76. 1982 Fig. 1. a-h.

≡Verticillium berkeleyanum P. Karst., Meddel. Soc. Fauna Flora Fennica 18:64. 1891

=Acremonium butyri (van Beyma) W. Gams, Cephalosporium-artige Schimmelpilze (Hyphomycetes) 126. 1971

≡Tilachlidium butyri van Beyma, Zentbl. Bakt. ParasitKde (Abt.II) 99:390. 1938

Teleomorphs: Nectria vilior Starb., Bih. Kongl. Svenska Vetensk.-Akad. Handl. 25, Afd. III, No. 1:28. 1899

=Nectria viridescens C. Booth, Mycol. Pap. 73:89. 1959

and Nectria berkeleyana (Plowr. & Cooke) J. M. Dingley, Trans. R. Soc. N.Z. 79:183. 1951

≡Hypomyces berkeleyanus Plowr. & Cooke, Grevillea 2:48. 1882

For further synonymy see Samuels (1976a), Gams (1971) and Domsch et al. (1980).

Colonies attaining a diameter of 21 - 28 mm in 12 days at 20°C in darkness on MEA.YE. When young, colonies yellow to light grey to white (2.5Y $^{7}/_{6}$, 5Y $^{7}/_{2}$ to $^{8}/_{2}$) and plectonematogenous in the centre, becoming yellow to pale yellow (2.5Y $^{7}/_{6}$ to 5Y $^{7}/_{3}$) and nematogenous towards the margins where the yellow tinted surface of the medium (which may reflect light) is sparsely covered with mycelium. If the colonies are exposed to light, the conidial droplets which are colourless to white in dark-grown cultures, become pinkish white (5YR $^{8}/_{2}$). Colonies finally

Fig. 1. Acremonium berkeleyanum (P. Karst.) W. Gams
(isolates: 9N (UM74-90), 129N (UM74-36), SC0080)

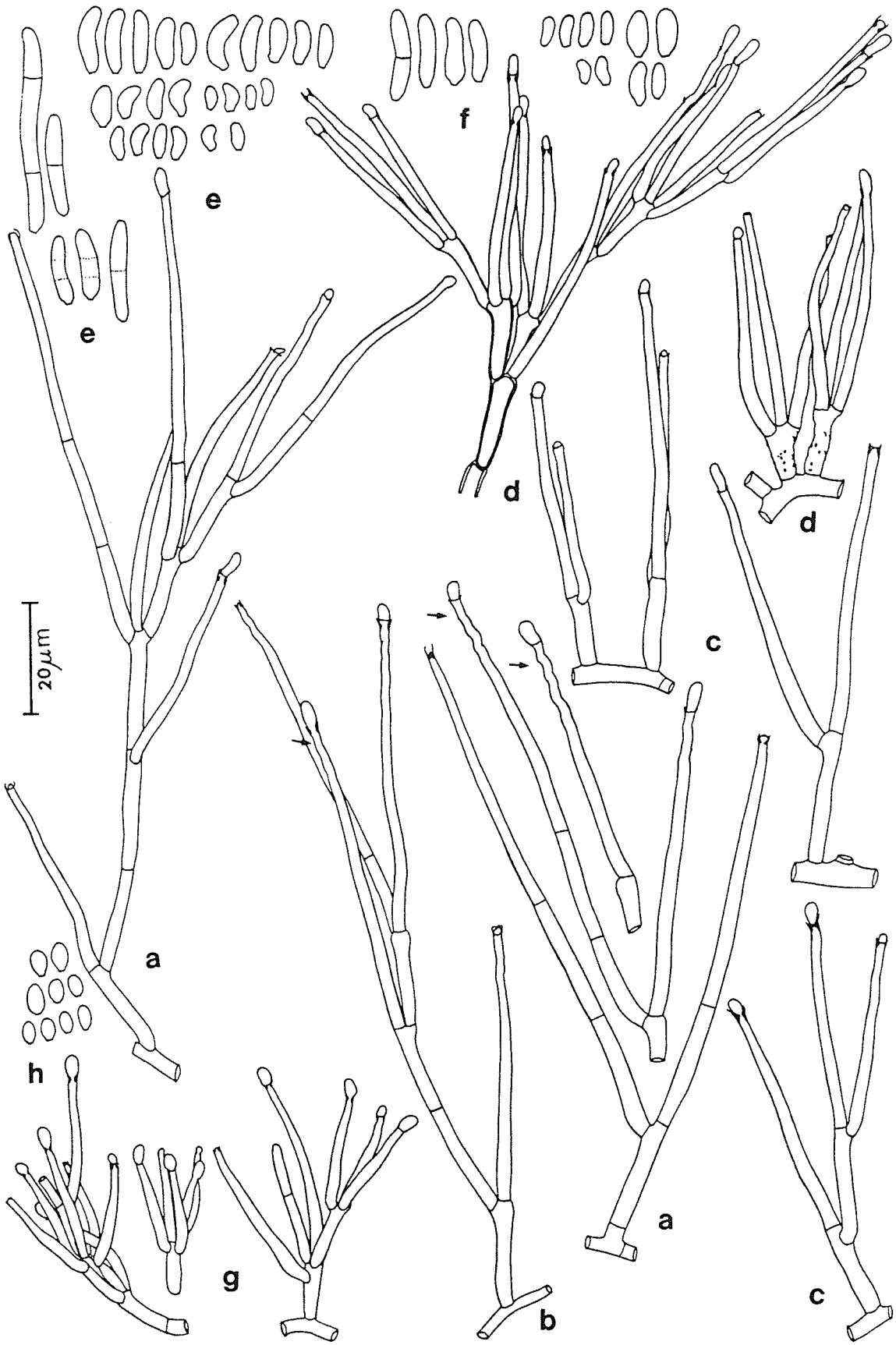
a-d. Phialophores; undulate apices of phialides («-); convergent phialides (d).

e-f. Phialoconidia.

g. Portions of phialophores from sporodochia; short phialides.

h. Phialoconidia from sporodochia.

Isolates as illustrated: 9N (UM74-90): a, e.
129N (UM74-36): c, d, f.
SC0080: b, g, h.


e
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a
c

becoming olive to light olive brown (5Y $^{5}/_{3}$ to 2.5Y $^{5}/_{4}$), but sometimes reddish brown (5YR $^{5}/_{3}$); on aging the colonies may (1) become strongly synnematogenous developing thick, hyaline to brown strands with pinkish white (5YR $^{8}/_{2}$) apices, with the strands covered by conidiophores, or (2) they may form pink (5YR $^{8}/_{4}$) sporodochia; medium surface from yellow to reddish brown to dark reddish brown (2.5Y $^{7}/_{6}$, 5YR $^{4}/_{3}$ to $^{3}/_{3}$). In reverse, when young, colonies are olive yellow (2.5Y $^{6}/_{6}$ to 5Y $^{6}/_{6}$) but gradually becoming brown (10YR $^{4}/_{3}$) and finally dark reddish brown to dusky red (5YR $^{2}/_{2}$, $^{3}/_{2}$ to 10R $^{3}/_{3}$). Odour indistinct and an exudate is present in young colonies as small, clear drops. Colonies grown in alternating light and darkness are zonate. A yellow to reddish-brown pigment diffuses into the medium and this is sometimes followed by retardation of growth. The pigment appears as minute, densely aggregated drops of a yellow, oily-appearing substance in the medium between the submerged hyphae. Hyphae hyaline or yellow; smooth-walled or partly encrusted with yellow deposits on their surface; 1.8 - 4.8 μm in diameter; on aging, some hyphae may become light brown, up to 7.0 μm in diameter and often constricted at the septa; when funiculose, the strands are 8 - 180 μm in diameter. Chlamydospores were not seen. Phialophores semi-macronematous to macronematous, and basitonously branched; hyaline, smooth-walled; stem short, usually consisting of a single basal cell but sometimes of 2 or 3 cells; branches and phialides are divergent. Semi-macronematous phialophores vary from being simple with 1 - 2(3) terminal phialides (Fig. 1. a,c) to more complex forms with several series of branches and phialides wherein the lateral

branches form the apex (cymose branching) as the main axis is earlier terminated by a phialide (Fig. 1. a,b,d); 60 - 220 x (1.8)2.4 - 4.0(4.3) μm. The macronematous phialophores sometimes arranged in sporodochia; the lower branches then divergent, but more densely branched apically and terminating in short metulae each of which gives rise to 3 - 5 short phialides (Fig. 1. g). Conidiogenous cells monophialidic; hyaline to yellow and smooth-walled; integrated or discrete; subulate, often wavy in outline below the apex (Fig. 1. a,b «-); 16 - 70 x 1.7 - 3.2 μm tapering to 1.2 - 1.8(2.0) μm at the apex; collarette indistinct, 0.5 - 1.5 μm long. Phialoconidia aggregate in slimy drops; 1-celled but rarely 1 to 2-septate; hyaline and smooth-walled; usually slightly curved, oblong-elliptical to oval; apex rounded and base indistinctly pedicellate or truncate. Ameroconidia measuring (3.5)4.0 - 13.5 x (1.7)2.0 - 3.4(4.4) μm (Fig. 1. e,f); septate conidia measuring 13.0 - 19.0 x 2.8 - 4.0 μm (Fig. 1. e,f).

HOSTS: Gnathotrichus retusus Lec., Pinus sylvestris L.

CULTURES EXAMINED: **Norway:** 9N (UM74-90), isolated from P. sylvestris, near As, Akershus, collected in May 1974; 129N (UM74-36), isolated from P. sylvestris, near Ski, Akershus, collected in October 1973. **United States:** SC0080, washed from the head of G. retusus, caught in Andrews Experimental Forest, Oregon, 7 November 1986.

A. berkeleyanum is a highly variable species that has been recorded

from a variety of substrata. Its teleomorph, Nectria berkeleyana (Plowr. & Cooke) J. M. Dingley, is reported from Stereum species in New Zealand (Dingley 1951), and in Europe, and the USSR (Gams & van Zaayen 1982; Samuels 1976a). The other teleomorph, Nectria vilior Starb. (as N. viridescens C. Booth), is reported from various deciduous and coniferous trees and decaying wood in Europe and Canada (Booth 1959; Gams 1971).

A. berkeleyanum has been isolated from a variety of soils, from butter, raw milk, leaves, dung, and an insect (Domsch et al. 1980; Gams 1971; Tubaki 1965). In addition to occurring on Stereum species, it has been found associated with a variety of other fungi (Fergus 1978; Gams 1971; Hawksworth 1981) and Rudakov (1978) considered A. berkeleyanum to be a facultative necrotroph.

Previous associations with stained wood were noted by Sasaki & Yoshida (1971) who isolated A. berkeleyanum from brown stained Betula maximowiczii Regel. and Tilia japonica Simk. wood in Japan. Nakashima (1971) recovered it from a few young females of the ambrosia beetle Crossotarsus niponicus Blandford in Fagus crenata Blume. In the latter case it was one of the fungi which grew after the beetles had been partially surface sterilized; that suggests the beetles may have protected these fungi from adverse conditions, perhaps by storing them in their mycangia. A further record of its association with bark inhabiting insects is that of Carroll (1987) who isolated it from unhatched gypsy moth eggs.

In creating the combination A. butyri, Gams (1971) noted that the

fungus identified by Tubaki (1955) as Cephalosporium mycophilus (Corda) Tubaki (≡Hyalopus mycophilus (Corda) Corda), actually had nothing to do with Corda's organism, but in reality was a misidentified example of A. butyri. A. berkeleyanum (as A. butyri) was also shown to be the anamorphic state of N. viridescens; cultures derived from ascospores of that species (Booth 1959) having produced cultures typical of it (Gams 1971).

Gams (in Gams & van Zaayen 1982) stated that A. butyri is identical to Verticillium berkeleyanum P. Karst., the presumed anamorph of Hypomyces berkeleyanus Plowr. & Cooke (≡Nectria berkeleyana (Plowr. & Cooke) J. M. Dingley), which Samuels (1976a) considered a true Hypomyces species. Thus the new combination Acremonium berkeleyanum (P. Karst.) W. Gams was created. Gams & van Zaayen (1982), however, disagree with Samuels' opinion and follow that of Dingley (1951) who excluded the species from the genus Hypomyces because the ascospores have rounded ends and are therefore typical of the genus Nectria.

While Gams judgement regarding the identity of A. butyri with A. berkeleyanum is not questioned, it is in fact unclear whether A. berkeleyanum is the anamorph of H. berkeleyanus. Clearly Karsten's (1891) opinion was based on an association of V. berkeleyanum with H. berkeleyanus rather than on cultural studies, and Gams (in Gams & van Zaayen 1982) does not specifically state he obtained A. berkeleyanum from ascospore cultures of N. berkeleyana. We are not sure at this point whether anyone has actually made this connection culturally.

Samuels & Dumont (1982) proposed the synonymy of Nectria

viridescens with N. vilior based on their identical anamorphs. There is, however, a consistent difference between north temperate and tropical/subtropical (including New Zealand) collections of the fungus, i. e. the ascospores of the former group are finely spinulose but those of the latter are distinctively tuberculate (Samuels pers. comm.). Nectria cosmariospora Ces. & de Not., a species that resembles N. vilior, has tuberculate ascospores which are larger than those of the latter. Its anamorph was treated by Gams (1971) as Verticillium olivaceum W. Gams.

As none of the three isolates examined in this study produced either protoperithecia or perithecia, nor were they derived from ascospores or found directly associated with the teleomorph in nature, following Domsch et al. (1980) the anamorph name is used.

Although one of the three isolates identified herein as A. berkeleyanum (isolate 129N) produces only a very limited amount of pigment, remains beige with pale yellow conidial drops, and has more compactly arranged phialides (Fig. 1. c,d) than the other two isolates, the conidial shape and branching pattern of the conidiophores of all the isolates resemble those described for A. berkeleyanum. Isolate SC0080 is the most robust of the three, and its colonies become reddish brown with age. When the isolates herein assigned to A. berkeleyanum form sporodochia or conidiophores highly branched at the apex, the individual phialides are usually slightly convergent, shorter, and abruptly narrow to a thin neck; the neck is about $^1/_3$ of the phialide. Conidia formed on such phialophores (Fig. 1. h) are often more oval than cylindrical,

but fall within the variety of shapes and sizes reported for the species (Gams 1971; Booth 1959).

A. berkeleyanum, is most likely the correct species for these isolates, as it is one of the yellowish olive species belonging to the section Nectrioidea W. Gams. Three other species to which these isolates appear to have some similarities are Tilachlidium brachiatum (Batsch: Fr.) Petch, Acremonium cymosum W. Gams, and Verticillium olivaceum W. Gams. However, the isolates examined here grow more rapidly than T. brachiatum, and in spite of their plectonematogenous to synnematogenous sporulation, the strands that they produce are clearly not true synnemata as are found in T. brachiatum. A. cymosum differs in producing more abundant aerial mycelium, and in having a much delayed onset of conidiogenesis in comparison to these isolates. And since these isolates produced conidiophores which were primarily basitonously branched and the basal segments thin-walled, they could be separated from the otherwise rather similar V. olivaceum.

A. berkeleyanum is known as a mycophilic species, often found growing on larger lignicolous fungi. However, on a few occasions it has been found in associations with insects, including those which are known to have a part of their life-cycle in or on trees. It has been isolated at least once from stained wood and several times from decaying wood. Therefore, finding A. berkeleyanum in bark beetle galleries should not be surprising.

Acremonium curvulum W. Gams, Cephalosporium-artige Schimmelpilze (Hyphomycetes). 57. 1971 Fig. 2. a-e.

Colonies attaining a diameter of 32 - 36 mm in 12 days at 20°C in darkness on MEA.YE. When young, colonies are white (10YR $^{8}/_{2}$) and plectonematogenous in the centre with thin flexuous strands, and a white (2.5Y $^{8}/_{2}$) margin which is appressed and phalacrogenous; the mycelium is finally covered by slimy conidial masses ranging from discrete sectors in mainly plectonematogenous, white (10YR $^{8}/_{2}$) colonies, to the whole surface in those colonies which are ultimately yellow (2.5Y $^{7}/_{6}$) in colour. Upon exposure to light the slimy areas become pink (5YR $^{7}/_{3}$ to $^{8}/_{4}$), with the plectonematogenous areas being somewhat lighter (5YR $^{8}/_{3}$). Conidia aggregate in clear droplets at the apex of individual phialides. In reverse, the colonies are very pale brown to white (10YR $^{8}/_{3}$ to $^{8}/_{2}$) when grown in darkness, but become pink (5YR $^{8}/_{4}$ to $^{7}/_{4}$) upon exposure to light. A sweet, yeasty odour is present. Minute, evenly distributed colourless droplets, about 0.5 - 0.7 µm in diameter, of an oily-appearing substance are found in the agar medium within the colonies. Hyphae hyaline; walls smooth and sometimes thickened; 0.9 - 4.0(4.8) µm in diameter; when funiculose, the strands are 5 - 20 µm in diameter, and consist of fairly wide hyphae. Chlamydospores were not seen. Phialophores micronematous or semi-macronematous; hyaline and smooth-walled; with 1-3 phialides developing from a 10 - 18.5 x 2.4 - 3.6 µm basal cell; 45 - 75 µm high including the basal cell (Fig. 2. a,b). Conidiogenous cells monophialidic; hyaline and

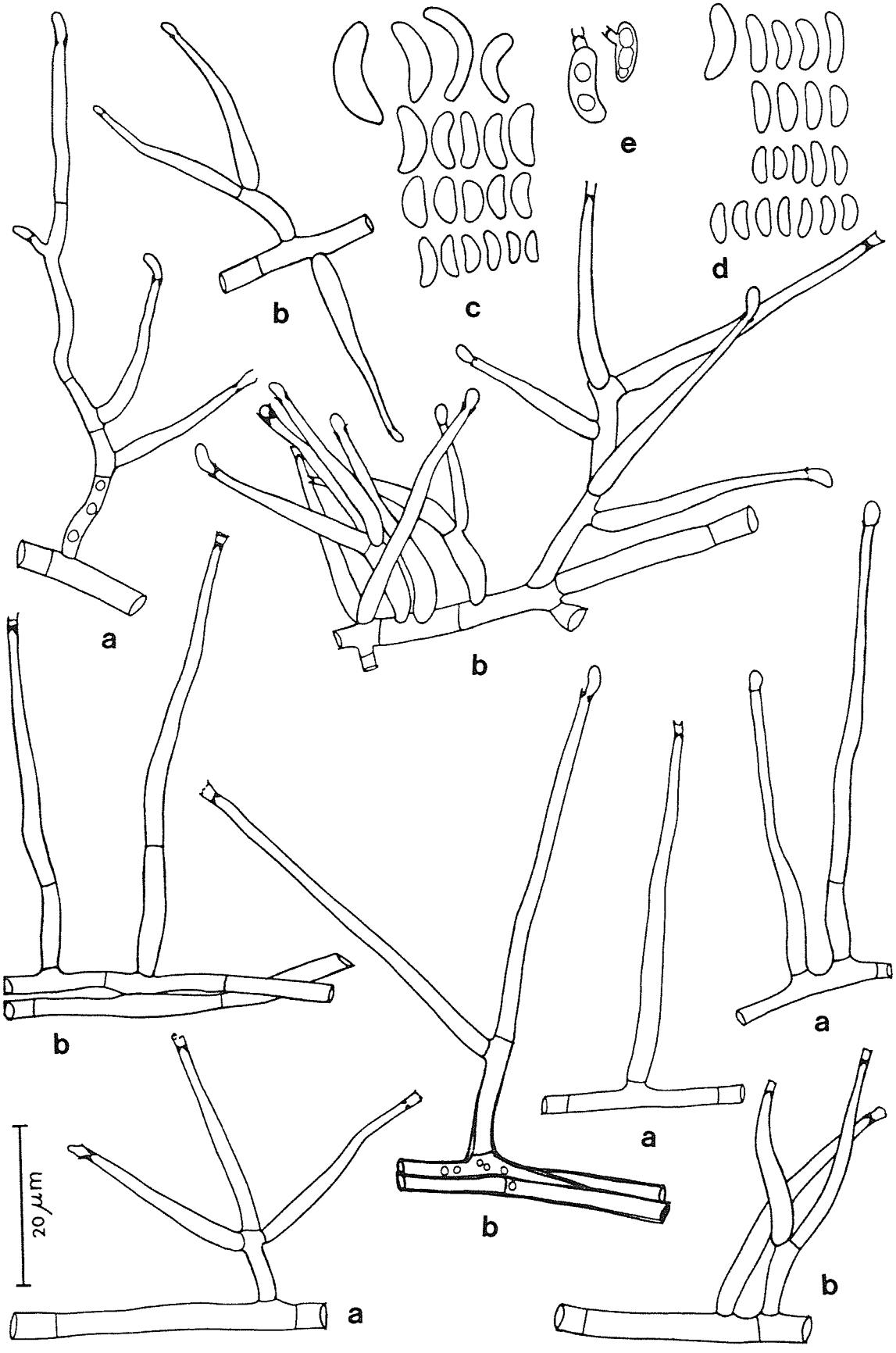
Fig. 2. Acremonium curvulum W. Gams
(isolates: 42a, 48, 98a)

a-b. Phialophores.

c-d. Phialoconidia.

e. Phialoconidia with adelophialides producing secondary conidia.

Isolates as illustrated: 42a: a, d.
48: b, c.
98a: e.


a
b
c
d
e
b
b
a
b
a
a
b
a
b
20 µm

smooth-walled; integrated or discrete; subulate; 13 - 52 x 1.7 - 2.6(2.9) μm tapering to 0.9 - 1.5 μm at the apex; or when submerged in the medium adelophialidic and 2.4 - 4.0 x 1.3 - 1.6 μm; collarette indistinct and 1.0 - 2.8 μm long. Phialoconidia aggregate in slimy drops; 1-celled, hyaline, and smooth-walled; curved and almost orange section-shaped in side view; 4.0 - 7.5(10.5) x (1.4)1.6 - 2.4(3.0) μm (Fig. 2. c,d). Similar appearing secondary conidia develop from phialidic pegs on swollen primary conidia (Fig. 1. e).

HOSTS: Pinus elliottii Engelm., Pinus radiata D. Don.

CULTURES EXAMINED: **New Zealand:** 42a, isolated from P. radiata, Compartment 37, Woodhill State Forest, Auckland, collected 4 May 1982; 48, isolated from P. radiata, Compartment 75, Woodhill State Forest, Auckland, collected 14 May 1982; 89a, isolated from P. radiata, off Road 41, Whangapoua State Forest, Coromandel, collected 19 May 1982; 68, 68bi, 68bii, isolated from P. elliottii, Camp Gully Rd., Tairua State Forest, Coromandel, collected 21 May 1982.

A. curvulum has been isolated from a variety of soil types, a water sample, the leaves of Metrosideros collina (Forst.) Gray var. polymorpha (Gaud.) Rock, and a rust infected Lolium sp. It is known from Europe, Nigeria and the U.S.A. (Baker et al. 1979; Gams 1971; Huang & Schmitt 1975; Wallace & Dickinson 1978). Furthermore, Andrews et al. (1982)

recovered it from 6 - 94 % of the Eurasian water milfoil plants, Myriophyllum spicatum L., sampled from 9 lakes in Wisconsin, U.S.A., where it was both epiphytic and endophytic on healthy plants, and pathogenic to those under stress.

A. curvulum has been isolated from grassland soil in New Zealand (Gams 1971).

A. curvulum was classified in the section Acremonium (=Simplex) by Gams (1971), and its curved or sickle-shaped conidia formed in heads, and the yellow-orange colony colour were the characters used to separate it from other species of that section. A morphologically similar species is the tropical A. recifei (Leão & Lôbo) W. Gams, which Gams assigns to the section Nectrioidea; it differs from A. curvulum by forming branching phialophores and producing less pigment.

No major differences were found between the six New Zealand isolates; each produced slime covered areas, some more than others. According to Gams (pers. comm.), the New Zealand isolates have unusually wide hyphae and might therefore represent a distinct group within A. curvulum which he now considers to be an aggregate species.

This appears to be the first record of A. curvulum's isolation from bark beetle galleries, and from two of the four wood samples from which it was isolated, no other species were recovered. Literature reports suggest this fungus occurs most frequently in wet habitats, and therefore might be able to grow in wood that has a high water content; such high water content might hinder growth of other species.

Acremonium rollhansenii spec. nov. prop. Fig. 3. a-g.

ETYMOLOGY: Named in honour of Finn and Helga Roll-Hansen, and their distinguished contributions to forest pathology.

Colonies attaining a diameter of 45 - 52 mm in 12 days at 20°C in darkness on MEA.YE. Pale yellow (2.5Y $^{8}/_{4}$ to $^{8}/_{6}$, 10YR $^{8}/_{6}$) and plecto-nematogenous to nematogenous in the centre where phialophores cover the surface of the medium; becoming reddish yellow (5YR $^{7}/_{8}$ to 7.5YR $^{7}/_{8}$) towards the margin where the aerial mycelium is sparser, and the reddish yellow tinted surface of the medium shines through; the colonies become mealy in texture when branched phialophores develop from the aerial mycelium. At first, conidia are formed in small, white to pale yellow, slimy drops which are relatively dry, but later often develop in thin, white chains at the apex of the individual phialides. In reverse, the yellowish red to reddish yellow (5YR $^{5}/_{8}$ to $^{6}/_{8}$ then 7.5YR $^{7}/_{8}$), pigment is more concentrated in the submerged mycelium than in the medium. Colonies sporulate more, but grow at reduced rates (34 mm in 12 days at 20°C) in alternating light and darkness. Odour mildly aromatic, or fruity. An exudate is present on the aerial mycelium as small to medium sized, clear to pale yellow drops. Hyphae hyaline to yellow; smooth at first, but on aging often becoming verruculose to verrucose, and sometimes appearing to be encrusted with a yellow material or flaky on the surface; (1.5)2.0 - 6.5 μm in diameter; when funiculose, strands are 8 - 25 μm in diameter and consist of individual hyphae 3.5 - 5.8(7.0) μm

Fig. 3. Acremonium rollhansenii spec. nov. prop.
(isolate: 109N (UM74-17))

a. Hyphae, one with a roughened surface, the other comprised of clavate hyphal cells.

b-c. Phialophores ranging from being simple and positioned at the apex of aerial hyphae (c) to more complex forms (b); proliferated phialides (≪-).

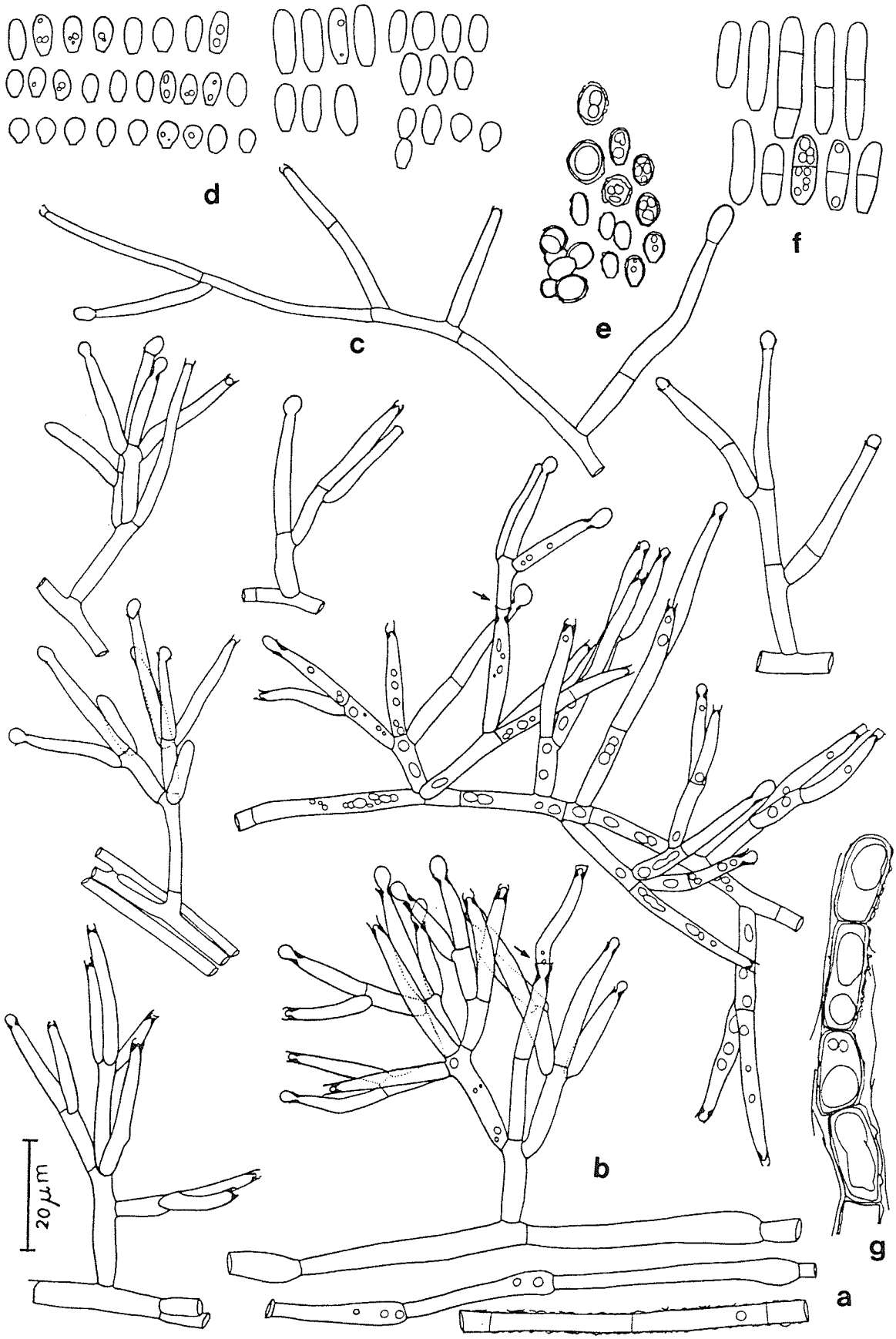
d. Phialoconidia; oblong and subglobose.

e. Inflated phialoconidia from aging colonies, surface rough and flaky, and contain large oil drops; some phialoconidia are strongly aggregated.

f. Germinating, septate conidia.

g. Inflated, thick-walled hyphal cells from the submerged mycelium of an aged colony.

Isolate as illustrated: 109N (UM74-17): a-g.


d
c
e
f
b
a
g
20 µm

wide that frequently anastomose. Older hyphae often produce additional septa, with the individual cells then often inflated and thick-walled, and up to 10 μm in diameter (Fig. 3. g). Hyphae composed of a series of clavate cells (Fig. 3. a) may occur. Chlamydospores were not seen, but the inflated hyphal cells which become thick-walled may function as such. Phialophores macronematous to semi-macronematous and micronematous; hyaline to yellow; smooth-walled to verrucose; usually consisting of a single basal cell but occasionally two basal cells are formed; the basal cells are 14 - 28 μm long and sometimes inflated. When the phialophores are simple, 1 - 3 phialides may arise from the basal cell, but most phialophores branch several times thus forming 1 - 8 series of phialides and branches, and measure 45 - 125 x 2.7 - 6.0 μm. The main axis is usually terminated early by a longer terminal phialide. From below the terminal phialide arise 1 - 2(3) divergent side branches which are also terminated early by a phialide. The branch continues to elongate by producing further lateral branches. At each branching point 1 - 2 phialides may be produced instead of branches, and as the phialophore branches further, the elements become shorter. Each branch of the ultimate series gives rise to 1 - 3(4) phialides. Thus while the complex phialophores are not very tall they are widely spread laterally (Fig. 3. b). Conidiogenous cells monophialidic; hyaline to yellow and smooth-walled; integrated or discrete; the long terminal phialides are sometimes subulate, but most phialides are short-subulate; 12 - 36 x 2.4 - 3.2(3.5) μm tapering to 1.6 - 2.0(2.2) μm at the apex and occasionally proliferating terminally (Fig. 3. b «-); collarettes

indistinct, 0.7 - 2.0 μm long, with a well developed periclinal thickening. The phialoconidia aggregate in drops or form false chains; 1-celled, hyaline, and smooth-walled; dimorphic, with both subglobose to obovate, and oblong-elliptical forms produced; 4.2 - 9.0(16.0) x (2.8)3.2 - 3.7(4.4) μm; apex rounded, but the base usually distinctly pedicellate or truncate (Fig. 3. d); on aging, the conidia may become coherent due to the presence of an apparently sticky material on their surfaces. When these conidia break apart, their walls appear rough and flaky; other aged conidia become inflated, thick-walled, yellow, and filled with oil; 6.5 - 8.0 x 4.8 - 7.0 μm (Fig. 3. e). Germinating conidia become inflated, often 1 - 2 septate, and are 10 - 23 x 3.3 - 4.3 μm (Fig. 3. f).

HOST: Pinus sylvestris

CULTURE EXAMINED: **Norway:** 109N (UM74-17), isolated from P. sylvestris, near Ås, Akershus, collected in October 1973.

A. rollhansenii clearly belongs in the section Nectrioidea of the genus Acremonium because: (1) its phialophores are extensively branched; (2) the conidia are hyaline; (3) the phialides are thin-walled; and (4) the colonies are easy to cut through. Employing Gams (1971) key to this section, the only species similar to A. rollhansenii is A. tsugae W. Gams.

A. rollhansenii does resemble A. tsugae in having divergent,

cymosely branched and laterally expanded phialophores which bear short-subulate phialides with short collarettes and distinctive periclinal thickenings. However, A. rollhansenii has a mild aromatic odour, best described as fruity, which is quite different from the soapy (Toiletteseife) odour that Gams (1971) reports is produced by colonies of A. tsugae growing on malt agar. A. rollhansenii develops less pigmented colonies than A. tsugae (W. Gams pers. comm.) and the conidia of the former often adhere in false chains in addition to the slimy drops typical of A. tsugae. The broadly obovate to subglobose conidia produced by A. rollhansenii are slightly larger in dimension than those of that type reported by Gams (1971) for A. tsugae, (4.3 - 6.5 x (2.8)3.2 - 4.0(4.5) and 3.7 - 5.6 x 2.3 - 3.5 μm respectively). However Denyer (1953), who provided a cultural description of A. tsugae as a Cephalosporium sp., said it had conidia which were 4.1 - 6.7 x 2.4 - 4.5 μm; Denyer's material was included by Gams (1971) in his study of the species. No oblong-elliptical conidia were reported in the type specimen by Gams, but Denyer reported "occasional cylindrical conidia" amongst the primarily oval to obovate ones. However, these cylindrical conidia were smaller than those found in A. rollhansenii. A. rollhansenii does produce the obovate conidia more abundantly than the longer oblong-elliptical conidia, but the longer conidia (7.0 - 16.0 μm long) are consistently present. Denyer (1953) found clavate hyphal cells in his Cephalosporium species; such cells were also present in A. rollhansenii.

While A. rollhansenii resembles A. tsugae in most major features,

it grows faster, produces less pigment, and its conidia adhere not only in moist drops but also regularly form chains. The surface of the conidia becomes flaky or irregularly verrucose, presumably due to drying of the remnants of some material surrounding the conidia. Perhaps the most distinguishing feature is the presence of much longer conidia than reported for A. tsugae.

Acremonium strictum W. Gams, Cephalosporium-artige Schimmelpilze (Hyphomycetes). 42. 1971 Fig. 4. a-e.

=Cephalosporium acremonium sensu auct. plur. non Corda.

Colonies attaining a diameter of 22 - 28 mm in 12 days at 20°C in darkness on MEA.YE. White (10YR $^{8}/_{2}$) and mostly phalacrogenous with a nematogenous centre and very limited aerial mycelium, or white (2.5YR $^{8}/_{0}$ to 5YR $^{8}/_{1}$) and plectonematogenous with a thin phalacrogenous zone at the appressed margin comprised of curved hyphal strands; the surface, especially the centre, covered with tomentose aerial mycelium. In light the colonies become light reddish brown or pink to reddish yellow (2.5YR $^{6}/_{4}$ or 5YR $^{7}/_{4}$ to 5YR $^{7}/_{6}$). At first the conidia are aggregated in droplets at the apex of individual phialides, but later such droplets coalesce forming slimy masses which make the mycelium appear moist and the surface of the medium slimy. In reverse, cultures are white to pale yellow (2.5Y $^{8}/_{2}$ to $^{8}/_{4}$) when grown in darkness, but pink to reddish yellow (5YR $^{7}/_{4}$ to $^{7}/_{6}$) when illuminated. Colonies are easy to cut through. Odour lacking. Hyphae hyaline, smooth, thin-walled, 0.8 - 2.5(3.2) µm in diameter; when funiculose, the strands are 4 - 65 µm in diameter, and consist of thin parallel hyphae. Chlamydospores were not seen. Phialophores micronematous or semi-macronematous; hyaline, smooth-walled; 16 - 69 x 1.4 - 2.0(2.2) µm (Fig. 4. a,b); usually bearing a single phialide which may be subtended by 1 - 2 basal cells; very rarely 2 phialides arise from the same basal cell. Conidiogenous cells monophialidic; integrated or discrete; hyaline and

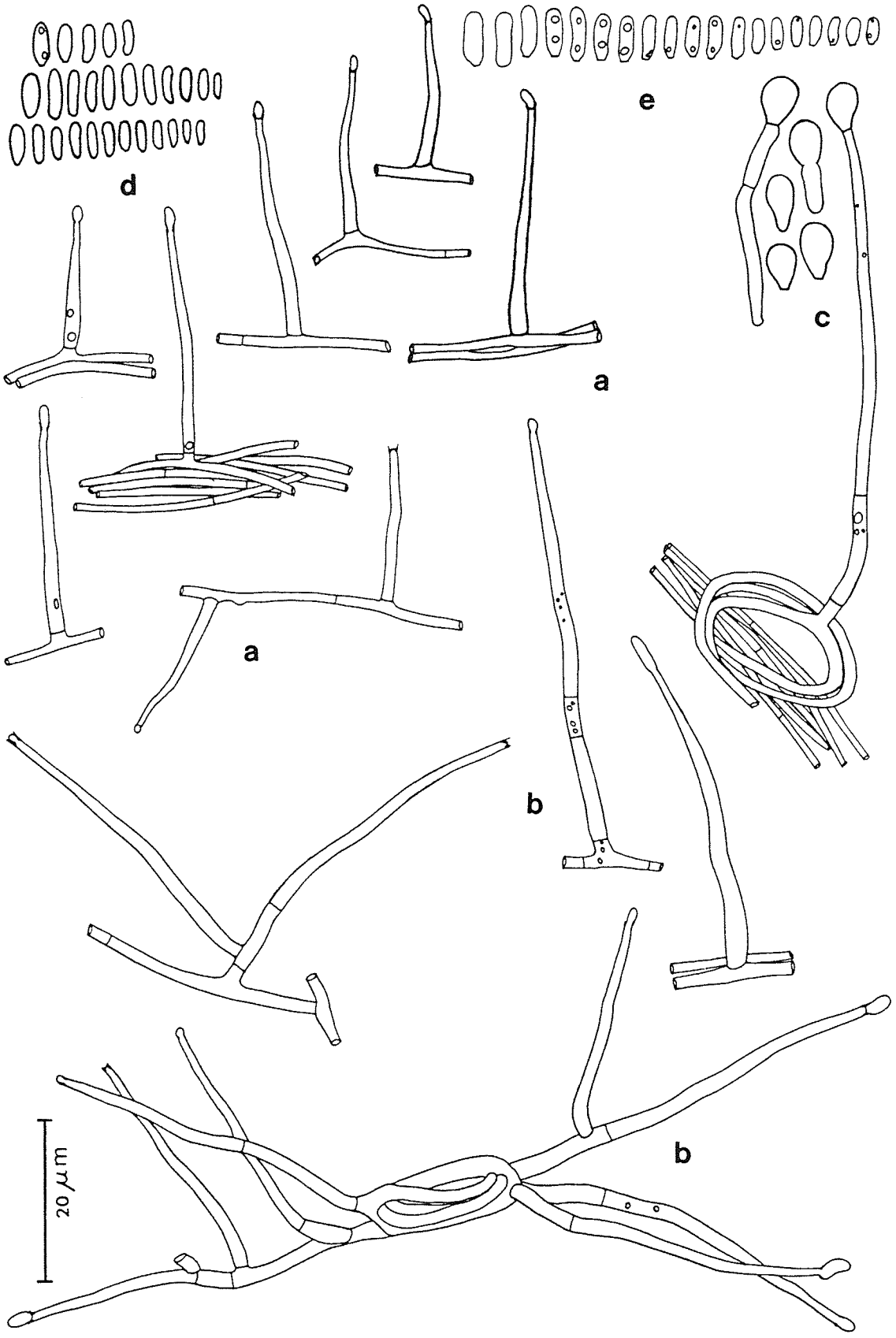
Fig. 4. Acremonium strictum W. Gams
(isolates: 51ci, 183c')

a-b. Phialophores; simple.

c. A phialide producing an inflated conidium and inflated, germinating conidia.

d-e. Phialoconidia.

Isolates as illustrated: 51ci: b, c, e.
183c': a, d.


d
e
c
a
a
b
b
20 µm

smooth-walled; subulate; 16 - 45 x (1.4)1.5 - 1.9(2.4) μm tapering to 0.8 - 1.0 μm at the apex; collarette usually lacking. Phialoconidia aggregated in slimy drops; 1-celled, hyaline, and smooth-walled; straight or slightly curved and chiefly cylindrical, but also oval or ellipsoidal; 3.0 - 6.5(8.0) x 1.0 - 2.0(2.4) μm; apex rounded, base either rounded or indistinctly pedicellate (Fig. 4. d,e). Larger, subglobose, obovate to obpyriform conidia, 5.5 - 7.0 x 4.0 - 4.8 μm (Fig. 4. c), were sometimes present.

HOSTS: Cupressus macrocarpa Hartw., Pinus taeda L.

CULTURES EXAMINED: New Zealand: 51ci, isolated from C. macrocarpa, Compartment 75, Woodhill State Forest, Auckland, collected 14 May 1982; 183c', isolated from P. taeda, Compartment 21, Riverhead State Forest, Auckland, collected 11 July 1982.

A. strictum is one of the most variable of the Acremonium species (note the variation in the conidial shape) which may be a reflection of the extremely diverse habitats, substrata, and hosts from which it has been isolated (Baker et al. 1979; Brandsberg 1969; Domsch et al. 1980; Dunn & Baker 1983; Gams 1971; Hayes 1965; Huang & Schmitt 1975; Visser et al. 1987). It is also an ubiquitous saprophyte on many senescent fungi (Hawksworth 1981), and has been reported both as a mycoparasite (Kenneth & Isaac 1964) and a competitive inhibitor of a mycoparasite (Gandy 1979).

Sieber (1989) reported A. strictum was one of the rarer endophytes in twigs of two coniferous tree species, and it has been isolated from stained wood (Gams 1971). And under the name Cephalosporium acremonium, it was isolated from a few females of the ambrosia beetle Crossotarsus niponicus Blandford in Fagus crenata Blume. These beetles presumably stored it in their mycangia (Nakashima 1971).

In New Zealand, Cephalosporium acremonium has been reported from different soil types (Ruscoe 1973; Thornton 1958, 1960, 1965) and from leaves of Nothofagus truncata (Col.) Ckn. (Ruscoe 1971).

Gams (1971) showed that the name Cephalosporium acremonium Corda, the type species of Cephalosporium Corda, could not be fixed, and he took up Acremonium Link for the majority of those species previously assigned to Cephalosporium. To assist in clarifying the identity of fungi previously assigned to C. acremonium, he erected A. strictum for those entities which typically lack chondroid coherent hyphae, and possess conidiophores with slender, unbranched phialides (i.e. simple phialophores) which are regular in outline and lack any wall thickening. The current limits of Acremonium were further discussed in Domsch et al. (1980), and the collections assigned to A. strictum herein generally agree with the description found in the latter publication.

Minor differences were noted between the two isolates obtained from New Zealand. Culture 183c' tended to have smaller conidia on average than 51ci, and the latter also occasionally produced inflated conidia which remained attached to the phialide apex or, when loose, appeared to be germinating (Fig. 4. c). Gams (1971) reported globose conidia were

formed in many of the isolates of A. strictum he examined, but as he considered them to be abnormal he did not give their dimensions.

Although it did not possess any unique distinguishing morphological features, Gams (1971) made A. strictum the type of the section Simplex; a section now a synonym of sect. Acremonium (Gams 1975).

Since A. strictum possesses very few morphological characteristics, other species which produce straight, cylindrical conidia on simple phialophores can be separated from it by the various additional structures they produce. These species are Monocillium tenue W. Gams which has thick-walled phialides and tough colonies; A. kilense Grütz which produces a brown pigment and chlamydospores but not too many conidia; and A. sclerotigenum (F. & R. Moreau ex Valenta) W. Gams which produces sclerotia (Gams 1971; Domsch et al. 1980).

There are only a few specific reports of A. strictum having been isolated from stained wood or from insects. However many studies involved in the isolation of fungi from insects or their galleries do list "Cephalosporium spp." amongst the recovered fungi (Baker & Norris 1968; Moore 1971; Shigo 1958) apparently without any attempt at specific identification. A. strictum could have been amongst such unidentified entities, and therefore its association with stained wood or insects could be more common than currently believed.

Aphanocladium W. Gams, Cephalosporium-artige Schimmelpilze (Hyphomycetes), 196. 1971

Type species: Aphanocladium album (Preuss) W. Gams

Teleomorphs are unknown or wanting.

The genus Aphanocladium was erected by Gams (1971) to accommodate A. album (Preuss) W. Gams (≡Acremonium album Preuss) and two additional species, A. aranearum (Petch) W. Gams and A. meliolae (Hansf.) W. Gams. It was to be characterized by species producing white, floccose colonies, and phialides arising singly or in verticils from the aerial hyphae. While the majority of the phialides were noted as being reduced and peg-like, some were seen to have inflated bases which narrowed to very thin necks, and were delimited from the subtending hyphae by septa. The conidia were described as being 1-celled, hyaline, and formed in basipetal succession in chains or drops.

Subsequently Gams (1973) showed that the presumptive phialides actually produced only a single conidium; these conidiogenous cells lacked periclinal thickenings and collarettes, and their method of conidial production was holoblastic, not enteroblastic as would be found in true phialides. Gams then also added a fourth species, A. spectabile W. Gams, and noted that in it more than one conidiogenous locus could occasionally form per conidiogenous cell; all such sites produced conidia holoblastically. He stated that species with catenate conidia would have to be placed in a separate, new genus. A. meliolae fits the

latter criterion, but Gams did not erect such a genus to accommodate this species.

Gams et al. (1984) reaffirmed the view that species of Aphanocladium "are characterized by solitary conidia produced either by flask-shaped phialides, or denticulate structures which may be interpreted as reduced phialides".

Von Arx (1986) examined several isolates of both A. aranearum and A. album, and concluded: (1) A. aranearum really should be considered a Beauveria, and he made the combination B. aranearum (Petch) von Arx; and (2) Aphanocladium should be considered a monotypic genus restricted to A. album. Strangely, von Arx did not mention either A. spectabile or A. meliolae in reaching these conclusions.

As defined by Gams, species of Aphanocladium differ from those of Engyodontium de Hoog in their production of solitary conidia on inflated phialide-like structures or reduced pegs, in contrast to the denticulate conidium production on polyblastic, subulate or acicular conidiogenous cells of the latter. These phialide-like structures of Aphanocladium species and their pattern of conidial production differ from those of true phialides typically found in species of Acremonium or Verticillium, in that a basipetal succession of conidia never develops. The pegs are also distinctive from the adelophialides or pleurophialides produced by the genera Lecythophora Nannf. or Cladorrhinum Sacc. & Marchal respectively.

Members of the genus are fungicolous, having been isolated from species of the Myxomycota, Agaricales, Ascomycotina and Urediniomycetes,

but they have also been isolated from spiders, insects and insect egg-masses, nematode cysts, soils, and dead plant leaves.

Since 1971, one variety of A. aranearum, a species of Beauveria fide von Arx (1986) and three more Aphanocladium species have been described. However, in view of the unsettled state of the generic concept of Aphanocladium, only further comparative studies of the organisms which have been assigned to this genus and others of the genera Engyodontium and Beauveria, will determine the relationship between these fungi. Hopefully, such studies will clarify whether A. album is so unique that Aphanocladium becomes a monotypic genus, or if some of the other species belong there too.

Aphanocladium album (Preuss) W. Gams, Cephalosporium-artige Schimmelpilze (Hyphomycetes). 196. 1971 Fig. 5. a-f.

≡Acremonium album Preuss, Sturm Deutschl. Fl. Pilze, 6:17. 1848

For further synonymy see Gams (1971).

Colonies attaining a diameter of 27 - 30 mm in 12 days at 20°C in darkness on MEA.YE. Colonies white (2.5Y $^{8}/_{2}$ (centre), $^{8}/_{0}$ (towards the margin)) or, if surface hyphae are sparse, pinkish grey (5YR $^{7}/_{2}$) in the centre; floccose, lacking any evidence of conidial production, hyphae sometimes undulate. In areas where the aerial hyphae have been scraped off or the colony slashed, small, compact, whitish-yellow nearly globose phialophores may develop. In reverse, the centres of the colonies are light brown (7.5YR $^{6}/_{4}$), sometimes becoming pinkish grey to reddish grey (7.5YR $^{6}/_{2}$ to $^{5}/_{2}$), but fading to very pale brown (10YR $^{7}/_{4}$, $^{8}/_{3}$) at the margins. Colonies grown on OA and RFA are white (2.5Y $^{8}/_{0}$), and usually produce more abundant aerial hyphae than colonies grown on MEA.YE. Odour indistinct. An exudate is present as small drops at the margins, or as abundant medium sized drops in the centre. Hyphae hyaline and smooth-walled; aerial hyphae often gently undulate and measuring 1.2 - 3.2 μm in diameter; submerged hyphae may become pale brown and filled with an oily substance, and are sometimes constricted at the septa; up to 5.5 - 6.5 μm in diameter. Chlamydospores were not seen. Conidiophores micronematous or rarely macronematous; hyaline and smooth-walled; the former are represented as conidiogenous cells which arise directly from the aerial hyphae, either laterally or terminally, and are

Fig. 5. Aphanocladium album (Preuss) W. Gams
(isolate: 110aiii)

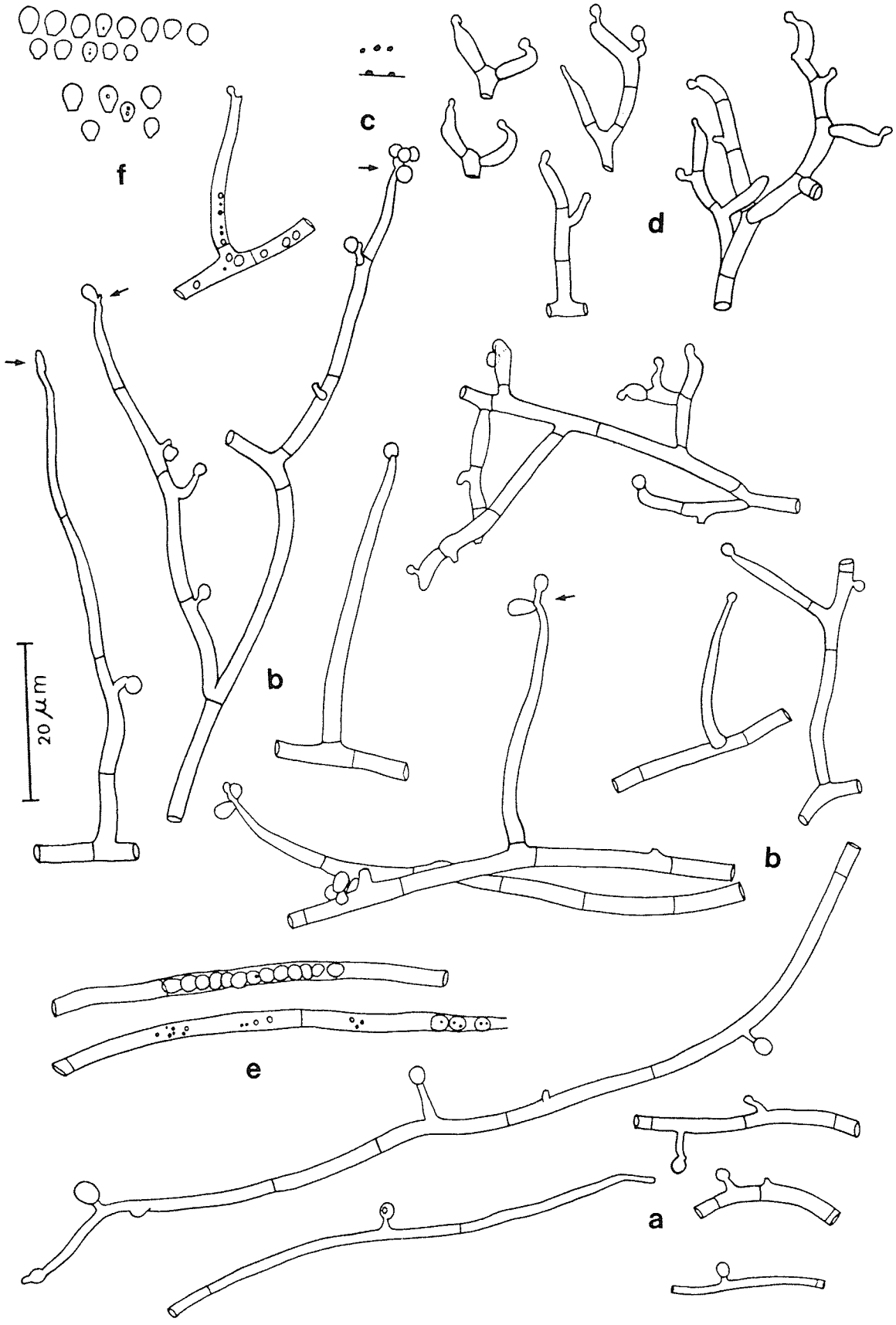
a-b. Micronematous conidiophores; (a) pegs, (b) longer conidiogenous cells; (b) conidiogenous loci which appear to have increased in length («-).

c-d. Macronematous conidiophores; (c) tiny globose conidiophores, habit sketch; (d) portions of such conidiophores, short-cylindrical to obovate conidiogenous cells, pegs and short branches.

e. Intra-hyphal conidia.

f. Conidia.

Isolate as illustrated: 110aiii: a-f.


f
c
d
b
b
b
20 µm
e
a

usually reduced to peg-like structures (Fig. 5. a,b); the latter are globose (Fig. 5. c) and consist of repeatedly branched systems of short cells which may produce lateral pegs, but bear 1 - 2 terminal phialide-like structures (Fig. 5. d). Conidiogenous cells neither produce periclinal thickenings nor clearly increase in length, and thus their mode of conidiogenesis is unclear; of three morphological types, (1) nearly cylindrical pegs, 1.2 - 5.6 x 0.8 - 1.2(1.6) μm tapering to 0.6 - 0.8(1.0) μm at the apex (Fig. 5. a), (2) acicular to cylindrical; 11 - 38 x 1.2 - 2.1 μm tapering very gradually to 0.7 - 1.0(1.4) μm at the apex (Fig. 5. b), (3) short-cylindrical to obovate, narrowing abruptly to very short and sharply curved necks; 3.6 - 10.5 x 1.5 - 2.3 μm becoming 0.7 - 0.9 μm at the apex (Fig. 5. d); collarettes lacking. Intra-hyphal conidia were observed once (Fig. 5. e). Conidia probably holoblastic and produced singly; 1-celled, hyaline, and smooth-walled; globose, subglobose to obovate; 1.8 - 3.2(4.0) x (1.3)1.7 - 2.5 μm, with an indistinctly apiculate to truncate base (Fig. 5. f).

HOST: Cupressus macrocarpa

CULTURE EXAMINED: **New Zealand:** 110aiii, isolated from C. macrocarpa, Compartment 14, Woodhill State Forest, Auckland, collected 25 May 1982.

This species has been isolated from members of the Myxomycota, Agaricales, Erysiphales, and Urediniomycetes (von Arx 1986; Biali et al. 1972; Gams 1971; Hawksworth 1981); from air, soils, leaves, and soybean

nematode cysts (Anon 1975; Bissett & Parkinson 1979a; Carris et al. 1989; Gams 1971; Gochenaur 1978; Lacey 1981). Carroll (1987) isolated A. album from egg-masses of the gypsy moth and reported the species as being occasionally associated with insects, but whether it is parasitic on insects is unknown.

As noted above, the genus Aphanocladium was erected for Acremonium album Preuss because it has a distinctive method of conidiogenesis, the conidiogenous cells, or "phialides," of A. album are not thickened at the apex, lack collarettes, and only produce a single conidium. Therefore this type of conidial ontogeny is really holoblastic, and lacks any proliferation of the conidiogenous locus. Nevertheless, it appears that some of the conidiogenous cells in the New Zealand isolate may produce more than one conidium as their apices appeared to have increased slightly in length, suggesting sympodial proliferation (Fig. 5. b «-). However, since no detailed investigation of conidial ontogeny was undertaken the significance of such structures is uncertain.

This isolate did produce a brown to pinkish-grey pigment which is presumably the same pigment mentioned by von Arx (1986). The conidia resembled those described by Gams (1971) but were shorter than those von Arx (1986) reported.

Previous reports of A. album from New Zealand, or of it having been isolated from bark beetle galleries or from coniferous wood have not been found. The only report of its occurrence in association with bark-inhabiting insects is that of Carroll (1987). However, since it is a fungicolous species it could well be growing on one of the other fungi

present in the galleries.

Beauveria Vuill., Bull. Soc. bot. Fr. 59:40. 1912

Type species: Beauveria bassiana (Bals.-Criv.) Vuill.

Teleomorphic genus: Cordyceps (Fr.) Link

The genus Beauveria is comprised of species which produce white, fairly slow growing colonies that are floccose, lanose, or powdery in texture. Sometimes they are plectonematogenous, but they rarely produce synnemata and, on aging, may become yellowish or occasionally pinkish. The conidiogenous cells (sympodulae) usually arise in clusters from inflated basal cells, or singly and in whorls from the aerial mycelium. They are subglobose or elliptical to cylindrical, and develop thin, geniculate, denticulate rachises at their apices as a result of sympodial proliferation during conidium production. The conidia are 1-celled, hyaline, smooth-walled, and globose to elliptical (de Hoog 1972; Domsch et al. 1980).

Most Beauveria species are entomogenous with a fairly wide host range (including bark beetles), but are also well adapted to a saprophytic existence, e.g. on chitin fragments in the soil (Evans 1982). However, a few are known only as soil saprophytes (Samson & Evans 1982). Some of the species have been used as alternatives to chemical control of certain insect pests. Such fungi shorten the life span of the adult insects, and increase the mortality rate of their larvae; this causes long-term deleterious effects on the host population (Roberts & Humber 1981).

B. bassiana, first described by Link in 1809 as Sporotrichum densum Link, has been recognized as an insect parasite since 1835 when, as Botrytis bassiana Bals.-Criv., it was identified as the cause of what is now called disastrous muscardine in silkworms. Because of its unique characteristics the genus Beauveria was erected for this species by Vuillemin in 1912.

Since then numerous species have been placed in Beauveria but, when critically examined (Benham & Miranda 1953; de Hoog 1972; MacLeod 1954; Petch 1924), most of them were reported to lack stable characters distinct enough to permit their separation into different species. Thus of the fourteen Beauveria species studied by MacLeod (1954), twelve were reduced to synonymy with either B. bassiana or B. brongniartii (Sacc.) Petch (as B. tenella (Sacc.) MacLeod). A third species, B. alba (Limber) Saccas (treated by MacLeod (1954) as Tritirachium album Limber), was considered a good Beauveria species by de Hoog (1972) because it lacked pigmented aerial hyphae and possessed denticulate rachises; these characteristics separated it from species normally assigned to Tritirachium Limber. B. alba, which lacks the inflated conidiogenous cells found in other Beauveria species, was subsequently transferred to the genus Engyodontium de Hoog (1978) in an attempt to make Beauveria a more homogeneous genus.

Von Arx (1986) transferred six species of the genus Tolypocladium W. Gams to Beauveria. His reason for doing so was that in fresh isolates of some of the Tolypocladium species, the conidiogenous cells proliferate (von Arx 1986, Fig. 1b p. 154 and Fig. 2a p. 155) and the

structure of the conidiophores resembles that found in species of Beauveria. However, species of Tolypocladium form their conidia in slimy drops, and the proliferation of their conidiogenous cell apices seems to be a rather transient character as most isolates usually possess typical phialides. Mugnai et al. (1989), on the basis of biochemical and morphological characters of one Tolypocladium species compared to several isolates of seven Beauveria species, expressed doubt that Tolypocladium should be considered a synonym of Beauveria.

To date, eight species of Beauveria have been described (plus six additional species if Tolypocladium is truly a synonym of Beauveria), and one species, B. aranearum (Petch) von Arx (≡Aphanocladium aranearum (Petch) W. Gams), has recently been transferred to this genus (von Arx 1986, 1988); the latter, however, seems to differ somewhat from more typical members of the genus.

Until recently, members of the genus were known primarily as anamorphic species, the one exception being the Cordyceps-like teleomorph (Domsch et al. 1980) reported for B. bassiana by Schaerffenberg (1955 in de Hoog 1972). However, Shimazu et al. (1988) found stromata of a new Cordyceps species on cadavers of Anomala cuprea Hope which had been killed by B. brongniartii. They isolated single ascospores and established the teleomorph-anamorph connection in culture, thereby proving the relationship with members of the Clavicipitaceae predicted by von Arx (1986, 1988).

Beauveria taxonomic sp. 1. Fig. 6. a-g.

Colonies attaining a diameter of 37 - 44 mm in 12 days at 20°C in darkness on MEA.YE. At first white (2.5Y $^{8}/_{0}$ to $^{8}/_{2}$), floccose and fluffy, but after 7 to 10 days white, globose conidiophores are produced in the centre of the colonies and, as conidial production progresses, the single hyphae bearing the conidiophores collapse and the surface becomes mealy in texture. Colonies then sometimes appearing pinkish white (5YR $^{8}/_{2}$) in mealy areas, but remaining white or becoming light grey to pale yellow (2.5Y $^{7}/_{2}$ to $^{7}/_{4}$) in floccose areas; these may finally become appressed and yellow (10YR $^{8}/_{8}$ to 2.5Y $^{8}/_{6}$). In reverse, colonies are pale yellow (2.5Y $^{8}/_{4}$). Odour lacking. An exudate is present as small clear drops, and small rectangular to pyramidal crystals are found in the medium surrounding the colony margin. Hyphae hyaline and smooth-walled; aerial hyphae 1.0 - 3.5 μm in diameter, submerged hyphae up to 5.5 μm wide; strands lacking, but individual aerial hyphae anastomose frequently, and hyphae comprised of a series of 3.5 - 6.5 μm wide, clavate cells (Fig. 6. b) are fairly common. Chlamydospores were not seen. Conidiophores sympodial and macronematous, semi-macronematous or micronematous; hyaline and smooth-walled. Macronematous conidiophores are globose to elliptical and 25 - 50 μm in diameter (Fig. 6. a); comprised of clusters of short, cylindrical basal cells, each usually bearing an additional terminal globose cell. Therefore the stem is two-celled, and along its length and apically it bears globose cells from which the ultimate series of smaller globose cells

Fig. 6. Beauveria taxonomic sp. 1.
(isolates: 168c, 168d)

a. Macronematous conidiophores; globose to elliptical, habit sketch.

b. Aerial hyphae; clavate cells.

c-d. Macronematous conidiophores; (c) portions of globose conidiophores, sympodulae globose to subglobose with long denticulate rachises; (d) details of the basal cells found within structures illustrated in (c).

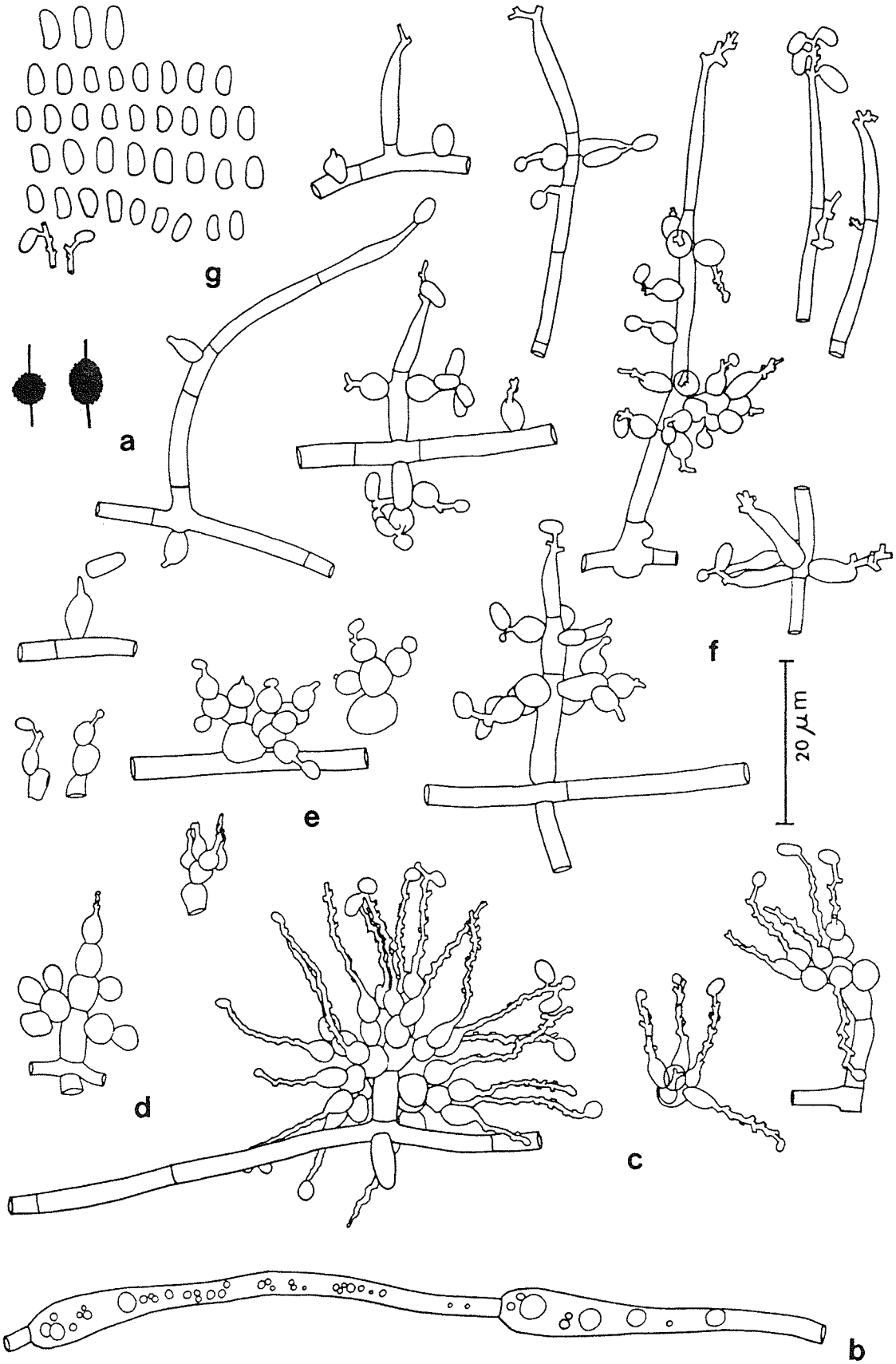
e. Young sympodulae on globose basal cells.

f. Micronematous to semi-macronematous conidiophores; subcylindrical to narrowly naviculate sympodulae are positioned terminally on the lateral branches.

g. Sympodioconidia; including those still attached laterally to the denticle.

Isolates as illustrated: 168c, d: a-g. *

* Figure shows both isolates since they were virtually identical and specific isolate designation was not deemed necessary.


a
b
c
d
e
f
g
20 µm

and occasional sympodulae arise (Fig. 6. d). Each of these ultimate globose cells bears up to 5 globose sympodulae (Fig. 6. c). Micronematous and semi-macronematous conidiophores are comprised of a single sympodula, or of lateral and terminal sympodulae on short basal cells (Fig. 6. e) or on longer lateral branches; the terminal sympodulae are usually subcylindrical to narrowly naviculate (Fig. 6. f). Conidiogenous cells sympodial (sympodulae); smooth-walled and hyaline; usually globose, subglobose, or short-elliptical and 2.8 - 3.6(4.7) x 2.4 - 3.2(3.5) μm (Fig. 6. c,e); but occasionally subcylindrical to narrowly naviculate and 6.5 - 12.5 x (1.8)2.0 - 2.8 μm (Fig. 6. f); both types produce the conidia on 0.8 - 1.0 μm wide, geniculate, denticulate rachises which may be up to 15 μm long, the denticles being 0.5 - 0.7 x 0.6 - 0.9 μm. Sympodioconidia dry, 1-celled, hyaline, and smooth-walled; cylindrical to narrowly reniform, and then one side is flattened; (2.8)3.2 - 5.0 x 1.6 - 2.2 μm; usually widest at the base which is attached laterally to the denticles (Fig. 6. g); scars and pedicels lacking; the longest (3.5 - 5.0 μm) conidia are produced by the cylindrical sympodulae.

HOST: Pinus nigra Arnold

CULTURES EXAMINED: **New Zealand:** 168c, d, isolated from P. nigra, Compartment 1091, Kaingaroa State Forest, Taupo, collected 10 June 1982.

Based on the appearance of the conidiophores and the sympodulae,

this fungus is clearly a Beauveria species. Of B. amorpha (Höhn.) R. A. Samson & Evans and B. caledonica Bissett & Widden, the only two species with cylindrical to reniform conidia, it most resembles B. amorpha, as its colonies become yellow on aging, and it produces somewhat broader conidia than those reported for B. caledonica. However, when confirmation of identification of this fungus (as B. amorpha) was sought at CBS, Baarn, it was identified as B. brongniartii (R. A. Samson, pers. comm.), a species described by de Hoog (1972) as having ellipsoidal (rarely subglobose) conidia which are widest near or below the middle, sometimes with a pointed or apiculate base.

The shape of the conidia is one of the more reliable morphological characters by which several of the Beauveria species can be identified, although the colony colour is also useful in distinguishing between some species (Mugnai et al. 1989). Many other morphological characters, as noted earlier, are quite variable and not suitable for separation of taxa.

Since the conidial shape is an important character, the identification of this fungus as B. brongniartii was questioned because nowhere in the descriptions of that species (de Hoog 1972; MacLeod 1954; Mugnai et al. 1989) are its conidia reported as cylindrical to reniform. In attempt to properly assign this fungus to a species isolates were compared to isolates of both B. amorpha and B. brongniartii using endonuclease restriction fragment analysis of the ribosomal DNA (G. Hausner, pers. comm.). He found that the New Zealand isolates differed from isolates of both these species, although the isolates of

B. brongniartii were also highly variable. The full details of that study will be presented elsewhere.

On MEA.YE, the conidiophores formed by the New Zealand isolates were mostly of the globose macronematous type, but some were reduced, and these produced generally longer conidia than the former.

Many Beauveria species are well known as insect parasites. These isolates were obtained from the galleries of bark beetles in coniferous wood and could thus indeed be affecting the beetle population in that host tree.

Chalara (Corda) Rabenh., Deut. Kryptfl. 1:38. 1844; emend. Nag Raj & Kendrick, A monograph of Chalara and allied genera, 60. 1975

≡Torula (Pers.) Link subg. Chalara Corda, Icon. fung. 2:9. 1838

≡Torula (Pers.) Link sect. Chalara (Corda) Corda, Icon. fung. 5:5. 1842

=Thielaviopsis Went, Arch. voor de Java Suekerr. 4. 1893

=Chalaropsis Peyr., Staz. sper. agr. ital. 49:595. 1916

=Chaetochalara Sutton & Pirozynski, Trans. Br. Mycol. Soc. 48:350. 1965

For full synonymy see Nag Raj & Kendrick (1975).

Type species: Chalara fusidioides (Corda) Rabenh.

Teleomorphic genera: Ceratocystis Ellis & Halst., Ceratocystiopsis Upadhyay & Kendrick, Chaetosphaeria Tul. & C. Tul., Cryptendoxyla Malloch & Cain, Melanochaeta E. Müller et al. and Quasichona M.E. Barr & M. Blackwell; each of the foregoing have one or more species with a Chalara anamorph. A Chalara species has also been found associated with one or more species of the genera Mollisina Höhn. and Pyxidiophora Bref. & Tav. but the nature of such associations has not yet been clarified.

Primarily comprised of dematiaceous forms, the species of this genus are characterized by simple to rarely branched macronematous phialophores with terminal, or rarely lateral, integrated phialides. These produce catenate, cylindric, 1-celled or septate conidia with truncate ends which arise deep within a long collarette, and chlamydospores or setae are sometimes present. For full generic descriptions

see Ellis (1971) and Nag Raj & Kendrick (1975).

While most species are saprophytic on a variety of dead plant parts, some are important plant pathogens. In the latter case they may cause tree wilts, root rots of various crop plants, and storage rots of fruits and vegetables (Holubová-Jechová 1984); several of the Chalara species have species of Ceratocystis as teleomorphs.

Nag Raj & Kendrick (1975) list 58 Chalara species, some of which were species formerly assigned to Thielaviopsis Went or Chalaropsis Peyronel. In addition, Kirk & Spooner (1984) transferred 5 species from Chaetochalara Sutton & Pirozynski to Chalara. Since 1975 at least 15 new Chalara species have been described (Holubová-Jechová 1984; Kile & Walker 1987, table 3.; Kirk 1985, 1986) and an additional three organisms were listed but not formally described as Chalara species by Matsushima (1975). Thus there are probably at least 78 Chalara species. Additionally, eight Ceratocystis species and one Ceratocystiopsis species are also reported to have Chalara anamorphs (Upadhyay 1981), and Chalara anamorphs are also known for Quasichona reticulata Barr & Blackwell (Blackwell & Gilbertson 1985), and Cryptendoxyla hypophloia Malloch & Cain (Nag Raj & Kendrick 1975). A Chalara state is also reported as a synanamorph of Melanochaeta aotearoae (Hughes) E. Müller et al., but this only develops in culture (Müller & Samuels 1982). Chalara states have also been found associated with Mollisina uncinata Arendholz & R. Sharma (Helotiales) (Arendholz & Sharma 1980) and three species of Pyxidiophora Bref. & Tavel (Lundqvist 1980), but the potential anamorphic status of these has not yet been clarified.

Minter & Holubová-Jechová (1981) considered members of the genus Chalara to be important saprophytes of pine needles, twigs, and cones. They reported that the Chalara state of Ceratocystis autographa Bakshi was the most commonest of at least ten Chalara species known from decaying pines. However, even though species of the genus are common on rotten wood and bark of various conifers, according to Nag Raj & Kendrick (1975) they are rarely found in stained wood. One exception was the association of Chalara australis J. Walker & G.A. Kile with discoloured wood, found following an insect attack on Nothofagus cunninghamii (Hook.) Oerst. in Tasmania (Kile & Walker 1987).

Chalara state of (?) Ceratocystis autographa Bakshi, Ann. Bot., N.S. 15:58. 1951 Fig. 7. a-g.

Colonies attaining a diameter of 25 mm in 21 days at 20°C in alternating light and darkness on MEA.YE. The young colonies are grey (5Y $^{5}/_{1}$), and usually have small hyphal aggregations arising from the compact colony margin; becoming greyish brown (2.5Y $^{5}/_{2}$) in those areas where aerial mycelium is abundant, but dark grey (5Y $^{4}/_{1}$) in phalacrogenous areas. Usually plectonematogenous to synnematogenous, with the size of the strands varying according to culture conditions. As the conidial production continues, the colony surface becomes mealy in appearance, light grey (2.5Y $^{7}/_{0}$) in colour, and is covered with numerous white conidial chains which sometimes encircle the phialide apex. In reverse, the young colonies are grey to dark grey (5Y $^{5}/_{1}$ to $^{4}/_{1}$), often with some of the centre yellowish red (5YR $^{5}/_{8}$), later dark grey (5YR $^{4}/_{1}$) with yellowish red (5YR $^{4}/_{6}$) areas, and sometimes becoming black (5YR $^{4}/_{1}$) on aging. Odour lacking and an exudate is present as clear drops. A yellow to rusty-red crystalline material often develops exogenously, either in discrete patches or generally on the colony surface; crystalline deposits may also be present on the surface of the hyphae, or may fill individual hyphal cells. Abundant crystal production is frequently associated with retardation of growth. Hyphae hyaline to brown; walls are smooth to verruculose, or finely encrusted; 0.9 - 3.2 μm in diameter (Fig. 7. a); rarely aging hyphae may became brown and constricted at the septa (moniliforme) and they are up

Fig. 7. Chalara state of (?) Ceratocystis autographa Bakshi (isolate: 85dii''')

a. Hyphae; verruculose.

b. Micronematous phialophores; phialides arising from a small protuberance, or directly from undifferentiated hyphae, sometimes lacking a basal septum.

c. Semi-macronematous phialophores; phialides arising from a stem; secondary phialides («-).

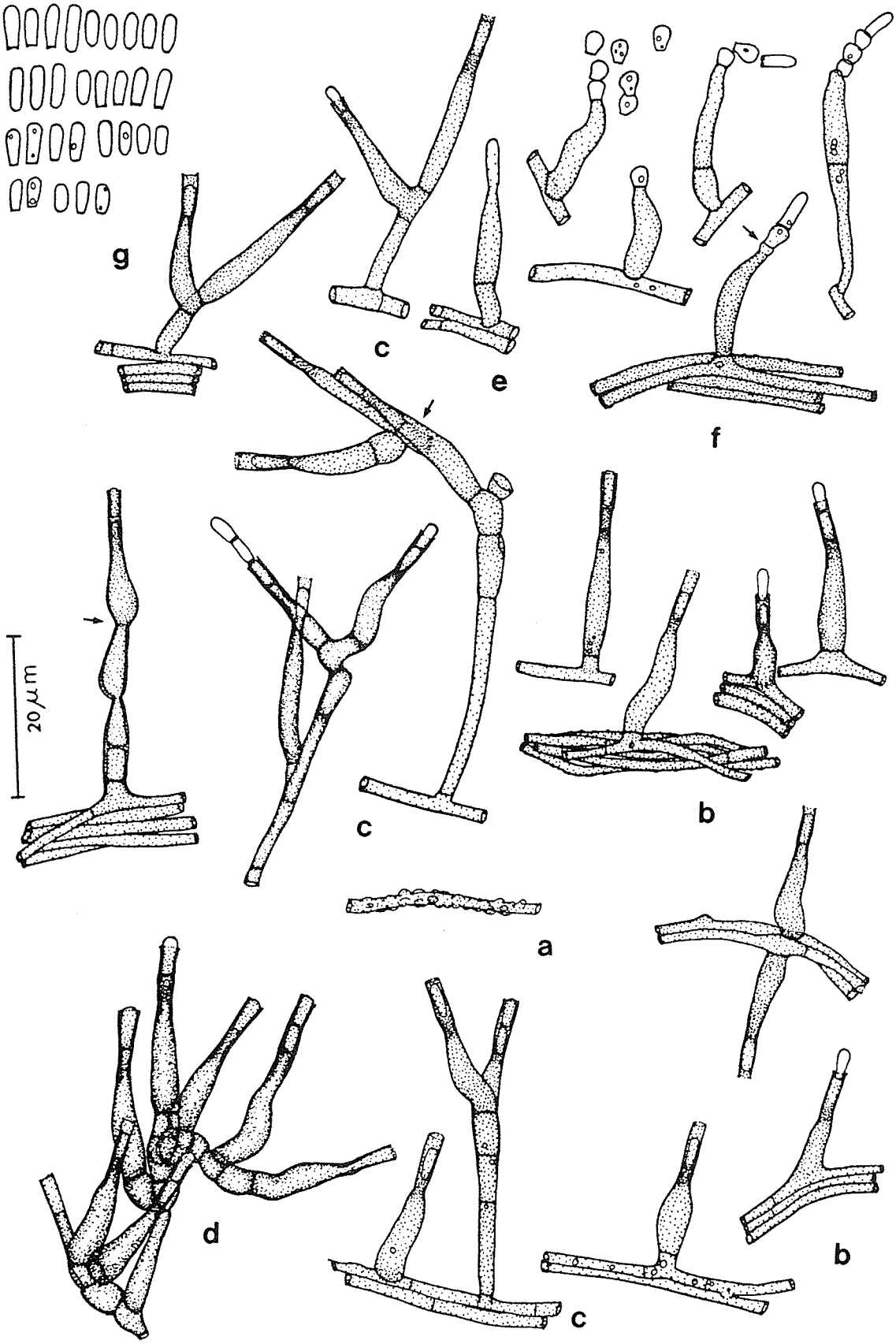
d. Complex phialophores from an aging colony.

e. Young phialide prior to conidial production.

f. Conidiogenous cells producing subglobose conidia in short chains; the slight swelling at the apex («-) indicates the third conidium being produced; the first conidium produced by each conidiogenous cell is cylindrical.

g. Phialoconidia.

Isolate as illustrated: 85dii''': a-g.


g
c
e
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20 µm
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c
b

to 4.7 μm in diameter. The hyphae are commonly funiculose, with 5 - 25 μm wide strands, but when they are discrete and tapering at the apex, their basal diameter may be up to 100 μm. Chlamydospores were not seen. Phialophores semi-macronematous or micronematous; light to dark brown, occasionally darker than the subtending hyphae, but usually evenly pigmented; smooth-walled; 20 - 40 μm long including the terminal phialide, and having a 0 - 2(3) septate stem which is 3.2 - 24 x 2.6 - 3.2 μm long, and bears phialides either singly or in pairs (Fig. 7. c); in young cultures the stems may be reduced to a small protuberance on the hyphae, or be lacking entirely (Fig. 7. b). As the culture ages, more complex phialophores (Fig. 7. d) often develop. Conidiogenous cells monophialidic; discrete, integrated, or adelophialidic; smooth-walled; brown but with a darker band extending above and below the slight constriction at the base of the collarette; subcylindrical, obclavate to navicular, and becoming slightly constricted at the base of the cylindrical collarette; 14 - 24 x 2.5 - 3.4(4.0) μm tapering to 1.3 - 1.6 μm, including the 5.5 - 7.5(9.0) μm long collarette which is 1.6 - 1.9(2.2) μm wide at the apex. Secondary phialides often proliferated laterally or, less frequently, percurrently from the primary ones (Fig. 7. c «-). In young cultures, conidiogenous cells which are similar in appearance but lack collarettes develop occasionally (Fig. 7. f); these produce conidia in short chains and are 11.3 - 16.3 x 2.6 - 3.3 μm, tapering to 1.5 - 1.6 μm at the conidiogenous site; the latter phialides are far less abundant than the Chalara-type. Phialoconidia catenate; 1-celled, hyaline, and smooth-walled; of three kinds, (1) most

are short-cylindrical with an obtuse apex and somewhat rounded base and measure 3.3 - 5.6(6.2) x 1.5 - 1.7(1.8) μm, (2) some clavate with obtuse apex and truncate base with barely distinguishable frills measuring 4.0 - 5.2(6.5) x 1.6 - 2.2 μm (Fig. 7. g), (3) rarely conidia are produced exogenously at the apex, also presumed to be phialoconidia, subglobose, truncate at the base and 2.8 - 3.2 x 2.1 - 2.4 μm (Fig. 7. f).

HOSTS: Juniperus communis L., Larix leptolepis Gord., Pinus radiata.

CULTURES EXAMINED: **New Zealand**; 85dii''', isolated from P. radiata, near Onemana, Tairua State Forest, Coromandel, 20 May 1982. **Europe: Netherlands**; CBS 670.75, from decaying J. communis needles, Lheedorp (Dr.), November 1975. SPECIMEN EXAMINED: **United Kingdom**; IMI 20162 (type specimen) isolated from bark beetle galleries in L. leptolepis, Blair Atholl, Perthshire, Scotland, date on specimen 24 December 1947.

C. autographa was first isolated from bark beetle galleries in dying L. leptolepis in Scotland (Bakshi 1951), and the teleomorph only appears to have been recovered once since then; from stained wood of Pimenta officinalis L. in Jamaica, associated with the pathogen Ceratocystis fimbriata Ellis & Halst. (Leather 1966). However, a fungus that may be its Chalara anamorph has been recovered from decaying juniper and pine needles in Czechoslovakia, the U. K. and the Netherlands (Gams & Holubová-Jechová 1976; Minter & Holubová-Jechová 1981).

Hunt (1956) examined both the type specimen and a culture derived

from the same source. He noted the typical hyphal strands and, in contrast to Bakshi, reported the "exogenous" conidia were formed in clusters at the apex of differentiated, septate conidiophores, which were 50 x 1 - 1.5 μm. Hunt's measurements for the globose to subglobose, exogenous conidia were 1.5 - 2.5 x 1.5 μm, much smaller than the range given by Bakshi (1951). Upadhyay (1981) clarified the nature of the exogenous conidiogenesis stating it was sympodial and resembled species of Hyalorhinocladiella. No evidence of sympodial conidiogenesis was found in the New Zealand isolate, nor in the culture CBS 670.75, obtained for comparison from the Centraalbureau voor Schimmelcultures, Baarn.

Bakshi (1951) and Hunt (1956) referred to the phialophores as endoconidiophores but it was not until Nag Raj & Kendrick (1975) examined the type specimen that the phialidic anamorphic state was transferred to the genus Chalara. The endoconidia were described as cylindrical by Hunt (1956), not barrel-shaped as stated by Bakshi, and he gave their measurements as 4 - 5.5 x 1.5 μm. However, Nag Raj & Kendrick (1975) were first to note the dark zone around the slight constriction at the base of the collarette, but they considered the phialoconidia to be short clavate. Gams & Holubová-Jechová (1976) and Holubová-Jechová (1984) stressed the presence of clavate phialoconidia and the dark zone at the base of the collarette as important diagnostic features of this species, but they did not note the presence of any subglobose conidia. Upadhyay (1981) examined the type specimen and reported the occurrence of cylindrical conidia with rounded or truncate

ends. Minter & Holubová-Jechová (1981) noted that there was some variation between collections and felt the various entities which have been assigned to this species may actually represent an aggregation of taxa.

To investigate whether a teleomorph might be produced when two different isolates were paired, the New Zealand isolate and CBS 670.75 were grown in paired cultures on different media, under alternating light and darkness. Replicate pairs were stored at 10°C for several months following fusion of the colonies. However, neither mature perithecia nor protoperithecia ever formed. Isolate CBS 670.75 produced less of the crystalline material than did the New Zealand isolate, and the crystals were formed mostly amongst the submerged hyphae. Microscopically, the two cultures were virtually identical except for the lack of phialide-like cells forming subglobose conidia at their apices in CBS 670.75. Examination of a slide prepared from the type specimen confirmed the shape of the phialides and their tendency to proliferate. Conidia were primarily cylindrical with rounded ends, fewer were subglobose, but the mode of conidiogenesis for the latter could not be ascertained from that slide.

Species of the genus Ceratocystis sensu lato are known for their pleoanamorphy, but C. autographa is unique in being the only species to combine a typical Chalara enteroblastic-phialidic anamorphic state, with holoblastic-sympodial conidiogenesis on simple conidiophores (Upadhyay 1981). Thus, based on its synanamorphs, C. autographa is intermediate between species comprising Ceratocystis sensu stricto, which have

Chalara-like anamorphs, and species of Ophiostoma H. & P. Sydow which produce other anamorphic forms (de Hoog & Scheffer 1984).

Such an intermediate species could be a valuable aid in the taxonomy of Ceratocystis sensu lato, but no live material of this species capable of producing the teleomorph seems to exist. Isolates such as the one from New Zealand, which only represent the Chalara form, may indeed be a separate species and then not at all related to species of Ceratocystis. Or, if not, this form may have lost the teleomorph from its life-cycle. Until the relationship of these Chalara isolates with C. autographa has been clarified, critical taxonomic decisions in the genus Ceratocystis should not be based on them. De Hoog & Scheffer (1984) further report that non-teleomorphic Chalara strains from the CBS culture collection apparently resemble other Chalara species without teleomorphs in being resistant to cycloheximide; this is in contrast to species of Ceratocystis sensu stricto which failed to grow on a medium containing it (Harrington 1981).

The subglobose conidia with truncate ends which are produced in young cultures of the New Zealand isolate, develop as follows. The first-formed conidium is cylindrical with a rounded apex and truncate base, and is identical in shape to the neck of a young phialide prior to conidiogenesis (Fig. 7. e); subsequent conidia of the chains are subglobose with a truncate base, and the conidium initial first appears as a swelling of the apex of the conidiogenous cell (Fig. 7. f «-). The conidiogenous cells correspond to the basal portion of the Chalara phialides, as if they lost the collarette, leaving the conidiogenous

locus at the apex. Similar conidiogenesis is illustrated by Nag Raj & Kendrick (1975, diagram, fig.8_{II} p.46) for the Chalara state of Ceratocystis paradoxa (Dade) C. Moreau.

The colony morphology is similar to that of C. microchona except for the presence of a yellow crystalline material; the shape of phialides is closest to C. constricta Nag Raj & Kendrick apart from the shorter collarettes and conidia; other Chalara species which produce small, 1-celled conidia, are not constricted at the collarette base.

The infrequent recovery of C. autographa from stained wood could be due to its very slow growth rate in culture allowing it to be easily overgrown by other organisms. The New Zealand isolate was recovered from a mixed culture where its presence was masked by the second species. The true C. autographa is one of the wood staining organisms vectored by bark beetles (Bakshi 1951), while the Chalara form is reported as a common saprophyte on decaying pines (Minter & Holubová-Jechová 1981).

Chalara crassipes (G. Preuss) Sacc., Syll. Fung. 4:335. 1886

Fig. 8. a-c.

≡Cylindrosporium crassipes G. Preuss, Linnaea 24:106. 1851

≡Chalara crassipes (G. Preuss) Lindau, Rabenh. Krypt.-Fl. 8:754. 1907

Colonies attaining a diameter of 54 mm in 21 days at 20°C in darkness on MEA.YE. When young somewhat appressed and grey (5Y $^{6}/_{1}$) in the centre with a white (5Y $^{8}/_{2}$) margin; later becoming white (2.5Y $^{8}/_{0}$) in the centre as dense hyphal tufts cover the darker surface of the medium, but remaining greyish brown to light greyish brown (2.5Y $^{5}/_{2}$ to $^{6}/_{2}$) towards the margin of the colony where fewer aerial hyphae develop; the ultimate margin remains white (5Y $^{8}/_{2}$) and appressed. The dark brown phialophores develop only after 2 - 3 weeks, arising singly or in rows from the mycelium, and make the surface of older cultures appear nematogenous and light grey (10YR $^{7}/_{1}$) in the centre, but grey (10YR $^{5}/_{1}$) and gradually becoming phalacrogenous towards the appressed edge. The conidia are catenate; the chains white, and rather inconspicuous at first, but later long, flexuose, undulate, or circular. In reverse, the young colonies are grey (2.5Y $^{5}/_{1}$), but on aging they become dark grey (2.5Y $^{4}/_{0}$) in the centre with the margins remaining white (2.5Y $^{8}/_{2}$). Colonies growing on cellulose medium sporulate readily. Odour mild, exudate lacking. Hyphae hyaline and smooth-walled; 1.5 - 5.5 μm in diameter; often becoming brown and verruculose on aging. Chlamydospores were not seen. Phialophores macronematous, mononematous; their walls

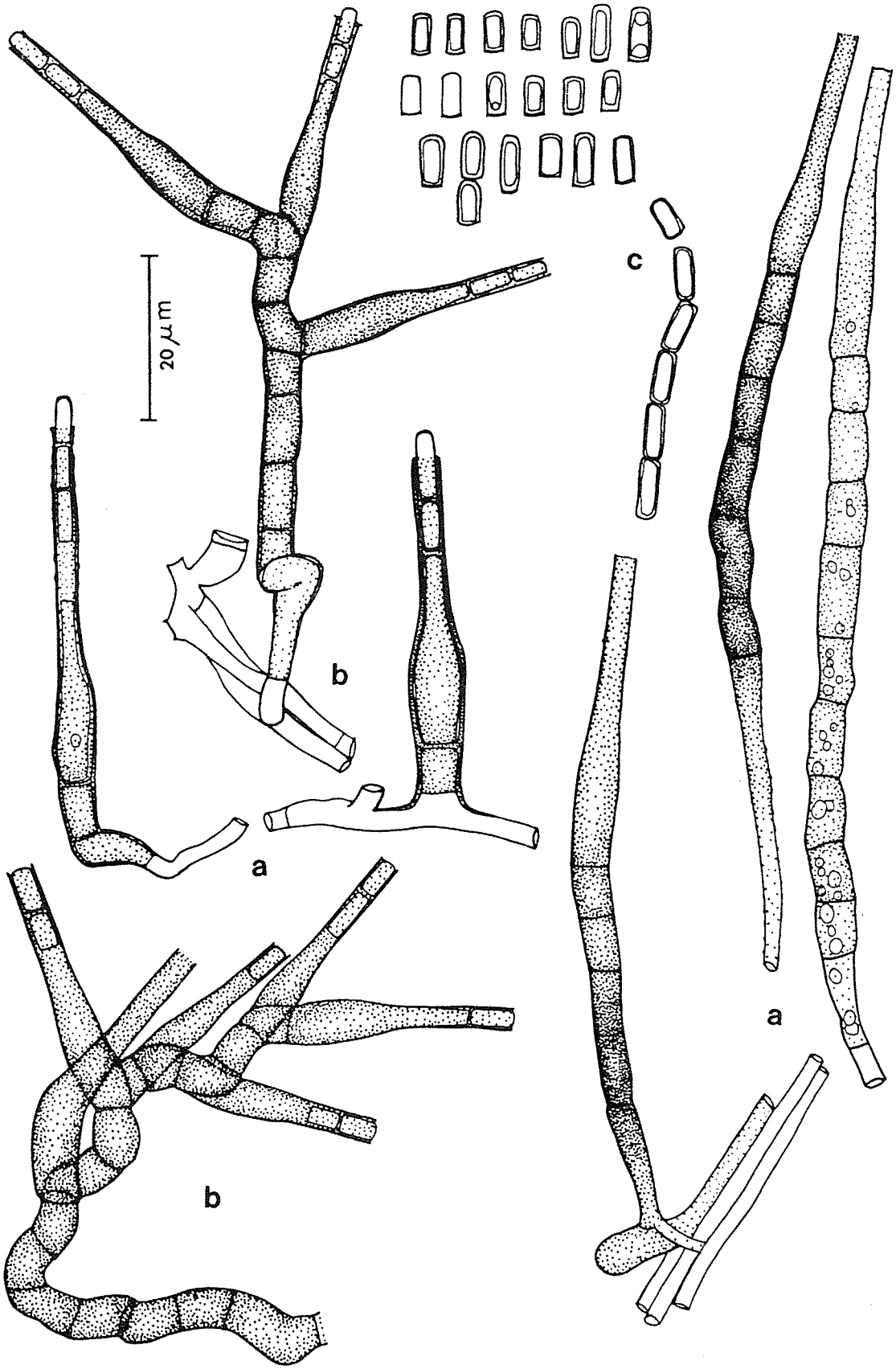
Fig. 8. Chalara crassipes (G. Preuss) Sacc.
(isolate: 141a')

a. Simple phialophores.

b. Branched phialophores.

c. Phialoconidia.

Isolate as illustrated: 141a': a-c.


20 µm
a
b
b
c
a

smooth, slightly thickened and sometimes finely verruculose in the lower part; uniform brown or pale brown in colour, but sometimes the basal cell lighter brown, and the stem then dark brown except for the terminal 1 or 2 cells and the terminal phialide which are then paler in colour (Fig. 8. a); usually simple, but occasionally producing a few lateral phialides (Fig. 8. b); usually 4 - 8 septate, but 1 - 13(17) septate phialophores are also produced; the stems are occasionally slightly constricted at the septa. The phialophores which often arise from an abruptly inflated hyphal cell of either a thin hyaline or a brown hyphae, measure 40 - 115(145) x 4.2 - 5.5 μm including the terminal phialide. Conidiogenous cells monophialidic; brown and smooth-walled; integrated; subcylindrical but tapering towards the base of the collarette; 20 - 40(45) x 4.2 - 5.5 μm but tapering to 2.4 - 3.2 μm at the base of the collarette. The collarettes are cylindrical and 10 - 22(26) μm long, but the basal portion of the phialides is 7.5 - 20 μm long; ratio of mean collarette length to mean of basal portion is 1.15 : 1 . Phialoconidia catenate; 1-celled and hyaline; their walls are smooth and appear slightly thickened; oblong; 4.4 - 7.5(9.0) x (2.0)2.3 - 2.8 μm, with an obtuse apex and nearly truncate base; the corners at the base are divergent, but too short to be considered frills (Fig. 8. c).

HOST: Podocarpus sp.

CULTURE EXAMINED: **New Zealand:** 141a', isolated from Podocarpus sp., near Minginui, Urewera National Park, Taupo, 11 June 1982.

C. crassipes (as Cylindrosporium crassipes) was described from rotten coniferous wood in Germany by Preuss in 1851 (Nag Raj & Kendrick 1971), and was known only from the type specimen until Holubová-Jechová (1984) obtained a second collection from a dead herbaceous stem in England. This second collection was described as having broader phialophores and conidia than the type specimen (4.5 - 5.0 μm compared to 3.0 - 4.5 μm; conidia 2.0 - 2.5 μm compared to 1.0 - 1.5 μm respectively), but both have dark brown phialophores that are lighter brown towards the apex, thick-walled, 0 - 5 septate, and up to 65 μm long.

Although the New Zealand isolate has broader conidia and longer, broader phialophores (usually 70 - 95 μm, 4 - 8 septate) than those found in either the English or type collections, it was assigned to C. crassipes because in addition to other similarities with isolate 141a', that is the only Chalara species reported to have 1-celled, cylindrical conidia, long phialophores, a collarette slightly longer than the basal portion of the phialide, and to lack chlamydospores (Holubová-Jechová 1984; Kile & Walker 1987; Nag Raj & Kendrick 1975). Including the New Zealand isolate may expanded the concept of C. crassipes somewhat but it is not unusual for the concept of a species based on a single collection to be expanded to accommodate the variation uncovered in later collections thought to represent that species.

The cultural characteristics of relatively few Chalara species are

known, most species having been described from material growing on natural substrata. The New Zealand isolate is known only from culture, and since many fungi differ markedly in culture from their appearance on natural substrata, this isolate might also behave differently if it was grown on wood.

Although isolate 141a' did not produce a teleomorphic state in culture, its microscopic characters were quite different from those Chalara species described as anamorphs of Ceratocystis and Ceratocystiopsis species (Upadhyay 1981). Thus it is not likely to be ever connected with a species of Ceratocystis sensu lato.

Nag Raj & Kendrick (1975) consider C. affinis Sacc. & Berl. as the species which most closely resembles C. crassipes, but the conidia of the latter are shorter and wider than those of the former species.

This appears to be the first record of C. crassipes from New Zealand, and the first record of it having been isolated from bark beetle galleries. The species has been presumed to be a saprophyte of various dead plant materials (including coniferous wood), but since it has been so rarely collected, its natural habitat range is simply a matter of speculation.

Chalara microchona W. Gams, Stud. Mycol. 13:73. 1976 Fig. 9. a-c.

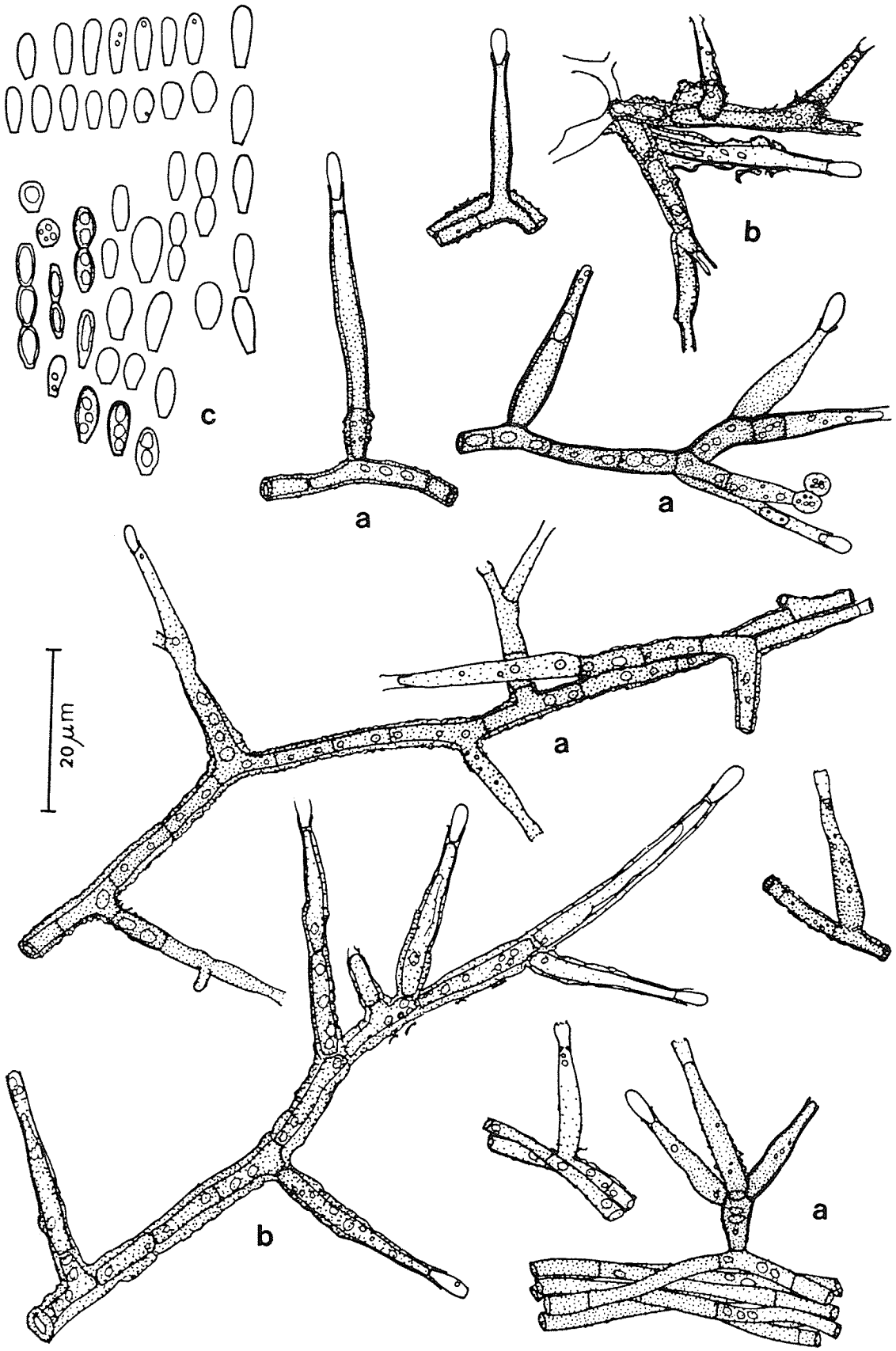
Colonies attaining a diameter of 14 mm in 14 days at 20°C in darkness on MEA.YE. When young, the colonies are light grey (5Y $^{7}/_{1}$) and nematogenous, becoming plectonematogenous and olive grey (5Y $^{5}/_{2}$) as growth continues; the conidia are produced in conspicuous white chains covering the colony surface. In reverse, colonies are grey (2.5Y $^{5}/_{0}$), at first, but become dark grey to grey (2.5Y $^{4}/_{0}$ to $^{5}/_{0}$) on aging. An odour is lacking, but an exudate is present as clear drops of varying size. Hyphae hyaline to brown; walls smooth to verrucose and sometimes with encrustations; 1.5 - 4.2 µm in diameter; commonly funiculose with strands up to 25 µm in diameter; submerged hyphae occasionally with swollen cells. Chlamydospores were not seen. Phialophores micronematous to semi-macronematous and 1-3 septate; darkest and often with conspicuously roughened walls at the base, but becoming lighter and smoother towards the apex (Fig. 9. a,b). Conidiogenous cells monophialidic or rarely polyphialidic; integrated or discrete, terminal or intercalary; when intercalary, adelophialidic. The longer phialides are subcylindrical to broadly subulate, but the shorter are obclavate; verrucose, brown, and sometimes thick-walled at the base but becoming smoother, lighter, and thin-walled towards the apex; 10.0 - 33 x 2.4 - 3.6 (3.9) µm including the collarette, tapering to 1.4 - 1.6 µm at the base of the collarette (Fig. 9. a,b). Collarettes distinct, obconical to funnel-shaped, and often with an incurved margin; 1.6 - 3.6 µm long and 1.7 - 2.5 µm wide. Phialoconidia catenate; 1-celled, hyaline, and

Fig. 9. Chalara microchona W. Gams
(isolates: 99b'', 99c'')

a-b. Phialophores.

c. Phialoconidia; both young, hyaline and smooth-walled conidia, and older, subhyaline conidia with somewhat thicker walls are figured.

Isolates as illustrated: 99b'': b, c.
99c'': a, c.


c
b
a
a
a
20 µm
b
a

smooth-walled, but sometimes subhyaline on aging; shape variable; obpyriform or short clavate to subcylindrical and (4.5) 5.0 - 7.3 (8.5) x (1.8) 2.0 - 2.6 (3.2) μm; or subglobose and 4.0 - 6.5 x 2.4 - 4.4 μm; all conidia with a truncate base (Fig. 9. c).

HOST: Pinus radiata

CULTURES EXAMINED: **New Zealand:** 99b'', c'', isolated from P. radiata, off Road 41, Whangapoua State Forest, Coromandel, collected 19 May 1982.

This species has previously been isolated from coniferous tree species and forest soils in Europe and Canada (Gams and Holubová-Jechová 1976; Holubová-Jechová 1984), but this appears to be the first report of its occurrence in New Zealand, and the first record of it having been isolated from bark beetle galleries.

When Gams (Gams & Holubová-Jechová 1976) erected the section Catenulatae within the genus Phialophora Medlar, primarily for those species with catenate phialoconidia, he highlighted the difficulty in clearly distinguishing between Phialophora species and some Chalara species. To solve this problem, the ontogeny of the conidial walls in the intermediate species such as C. microchona and more typical species of both Chalara and Phialophora must be determined. However, since growth characteristics of C. microchona and the Chalara state of Ceratocystis autographa Bakshi are very similar, C. microchona has been placed in Chalara rather than Phialophora.

The phialoconidia produced by the New Zealand isolates are longer than the measurements given in the original description, the maximum length being 5.0 μm according to Gams and Holubová-Jechová (1976), and both longer and wider than noted by Holubová-Jechová (1984). However, the conidial measurements given by these authors fall within the range recorded for the New Zealand isolates, and therefore the increased size range reported here is not considered to be significant.

When young conidial chains became dispersed in the mountant, a short frill could be seen at the apex of each conidium; the diameter of such frills corresponded to the width of the truncate base of the various conidia. An apical frill was never seen in mature conidia. This may suggest that the phialoconidia adhere in "true" chains and are formed by a wall-building ring (Minter et al. 1983) as are the conidia in various other Chalara species (Hawes and Beckett 1977).

This species appears to be saprophytic, occurring in coniferous wood and forest soils. It was isolated from a single wood sample in the New Zealand surveys and is thus apparently not a common inhabitant of the bark beetle galleries.

Dipodascus Lagerh., Jahrb. wiss. Bot. 24:549. 1892

=Magnusiomyces Zender, Bull. Soc. Bot. Genève, 17:41. 1925

=Zendera Redhead & Malloch, Can. J. Bot. 55:1707. 1977

Type species: Dipodascus albidus Lagerh.

Anamorphic genus: Geotrichum Link: Fr.

Most Dipodascus species (Endomycetales: Dipodascaceae) grow well in culture and have Geotrichum anamorphs. Colonies are white, phalacrogenous to plectonematogenous, and usually dry, with delicate, branched chains of conidia $^{and}/_{or}$ gelatinous masses of ascospores borne at the ascal apices. Hyphae are hyaline, smooth-walled, and hygrophilic; the cells are non-amyloid, lack capsules, and chlamydospores or endoconidia are sometimes present. The conidiophores are micronematous or semi-macronematous, and consist of only a little differentiated stem bearing fertile branches. The frequently sickle-shaped branches often arise at sharp angles to the stem or form dichotomously. Conidium development is chiefly arthric, forming chains without intermediate sterile cells, but in some species, conidium formation is sympodial or percurrent. The naked asci develop as a result of gametangial fusion; the gametangia forming as lateral outgrowths of the hyphae, and an ascogenous hyphal system and ascocarps are lacking. The asci develop singly or in clusters, and are subglobose, conical, or cylindrical and contain two to numerous ascospores. Their walls are persistent, either evenly thickened or slightly thicker at the apex. The spores are released through an

apical pore and the empty asci may become reflexed at the apex. Ascospores are 1-celled, hyaline and smooth-walled, elliptical, broadly elliptical, or oblong-elliptical; a mucilaginous sheath or capsule is present.

De Hoog et al. (1986) provide additional ultrastructural and physiological data of use in delimiting the genus.

Originally only comprising species with long, tapering, multispored asci, such as are seen in the type species D. albidus Lagerh., the generic concept was broadened to include species with much shorter and broader asci which contain only a few spores (de Hoog et al. 1986). This resulted in Zendera Redhead & Malloch and Magnusiomyces Zender being synonymized with Dipodascus (de Hoog et al. 1986).

The genera Dipodascus and Galactomyces Redhead & Malloch are both members of the Dipodascaceae and have Geotrichum Link: Fr. anamorphs, but species of these genera differ in ascospore morphology and the mode of their release (de Hoog et al. 1986). Dipodascopsis Batra & Millner species resemble Dipodascus in ascus morphology, but differ by producing numerous, small, allantoid ascospores, in lacking anamorphs, and having encapsulated hyphal cells. Species of Endomyces Reess have galeate ascospores, and anamorphs which produce holoblastic conidia.

Dipodascus species have been isolated from slime fluxes of trees, galleries of wood-boring insects, other fungi, humans, decaying plant material, waste water, and from wine cellars (de Hoog et al. 1986). In their monograph of these fungi, these authors recognized 13 species of Dipodascus and noted most had anamorphs referable to the genus

Geotrichum; however, the majority of the latter were not named to species.

Dipodascus aggregatus Francke-Grosmann, Med. Stat. SkogsvFör. Inst. 41:30. 1952 Fig. 10. a-h.

=Dipodascus albidus Lagerh. f. minor Korf, Sydowia, Beih. 1:286. 1957

Anamorph: Geotrichum sp.

Colonies attaining a diameter of 25 - 28 mm in 12 days at 20°C in darkness on MEA.YE. White (10YR $^{8}/_{1}$) and synnematogenous in the centre, with moist aerial hyphae, while the rest of the colony is semi-translucent and flat, phalacrogenous to nematogenous, the surface of the medium being dotted with mucilaginous aggregations. These aggregations chiefly consist of ascospores, and between them are rather sparse white, delicate, branched conidiophores. In reverse, the colonies are semi-translucent. Odour indistinct. Exudate and crystals lacking. Hyphae hyaline, smooth-walled, and 2.5 - 7.5 µm wide; the primary hyphae usually markedly broader than the branches (Fig. 10. a); when funiculose, the strands taper towards the apex, are loosely packed, and consist of relatively thin hyphae. Asci are produced following paired fusion of clustered gametangia, thus while the asci are aggregated, they do not develop synchronously (Fig. 10. b). Asci polysporous; cylindrical to slightly broader at the irregularly bifurcate base; walls uniformly thickened, but lacking any structures in the rounded apex which simply ruptures to release the spores; (28)45 - 95 x (4.0)5.0 - 9.0 µm; the empty asci are cylindrical with a torn apex (Fig. 10. b «-). Ascospores hyaline, smooth-walled, and oblong to broadly

Fig. 10. Dipodascus aggregatus Francke-Grosmann
(isolate: 3C)

a. Broader, primary hypha with secondary thinner branches.

b. Asci in various developmental stages; torn apex of an empty ascus («-).

c. Ascospores.

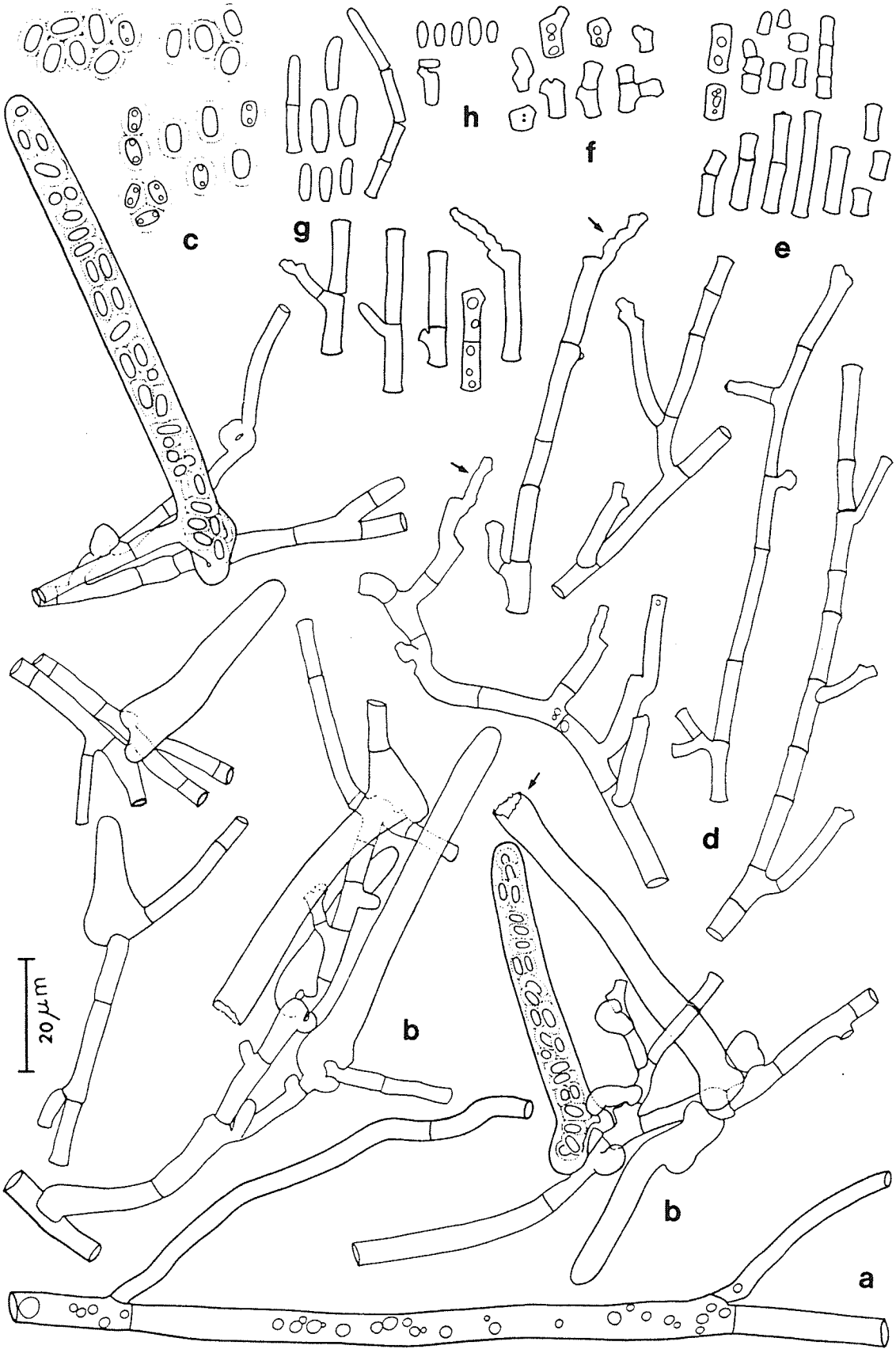
d. Portions of conidiophores; some with rachis-like proliferations («-).

e-f. Arthroconidia: both rectangular (e) and irregularly-shaped (f) conidia are illustrated; the latter are derived from the bases of disarticulating branches.

g. Holoblastic conidia and thin arthroconidia.

h. A primary conidium producing secondary conidia.

Isolate as illustrated: 3C: a-h.


a
b
b
c
d
e
f
g
h
20 µm

ellipsoid with a distinct mucilaginous sheath; 4.0 - 5.0(5.5) x 2.5 - 3.4 μm not including the sheath, but 6.0 - 7.3 x 4.8 - 6.0 μm including sheath (Fig. 10. c). Conidiophores thallic-arthric; micronematous to semi-macronematous; hyaline and smooth-walled; each consisting of a stem with a few branches and generally resembling the aerial hyphae (Fig. 10. d). Branches are converted to conidia by septation followed by schizolytic secession and are thus transformed into delicate, branched conidial chains. After conversion and secession of a branch, other branches may develop from the side of the previous secession scar, and this results in short, rachis-like proliferations (Fig. 10. d «-) of the branching point. When short, these secondary branches may secede intact as holoblastic conidia, when longer, they disarticulate as arthroconidia. Arthroconidia 1-celled, hyaline and smooth-walled; rectangular except for the terminal conidium on each branch which has a rounded apex; never inflated; 2.5 - 18.0 x 2.0 - 4.0 μm, with flat, indistinct scars on each end (Fig. 10. e). Conidia from branching points are more irregular in shape (Fig. 10. f). Cylindrical conidia that develop holoblastically are present in low numbers; these are 9.0 - 18.5 x 2.0 - 2.5 μm with a rounded apex and taper slightly at the truncate base (Fig. 10. g). Primary conidia may produce secondary conidia on short, sympodially proliferating pegs. Such conidia are short-cylindrical to slightly curved and measure 4.0 - 6.5 x 2.0 - 2.7 μm (Fig. 10. h).

HOST: Pinus contorta Dougl. ex Loud.

CULTURE EXAMINED: **Canada:** 3C, isolated from P. contorta, Hwy. 14, about 15 km west of Sooke, Vancouver Island, British Columbia, collected 17 September 1987.

First described from Sweden, where it was isolated from pupal galleries of Ips acuminatus Gyll. in Pinus sylvestris L. by Francke-Grosmann (1952), this species has been reported from many host/insect associations (Batra 1959, 1967; de Hoog et al. 1986; Tsuneda 1987), often specifically as an ambrosia fungus (either primary or auxiliary) (Batra 1967, 1987), and from other substrata (Batra 1959). It is well known from Europe and North America.

Batra (1959) described the cytology, morphology, and life history of this organism, although the mode of conidiogenesis (meristem-arthrospores) he reported was later considered to be of the typical thallic-arthric type (de Hoog et al. 1986). The conidiogenesis may continue by formation of new branches lateral to the secession scar of the earlier branch, and this results in a short, geniculate rachis with broad, flat scars. Tsuneda (1987), with the aid of scanning electron microscopy, demonstrated the pleomorphic nature of the anamorph, which was also reflected in the conidia of isolate 3C.

This isolate corresponds well with previous descriptions (Batra 1959; de Hoog et al. 1986), although both some of the asci and ascospores measured were slightly smaller than recorded previously.

D. aggregatus has cylindrical asci with a rounded apex, thus

differing from D. albidus Lagerh. which has longer, tapered asci with smaller and more numerous ascospores. D. aggregatus also has longer asci and larger, more numerous spores than D. geniculatus de Hoog et al.

D. aggregatus is one of the fungi commonly found in associations with bark-inhabiting insects, sometimes in mutualistic symbiotic relationships with ambrosia beetles, but often either simply growing in insects galleries, or on slime fluxes of injured trees (Batra 1987). Although isolated only once in this study, it is one of the species which is commonly recorded from this habitat.

Engyodontium de Hoog, Persoonia 10:53. 1978

Type species: Engyodontium parvisporum (Petch) de Hoog

Teleomorphic genus: Torrubiella Boud.

Species of the genus Engyodontium are characterized by white, delicate colonies; creeping to sub-erect often verticillate conidiophores; and subulate to cylindrical, polyblastic conidiogenous cells which produce small, hyaline, 1-celled conidia on denticles arising from elongating rachises (de Hoog 1978). Conidiogenesis is either progressive or retrogressive (Gams et al. 1984).

Engyodontium species are entomogenous, but are often found on spiders, and have also been isolated from soil, air, and humans (Gams et al. 1984; de Hoog 1972, 1978).

De Hoog (1978) based his concept of the genus on E. parvisporum (Petch) de Hoog, and also transferred Beauveria alba (Limber) Saccas to Engyodontium, but noted there were clearly defined differences between these species. Later Gams et al. (1984) broadened the generic concept somewhat by including species such as E. aranearum (Cavara) Gams et al., which in addition to forming the majority of its conidia on denticles, also produces some from true phialides.

Thus this genus appears to be a heterogeneous assemblage of species, particularly with respect to the method of conidiogenesis. Some, like E. album, form their conidia in a very organized fashion at the apices of discrete conidiogenous cells, others produce them on

denticles on the hyphae or from the apices of conidiogenous cells that are often irregular in shape.

Engyodontium differs from species of Verticillium sect. Prostrata W. Gams in producing holoblastic conidia on denticles, from Aphanocladium species by forming more than one conidium per conidiogenous cell, and from Beauveria species in lacking an inflated basal portion to the conidiogenous cells.

Currently at least six species have been placed in this genus, but at least one additional species has been provisionally assigned (Gams et al. 1984).

Engyodontium album (Limber) de Hoog, Persoonia **10**:53. 1978

Fig. 11. a-h.

≡Tritirachium album Limber, Mycologia **32**:27. 1940

≡Beauveria alba (Limber) Saccas, Revue Mycol. **13**:64. 1948

Colonies attaining a diameter of 30 - 32 mm in 12 days at 20°C in darkness on MEA.YE. Colonies white (2.5Y $^{8}/_{0}$); floccose and nematogenous; conidiogenesis most abundant at the surface of the medium; the dry conidia develop apically, as a wider, cream-coloured cylinder on the white, thin conidiogenous cells and resemble tiny bottle brushes (Fig. 11. a). In reverse, colonies are white to pale yellow (2.5Y $^{8}/_{2}$ to $^{8}/_{4}$), sometimes becoming light yellowish brown to reddish yellow (10YR $^{6}/_{4}$ to 5YR $^{7}/_{8}$) in small areas in the centre of aging colonies. Odour indistinct. Exudate present as small clear drops. Crystals lacking. Hyphae hyaline and smooth-walled; the aerial hyphae are 0.8 - 2.5 µm in diameter; the submerged hyphae (Fig. 11. b) are up to 3.5 µm wide, filled with oily appearing substances, loosely interwoven, and may be slightly inflated in an irregular fashion. Chlamydospores were not seen. Conidiophores are sympodial and micronematous to semi-macronematous; erect or prostrate, quite long and 1.0 - 2.3 µm wide, but resembling the aerial hyphae; the sympodulae arise in terminal whorls of 2 - 4; and rather widely spaced along the conidiophores (Fig. 11. a), either singly, 2 - 3 in whorls, or occasionally the 1 - 2 sympodulae are subtended by a short branch (Fig. 11. d,e,f). Conidiogenous cells sympodial (sympodulae), hyaline, and smooth-walled; subulate to

Fig. 11. Engyodontium album (Limber) de Hoog
(isolates: 79'', 136d')

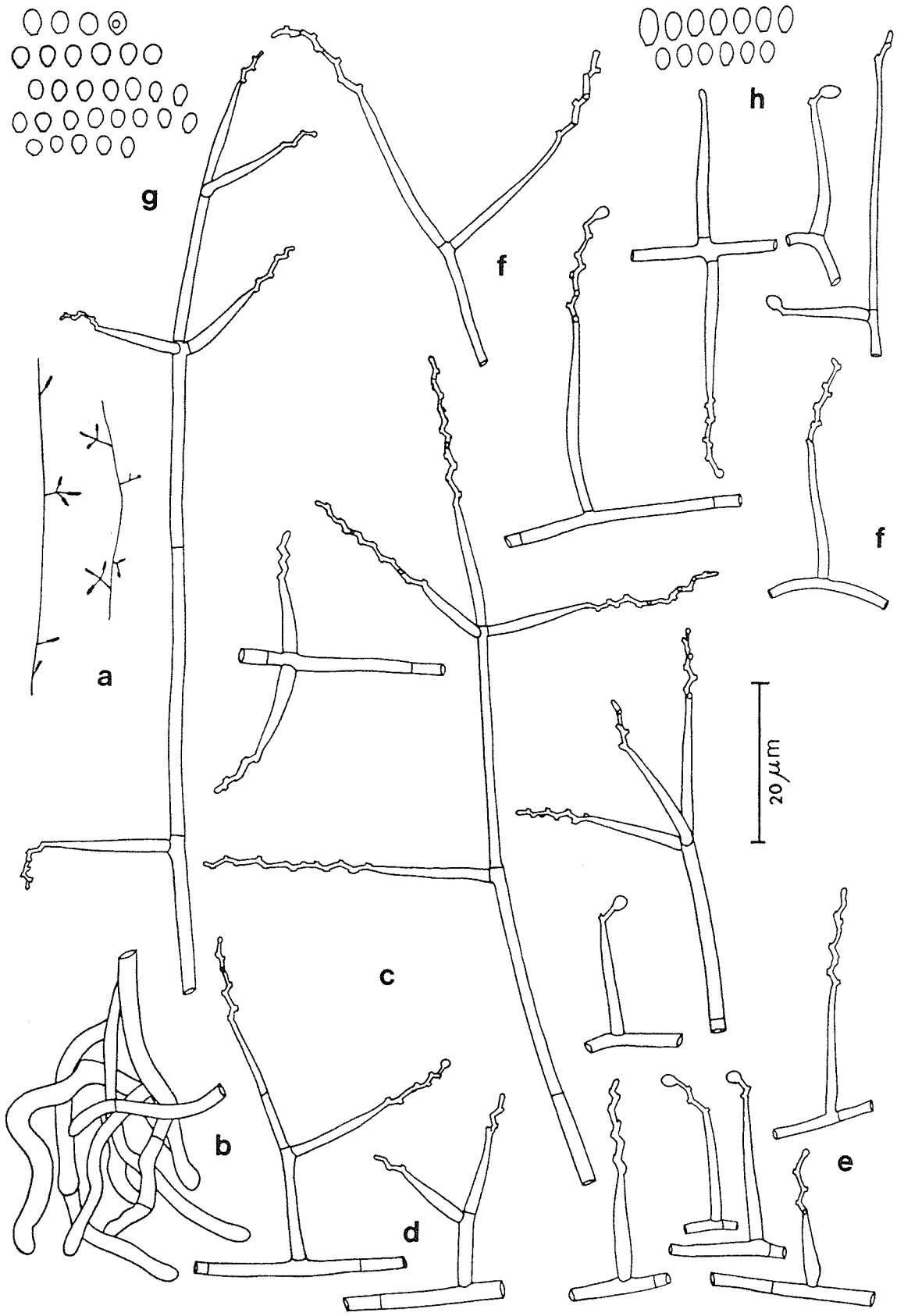
a. Conidiophores bearing conidia on the rachises; habit sketch.

b. Submerged hyphae.

c-f. Conidiophores; (c) with apical whorls; (d) sympodulae subtended by a short branch; (e, f) sympodulae borne singly or in pairs on undifferentiated hyphae.

g-h. Sympodioconidia.

Isolates as illustrated: 79'': b, c, d, e, g.
136d': f, h.


g
h
f
f
a
c
20 µm
b
d
e

subcylindrical and gradually tapering to the apex; 8.0 - 23 x 1.3 - 1.7(2.0) μm, producing the conidia on 0.7 - 0.9 μm wide geniculate, denticulate rachises which may become at least 20 μm long, the denticles being 0.5 - 0.7 x 0.6 - 0.9 μm. Sympodioconidia dry, 1-celled, hyaline, and smooth-walled; subglobose, 2.0 - 3.0 x 1.6 - 2.5 μm; sometimes indistinctly pedicellate and truncate (Fig. 11. g,h).

HOSTS: Pinus radiata, Podocarpus sp.

CULTURES EXAMINED: **New Zealand:** 79'', isolated from P. radiata, near Forest Headquarters, Tairua State Forest, Coromandel, collected 20 May 1982; 136d', isolated from Podocarpus sp., near Minginui, Urewera National Park, Taupo, collected 11 June 1982.

This species, described as Tritirachium album by Limber (1940) was first found growing in conjunction with Penicillium intricatum Thom which had been isolated from the cover of a book. Since then it has been isolated from diverse substrata e.g. humans, cat skin, soybean nematode cysts, fresco, soils, larch, peas, wheat, algae, and air (Anon 1975; Anon 1987a; Anon 1987b; Carris et al. 1989; de Hoog 1972; Matsushima 1975; Mugnai et al. 1989). Obviously, it is not restricted as to the type of material it can grow in or on! However, no previous records of E. album from New Zealand were located.

While the sympodially produced conidia developing on thin, denticulate rachises, combined with the verticillate arrangement of

subulate conidiogenous cells and the fine hyaline hyphae allows easy identification of representatives of this species, this combination of morphological characters also clearly sets it apart from those species more central to the genus Engyodontium.

Although originally assigned to Tritirachium, a genus which had been erected by Limber (1940) to accommodate species with whorls of conidiogenous cells, or branches bearing such cells, that produced conidia on zigzag-shaped rachises, geniculate, cicatrized fide de Hoog (1972), T. album was transferred to Beauveria by Saccas in 1948. De Hoog (1972) followed Saccas' treatment, but clearly other authors (MacLeod 1954; Matsushima 1975) did not consider it a Beauveria, and continued to refer to it as T. album.

Excluded from the genus Tritirachium because it lacks pigmentation in the aerial hyphae and possesses denticles on the rachises (de Hoog 1972), E. album differs from other Beauveria species in lacking an inflated portion in the conidiogenous cells, and in the fact these are arranged in whorls and not clusters. However, both the mode of conidiogenesis which results in the production of thin, geniculate, denticulate rachises, and the basic colony morphology of E. album are similar to what is found in Beauveria species.

De Hoog's (1978) transfer of this species to the genus Engyodontium de Hoog was apparently intended to make Beauveria a more homogeneous genus and, at the same time, place B. alba with other species which have narrowly cylindrical to subulate conidiogenous cells which produce conidia on denticles. However, E. album does not appear to resemble

closely the type species of Engyodontium, E. parvisporum (Petch) de Hoog. In that species the conidia are produced on very thin denticles formed on rachises which are nearly as wide as the basal portion of the conidiogenous cells. Gams et al. (1984) broadened the acceptable range of methods of conidiogenesis within the genus Engyodontium by including species which produce some conidia on denticles but others from true phialides. By doing so they reduced the diagnostic importance of conidiogenous cell morphology in this genus; species such as E. album which form their conidia on short denticles at the apices of subulate sympodulae being grouped with others that produce their conidia in a much more variable manner.

The description given above is based on isolate 79'', but isolate 136d' sporulated less, had longer and thinner sympodulae (14 - 30 x 0.9 - 1.5 μm), and produced subglobose to short-elliptical conidia that measured 2.4 - 3.3(4.0) x 1.6 - 2.1(2.4) μm (Fig. 11. h). These isolates, examined using endonuclease restriction fragment analysis of the ribosomal DNA (Georg Hausner pers. comm.), showed (virtually) identical patterns, thus confirming that such slight variation can easily be accommodated within this species as it is presently defined.

E. album differs from other Engyodontium species in only producing the conidia at the apices of the sympodulae on geniculate rachises which have regularly spaced, short, cylindrical denticles, and in having conidiophores with verticillate branching.

We are not aware of this species having been associated with wood or wood inhabiting insects before. As noted above, it has been

recovered from various substrata, including nematode cysts, but it does not appear to be entomogenous.

Erostella (Sacc.) Sacc., J. Mycol. 12:48. 1906 (May 31)

≡Erostella (Sacc.) Traverso, Fl. Ital. Cryptog. 1:156. (1905) 1906 (Oct. 15)

≡Calosphaeria subgenus Erostella Sacc., Syll. Fung. 1:101. 1882

Type species: Erostella minima (Tul. & C. Tul.) Traverso (lectotype)

Anamorphic genus: Where known, it is an intermediate between Acremonium Link and Phialophora Medlar.

A member of the Calosphaeriaceae, the only family of the Calosphaeriales, the genus Erostella is characterized by black globose ascomata which are either glabrous or ornamented with short, dark hyphae, and have papillate to elongate beak-like necks. The unitunicate, oblong to narrowly clavate, 8-spored asci have a thickened apex and truncate base, and develop in an acropetal succession from proliferating ascogenous hyphae; they thus appear clustered or spicate. The paraphyses are hyaline, smooth- and thin-walled, septate, broadest at the base, and gradually taper to the apex. The ascospores are 1-celled, hyaline and smooth-walled, and are allantoid or elliptical to oblong-elliptical.

In nature, the ascomata of Erostella species may occur singly or in irregular clusters immediately beneath the bark of the host, or in bark beetle galleries.

When known, the anamorphs grow well in culture and produce colonies which range from white to light grey, to light olive grey. They grow moderately fast, topographically are nematogenous to plectonematogenous,

and produce 1-celled, hyaline and smooth-walled conidia which aggregate in slimy drops at the apices of individual phialides. The phialides are variable, ranging from short and nearly cylindrical adelophialides (pegs), to medium-length obclavate to navicular phialides, or to longer subulate forms, but they all possess indistinct collarettes. The phialides form singly on the hyphae, or are produced singly or in pairs at the apices of short phialophores, and are then often subtended by adelophialides.

The species placed in this revived genus differ from species of the other genera of the Calosphaeriaceae primarily in the shape and manner of development of the asci and the ascogenous hyphae.

The type species, E. minima, was originally described as Calosphaeria minima Tul. & C. Tul. (1863), and although it was assigned to Calosphaeria Tul. & C. Tul., it differed markedly from Calosphaeria pulchella (Pers.: Fr.) Schroet. (=C. princeps Tul. & C. Tul.), the type of that genus, in the shape of the asci, and in the manner of their formation. C. pulchella has clavate asci with long, tapering stipes which appear to arise in fascicles from the same tissue as the paraphyses; this is quite different from that which had been described earlier for C. minima. Later, C. minima was transferred to the genus Togninia Berlese (1900), and subsequently it was incorrectly designated as the lectotype of that genus by Clements & Shear (1931). They overlooked the fact that Berlese had clearly stipulated T. ambigua Berl. was to be the type of his then new genus.

Attempts to locate the type material of T. ambigua and C. minima

were unsuccessful, but the original descriptions and illustrations (Berlese 1900, Tab. XII, Fig. 2 and Tulasne & C. Tulasne 1863, Tab. XIII, Fig. 23, 24) show that these two species are quite different. Since Togninia is based on T. ambigua, a species with clavate, stipitate asci tapering towards the base, Togninia is presumably a synonym of Jattaea Berl. (Dr. M. Barr pers. comm.) as that genus is currently delimited by Barr (1985). However, since C. minima is clearly different from members of Calosphaeria and Jattaea (Jattaea includes Togninia based on the latter's type), a separate genus is needed to accommodate C. minima and other species which have a similar arrangement of their asci. Erostella (Sacc.) Sacc. was erected for C. minima (Saccardo 1906; Traverso 1906), but later reduced to synonymy with Togninia sensu Barr (1985). However, as Togninia is now clearly a synonym of Jattaea Berl., Erostella is revived to accommodate C. minima and two related species.

The genus Erostella consists of its type, E. minima, and two additional species E. fraxinopennsylvanica (Hinds) comb. nov. prop. and E. novae-zelandiae sp. nov. prop. Illustrations and descriptions of some other species, i.e. Calosphaeria microsperma Ellis & Everh., C. socialis Berl. (Berlese 1900) and C. oxyacanthae (Sacc.) Traverso (Traverso 1906), suggest these species may also produce their asci in a similar spicate fashion, and they are possible additional candidates for transfer to Erostella. However, as there is no suggestion that they are associated with insects, they were not considered further during this study.

Erostella fraxinopennsylvanica (Hinds) comb. nov. prop.

Figs. 12A. a-h; 12B. a-h.

≡Ceratocystis fraxinopennsylvanica Hinds, Mycologia 67:719. 1975

≡Calosphaeria fraxinopennsylvanica (Hinds) Upadhyay, A monograph of Ceratocystis and Ceratocystiopsis 137. 1981

Anamorph: Variable, appearing to be intermediate between an Acremonium and a Phialophora species.

Colonies attaining a diameter of 57 mm in 21 days at 20°C in darkness on MEA.YE. When young, colonies are white (10YR $^{8}/_{1}$), but become light grey (2.5Y $^{7}/_{2}$ to 10YR $^{7}/_{2}$) in the centre; nematogenous to finely plectonematogenous and finely tufted. Conidia aggregate in hyaline droplets borne at the apex of individual phialides. In reverse, colonies are white (10YR $^{8}/_{2}$), but on aging become pale brown (10YR $^{6}/_{3}$) in the centre. Odour indistinct. Exudate is present as small, clear drops. Hyphae hyaline to light brown; smooth to verrucose; 1.5 - 5.5 μm in diameter; when funiculose, strands are 7 - 20 μm wide and composed of 2.0 - 3.5 μm wide hyphae. Chlamydospores were not seen. Phialophores micronematous, semi-macronematous, or rarely macronematous; hyaline to light brown; when brown, darkest towards the base; walls smooth to irregularly verrucose; 25 - 60 x 2.4 - 2.8(3.0) μm including the terminal phialide; phialophore axis 8 - 32 μm long, consisting of 1 - 4 cells, each of which gives rise to 1 - 2 lateral phialide(s) and/or an adelophialide (Fig. 12A. d), or the axis is lacking. Most phialophores

Fig. 12A. Erostella fraxinopennsylvanica (Hinds) comb. nov. prop. (isolate: ATCC 26664)

a-d. Micronematous to semi-macronematous phialophores; (a) adelophialides; (b) obclavate to naviculate phialides; (c) subulate phialides; (d) phialides subtended by short branches, or basal cells often with an adelophialide.

e. The only proliferating phialide found (≪-).

f. Macronematous phialophore.

g. Phialoconidia.

h. Inflated conidia producing secondary conidia on short adelophialides.

Isolate as illustrated: ATCC 26664: a-h.

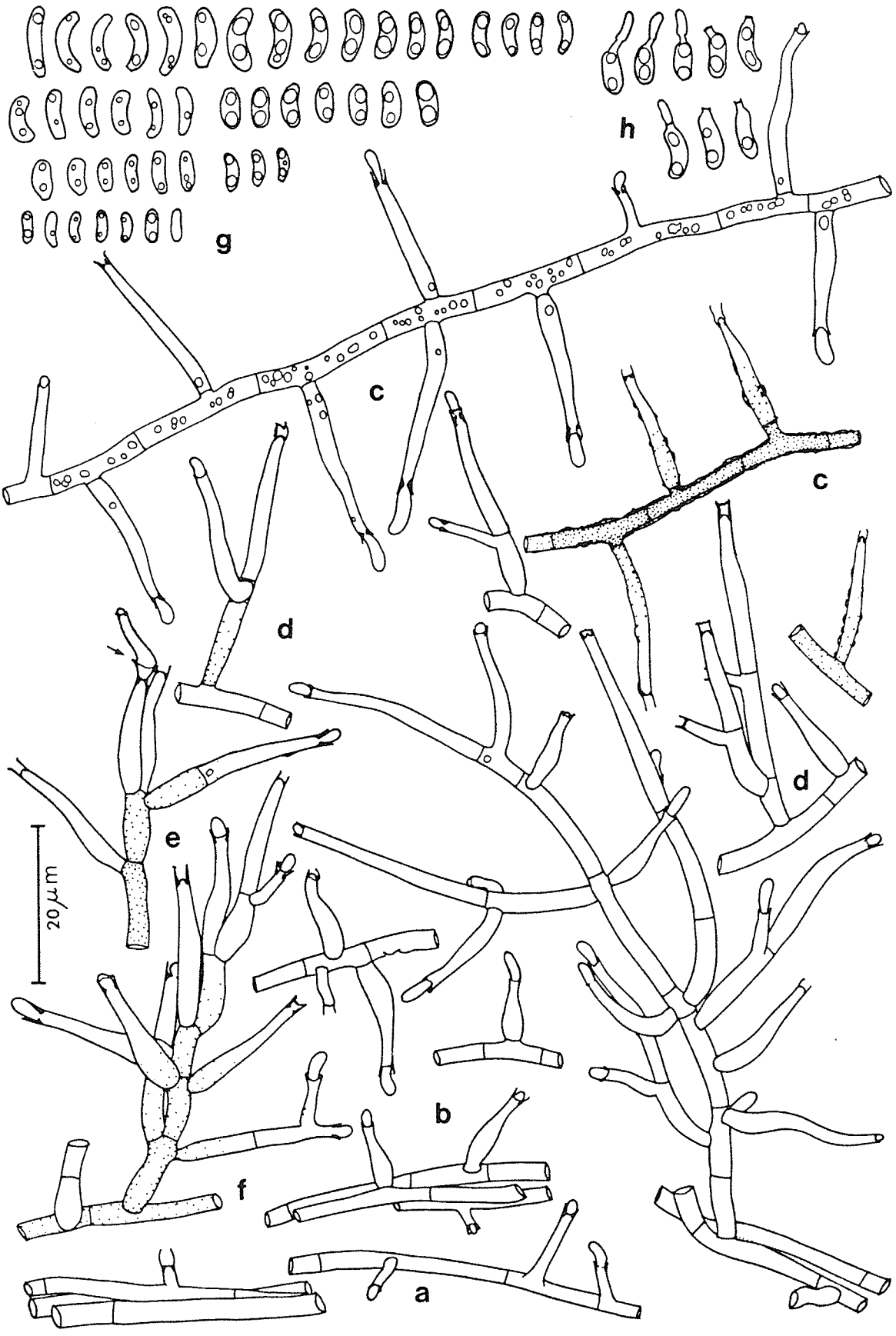

g
h
c
c
d
d
e
20 µm
f
b
a

Fig. 12B. Erostella fraxinopennsylvanica (Hinds) comb. nov. prop. (isolate: ATCC 26664)

a. Perithecia.

b. Hyphal appendages from the surface of a perithecium.

c. Outline of a perithecial neck showing the coarsely verrucose surface texture.

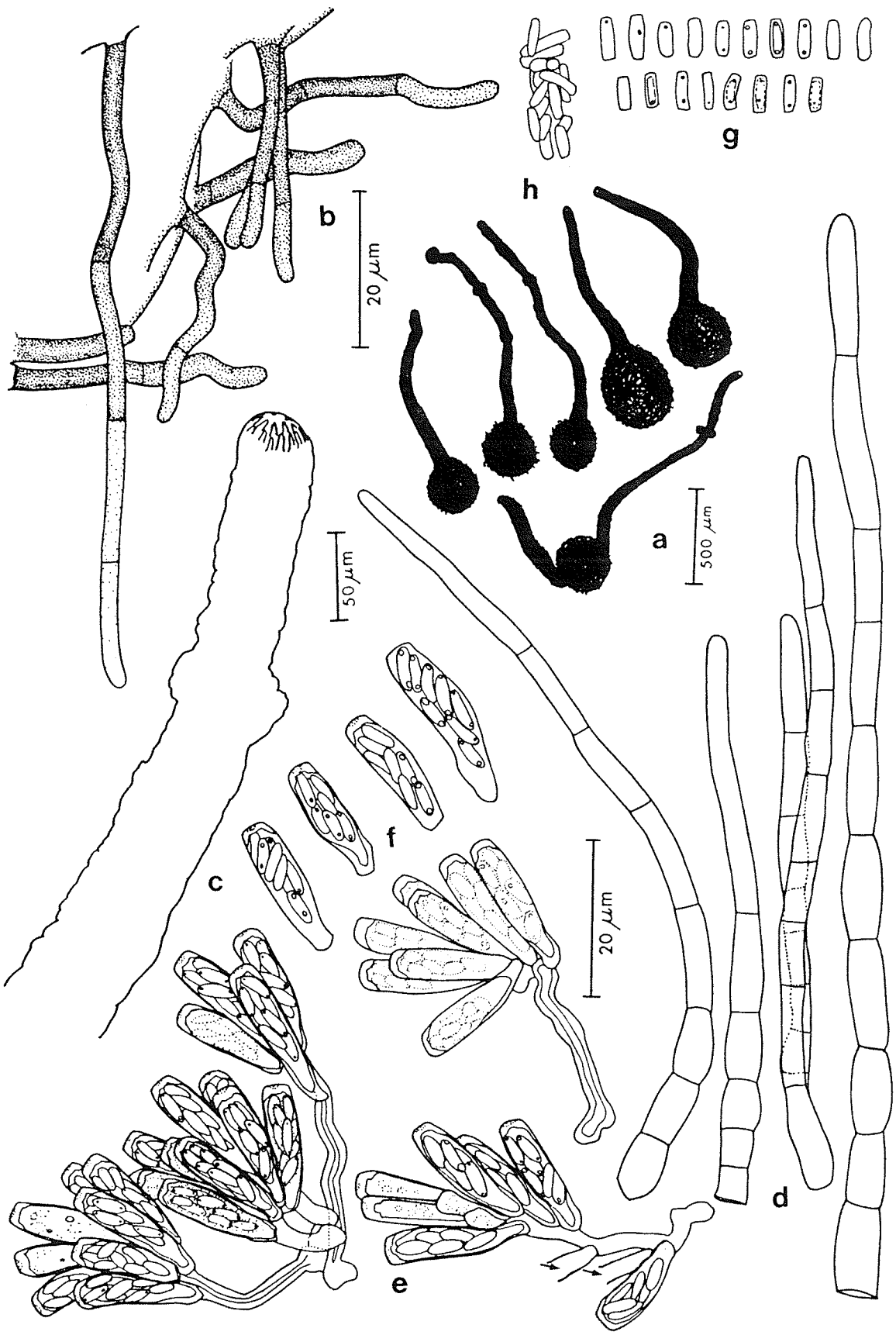
d. Paraphyses.

e. Asci arranged spicately on the generative hyphae, where the youngest asci are at the apex but the frills («-) on the lower portion were left by mature, now dehisced asci; note the inflated base of the generative hyphae.

f. Dehiscent asci.

g-h. Ascospores; some are shown clustered, as often appears to occur when spores are released from the asci.

Isolate as illustrated: ATCC 26664: a-h.


a
b
c
d
e
f
g
h
20 µm
50 µm
500 µm
20 µm

are semi-macronematous with 1 - 2 terminal phialides which are subtended by a single basal cell. This basal cell often also forms an adelophialide, and even more complex (macronematous) phialophores are also present (Fig. 12A. f). Conidiogenous cells are monophialidic; hyaline to light brown; walls smooth to verrucose; integrated or discrete. Phialides of three types: (1) adelophialides which are cylindrical or, occasionally, widest at the base then tapering to the apex, 1.0 - 9.0 x 0.9 - 2.3 μm, remaining the same or tapering to 0.9 - 1.7 μm at the apex (Fig. 12A. a); (2) obclavate to navicular, often narrowing abruptly to a short neck; 9.0 - 20.0 x 2.2 - 2.8(3.4) μm tapering to 1.3 - 1.6 μm at the apex (Fig. 12A. b); (3) subulate or slightly inflated at or just above the base, then narrowing gradually to a long neck, 17 - 28 x 2.0 - 3.2 μm tapering to 1.3 - 1.7 μm at the apex (Fig. 12A. c). All three types develop hyaline, nearly cylindrical collarettes that are 1.5 - 2.4 μm long and have a short periclinal thickening. Phialoconidia aggregate in slimy drops; 1-celled, hyaline and smooth-walled; most are cylindrical to allantoid, but a few are reniform to oblong-elliptical; (2.5)3.5 - 7.5(9.0) x 1.2 - 2.5 μm; apex rounded, base indistinctly pedicellate to rounded; usually containing 2(3) oil drops (Fig. 12A. g). Larger conidia (4.8 - 6.5 x 2.2 - 2.5 μm) often develop a short adelophialide which produces smaller conidia (microcyclic conidiogenesis) (Fig. 12A. h). Perithecia develop singly or aggregated after 2 - 4 months in culture; bases dark brown to black; globose to broadly-oval; 195 - 290 μm in diameter (Fig. 12B. a) and ornamented with 50 - 360 x 2.0 - 2.3(3.5) μm brown, septate, hyphal appendages which become hyaline

at the tip (Fig. 12B. b). Perithecia develop 1 - 2(3) black necks which are usually somewhat curved, coarsely verrucose (Fig. 12B. c), and taper gradually to lighter coloured apices; apices often proliferate secondarily on aging, and then appear nodulose; 400 - 900 x 55 - 67 μm wide at the base and tapering to 30 - 40 μm at the apex, but 50 - 70 μm wide across at the nodes. Asci arising from the generative hyphae which produce up to at least 24 asci in acropetal succession, and continue to elongate during ascus formation; the generative hyphae are hyaline, smooth-walled; 2.0 - 2.5 μm wide, and with an irregularly inflated, 2.8 - 3.5(4.0) μm wide base (Fig. 12B. e). Paraphyses hyaline, thin-walled and septate; 75 - 145 x (3.5)4.0 - 5.5 μm wide at the base and tapering to 1.7 - 3.0 μm at the apex (Fig. 12B. d). The paraphyses originate from the same pseudoparenchymatous tissue as the generative hyphae which produce the asci. Paraphyses dispersed amongst the young asci but, as the asci mature, they tend to collapse and become rather inconspicuous. Asci 8-spored; clavate with a nearly truncate apex and sides that are usually straight, but tapering, often abruptly, in the lower portion to a truncate base; base often appearing lateral as one side of the asci is often sharply curved; 16.5 - 21.0 x 4.0 - 4.8 μm (Fig. 12B. e). The apical complex is 0.9 - 1.7 μm thick, but its structure is indistinct. The asci appear to be dehiscent from the generative hyphae when mature. The ascospores are extruded from the ostiole in slimy masses; 1-celled, hyaline and smooth-walled; cylindrical to slightly curved; 4.0 - 5.2 x 1.6 - 1.8(2.0) μm; ends are nearly truncate (Fig. 12B. g,h).

HOST: Fraxinus pennsylvanica Marsh.

CULTURE EXAMINED: **United States:** ATCC 26664 derived from the type collection of Ceratocystis fraxinopennsylvanica, isolated from F. pennsylvanica (from a brown stained area associated with larval galleries of the bark beetle Leperisinus californicus Swaine), Bottineau County, North Dakota, 1970.

E. fraxinopennsylvanica has only been isolated once (Hinds & Davidson 1975), and as Upadhyay (1981) stated, it is obviously not a species of Ceratocystis sensu lato. The decision to transfer it to Erostella is based on the persistent nature of the asci, the way they are formed, the presence of paraphyses, and the nature of the perithecial necks. Presumably Upadhyay's decision for transferring it to the genus Calosphaeria was based on similar grounds, for although he gave no reasons for his decision, he certainly appears to have understood how the asci develop (see the addendum, Hinds & Davidson 1975, p.721).

Although E. fraxinopennsylvanica was not isolated during this study, it is included here because of its obvious close relationship with the new species E. novae-zelandiae, to describe the nature of its asci, paraphyses, and phialophores, and to clarify its relationship with some Calosphaeria species.

In culture, perithecial production occurred irregularly, and did not appear to be light-stimulated as in E. novae-zelandiae. However,

temporarily flooding the plates with water did assist perithecial induction, and some other external stimuli might also be effective. In E. fraxinopennsylvanica the long paraphyses are the first structures to develop in the young centrum, and the generative hyphae bearing the asci follow later. But in preparations made from mature perithecia, only the younger asci remain attached to the generative hyphae, with short frills which remain attached to the lower portion of the fertile area marking the former sites of the dehisced, older asci (Fig. 12B. e «-).

In contrast to members of the genus Calosphaeria, E. fraxinopennsylvanica has fairly straight ascospores, with spore measurements in the upper portion of the range reported by Hinds.

All the conidia are considered phialoconidia, and the "denticles" adelophialides because they have collarettes and periclinal thickenings. The shapes and sizes of the conidia both demonstrate continuous gradations, and thus the conidia cannot be easily separated into two groups as Hinds attempted to do. The larger conidia, those of Hind's exogenous group, are often produced within the medium where they may swell and sometimes undergo microcyclic conidiogenesis in situ (Fig. 12A. h). Not only do the phialides arise directly from the hyphae as illustrated by Hinds, they are also regularly subtended by one basal cell and, although less common, more complex phialophores do occur (Fig. 12A. d). The phialides do not proliferate, although very rarely a phialide can be seen subtended by an older one (Fig. 12A. e).

In paired cultures with other fungi, E. fraxinopennsylvanica was not able to overgrow the second organism nearly as well as did

E. novae-zelandiae in similar pairings, nor did it ever produce perithecia in such mixed cultures; E. novae-zelandiae did so.

Erostella minima (Tul. & C. Tul.) Traverso, Fl. Ital. Crypt. 1:156. (1905)1906 Fig. 13. a-d.

≡Calosphaeria minima Tul. & C. Tul., Sel. Fung. Carpol. 2:111-112. 1863

≡Calosphaeria (Erostella) minima Sacc., Syll. Fung. 1:101. 1882

=Calosphaeria alnicola Ellis & Everh., Proc. Acad. Nat. Sci. Philad. 1890:221. 1891

Ascomata globose to subglobose, immersed beneath the bark, and scattered to clustered; 225 - 490(525) μm in diameter; peridium smooth to covered with fine dark brown hyphae; papillate to beaked in culture. Asci unitunicate; oblong to slightly tapering; apex thickened but the base somewhat flattened; 8-spored, 20 - 30 x 4.5 - 6.0 μm; arising in acropetal succession from proliferating ascogenous hyphae (Fig. 13. a,b,). Ascospores 1-celled; uniseriate to biseriate; allantoid; hyaline; 5.0 - 6.5 x 1 - 2 μm (Fig. 13. d). Paraphyses hyaline; septate; broadest at the base and tapering towards the apex; 115 - 185 x 4.0 - 5.5 μm wide at the base, tapering to 1.5 - 2.5 at the apex; persistent (Fig. 13. a).

HOSTS: Various hardwoods in Europe and North America.

SPECIMENS EXAMINED: **United States:** New Jersey: N.A.F. 2514, Isotype, TRTC: (as Calosphaeria alnicola) Ellis & Everh., on dead alders, March 1889; **Canada:** Ontario: SSMF725-7179 (MFB6005), SSMF, TRTC: (as

Fig. 13. Erostella minima (Tul. & C. Tul.) Traverso
(collection: SSMF725-7179)

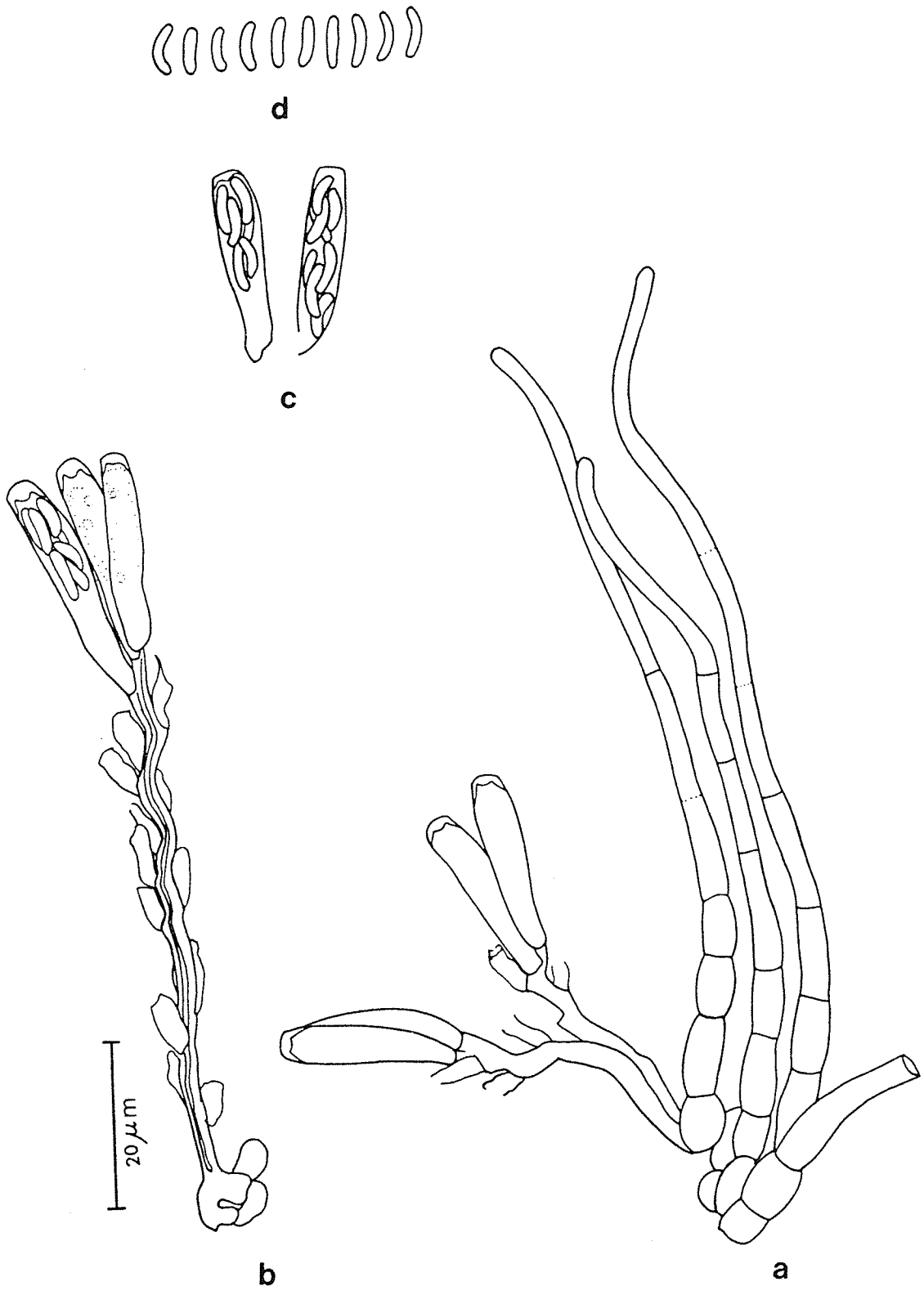
a. Paraphyses and asci.

b. Long generative hypha bearing the youngest asci at the apex, but frills below; note the inflated base.

c. Dehiscent asci with mature spores.

d. Ascospores.

Collection as illustrated: SSMF725-7179: a-d


d
c
20 µm
b
a

Calosphaeria minima) on Prunus, Madsen Mine, Baird Twp., 5 August 1960, E. Buchan; **Austria:** (as Calosphaeria minima) from dry branches of Salix, auf der Münchau by Hastenheim, Fuckel, Herbier Barbey-Boissier, 17, TRTC.

This description is based on examination of perithecia from collections SSMF725-7179 and N.A.F. 2514. This species was only examined on natural substrata where the neck of the perithecia was short, and can be described as papillate, although sometimes its length was equal to the thickness of the bark it penetrated. However, Barr (1985) identified cultures which Hoover-Litty & Hanlin (1985) had isolated from woodchips as C. minima. Here, the perithecia were described as having well developed beaks, but the nature of the anamorph was not reported.

The asci and paraphyses from the perithecia in the specimens which were examined were clearly similar in basic structure to those found in E. novae-zelandiae and E. fraxinopennsylvanica. The youngest asci remained attached to the apex of the generative hyphae, but the basal portion of these hyphae had frills where the earlier formed asci had seceded (Fig. 13. b). The asci had a thickened apex with indistinct structures, and the paraphyses were broadest at the base and somewhat constricted at the septa.

Tulasne & Tulasne (1863) described this species as usually lacking paraphyses, but accurately depicted the spicate arrangement of the asci on the generative hyphae. Berlese (1900) in Tab. XI, fig. 2, on the other hand, depicts the asci as developing directly from the basal cells

of the paraphyses, and not from the separate generative hyphae. Berlese was wrong, and Traverso (1906) also followed his interpretation. Because both the generative hyphae and the paraphyses originate from the perithecial wall, and, at first, when the generative hyphae are still short it is not always possible to distinguish the generative hyphae from the rest of the internal structures of the perithecium, such a misinterpretation of these structures can be understood. Barr (1985) briefly described the species and emphasised the nature of the proliferating ascogenous hyphae and the spicate arrangement of the asci, characters which separate this species from true Calosphaeria species.

This species is included for comparison with the other two species assigned to Erostella, and since no living material could be located, the anamorph of E. minima still remains unknown.

Erostella novae-zelandiae sp. nov. prop.

Figs. 14A. a-f, 14B. a, 14C. a-l.

Anamorph: Variable, appearing to be intermediate between an Acremonium and a Phialophora species.

Colonies attaining a diameter of 38 - 42 mm in 21 days at 20°C in darkness on MEA.YE. Colonies grown in darkness are grey (5Y $^{5}/_{1}$) at the centre, but more peripherally are pale yellow to light grey (5Y $^{8}/_{4}$ to 5Y $^{7}/_{2}$, 2.5Y $^{7}/_{2}$) and finally white (10YR $^{8}/_{1}$) at the margins. Colonies fairly flat, nematogenous to finely plectonematogenous, and consisting of hyphae and hyphal strands bearing short phialides producing conidia which aggregate in clear droplets at their apex. Colonies grown in alternating light and darkness are light grey, light brownish grey to grey and light olive grey (10YR $^{7}/_{1}$, $^{7}/_{2}$, $^{6}/_{2}$ to 5Y $^{6}/_{1}$ and $^{6}/_{2}$) and often develop grey to dark greyish brown (10YR $^{5}/_{1}$ to $^{4}/_{2}$) sectors. On aging, patches of white, loosely organized phialophores may develop. Cultures grown in the dark for three weeks, then transferred to alternating light and darkness for an additional three weeks, develop brown hyphal aggregations and brown to black protoperithecia on the surface; perithecia mature in a further four to six weeks. In reverse, dark grown colonies are grey (5Y $^{6}/_{1}$ to $^{5}/_{1}$) in the centre, white to pale yellow (5Y $^{8}/_{2}$ to $^{8}/_{3}$) towards the margin but become olive grey (5Y $^{5}/_{2}$) to dark grey (2.5Y $^{4}/_{0}$) on aging. The pigmentation develops earlier in colonies grown in light, but is uneven in distribution, being most intense in sectors. Odour indistinct, and an exudate may be

Fig. 14A. Erostella novae-zelandiae sp. nov. prop.
(isolate: 113bi)

a-d. Micronematous to semi-macronematous phialophores; (a) adelophialides; (b) obclavate to naviculate phialides; (c) subulate phialides, some subtended by short branches, or basal cells often with an adelophialide; (d) subulate phialide proliferating from an adelophialide («-).

e. Phialoconidia.

f. Inflated conidia some of which are producing secondary conidia by means of adelophialides.

Isolate as illustrated: 113bi: a-f.

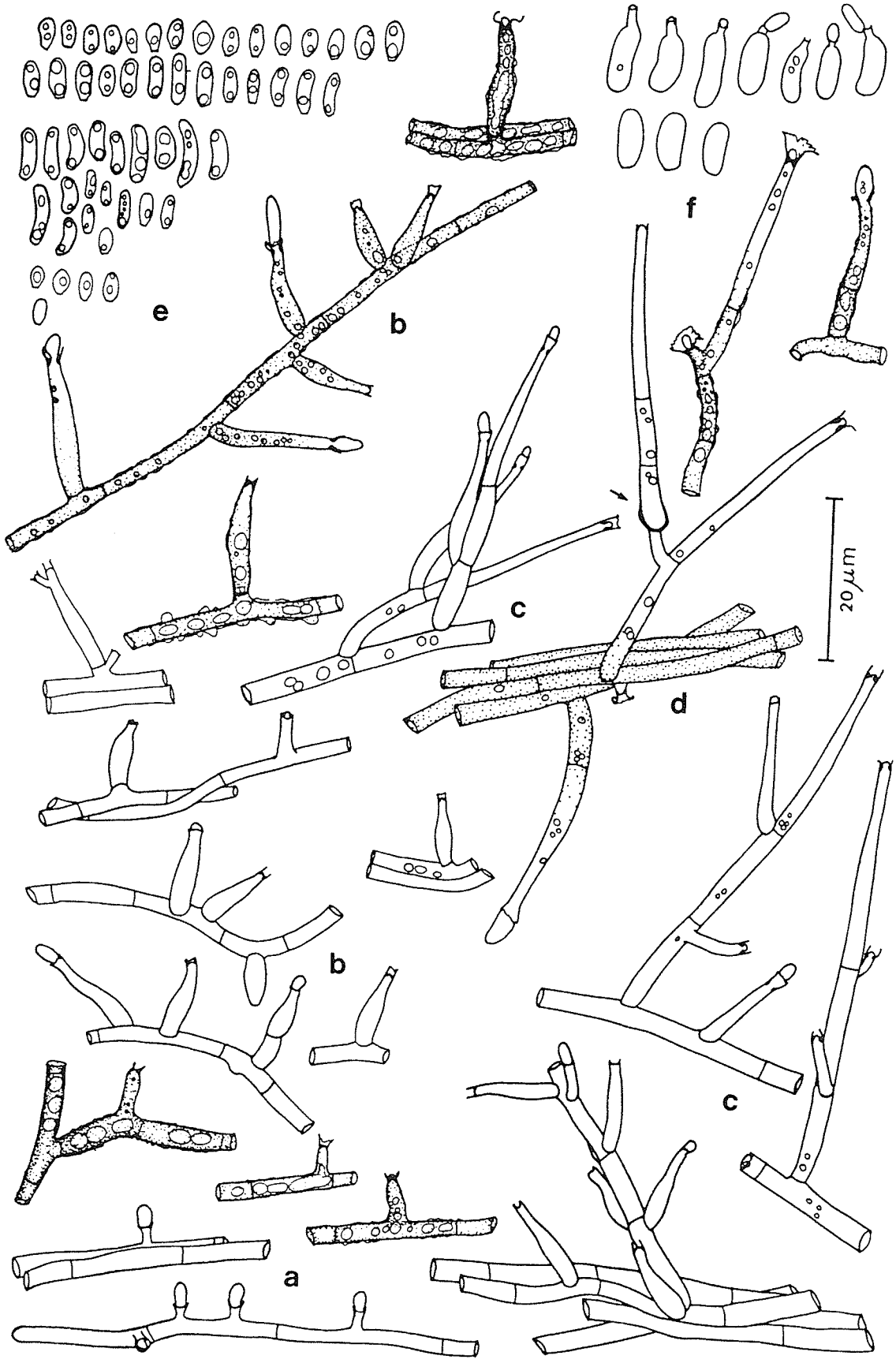

e
b
f
c
d
20 µm
b
c
a

Fig. 14B. Erostella novae-zelandiae sp. nov. prop.
(isolate: 113bi)

a. Complex phialophores from aged colonies; note the repeated proliferations of phialides, either forming short stem segments which often branch (≪-) or the new phialide is produced directly from the older one.

Isolate as illustrated: 113bi: a.

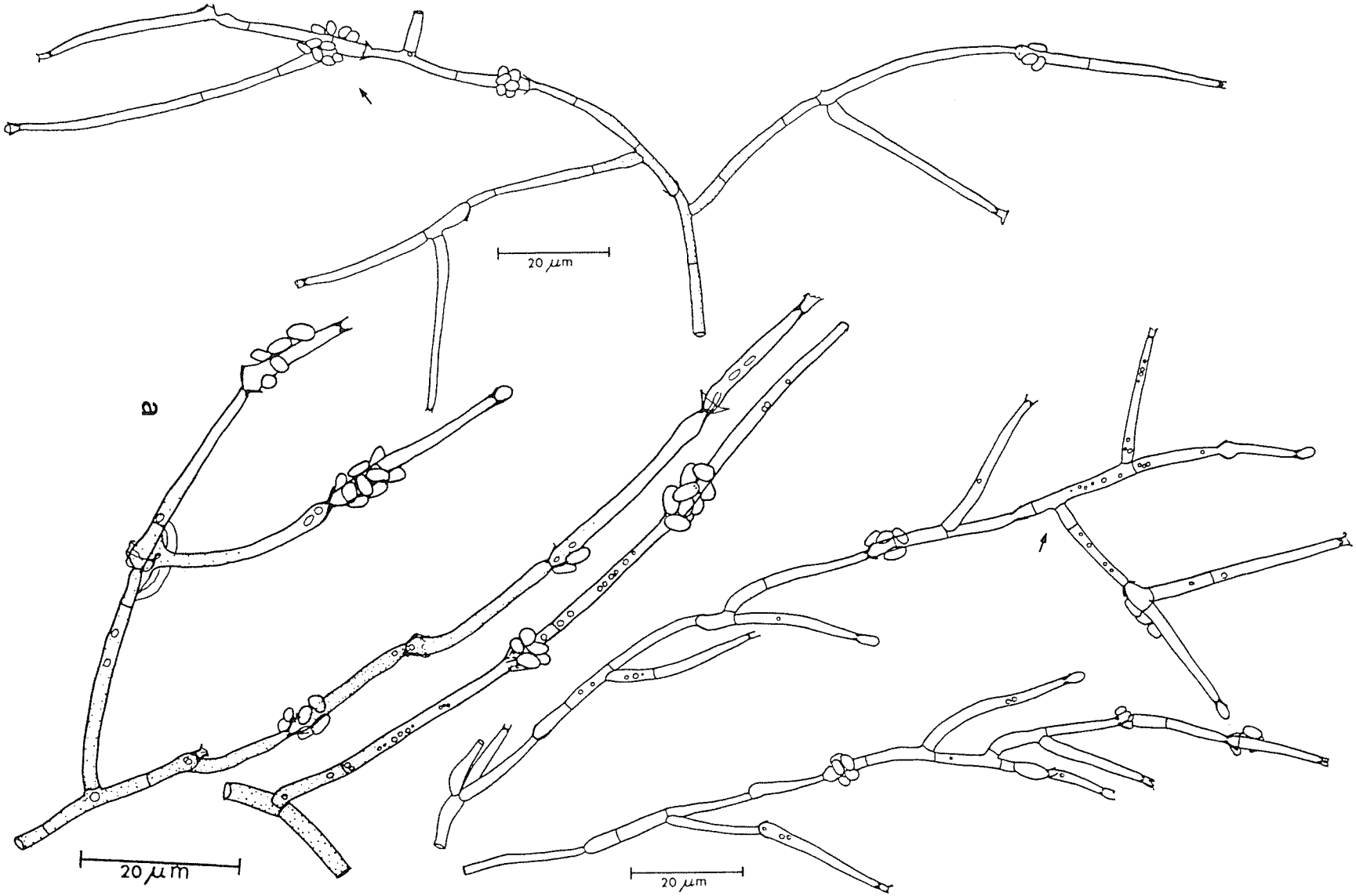

a
20 µm
20 µm
20 µm

Fig. 14C. Erostella novae-zelandiae sp. nov. prop.
(isolates: 105aii, 113bi)

a. Perithecia.

b. Hyphal appendages from the surface of a perithecium.

c. Outline of a perithecial neck showing the coarsely verrucose surface texture.

d. Hyphae from a young perithecial centrum.

e. Paraphyses.

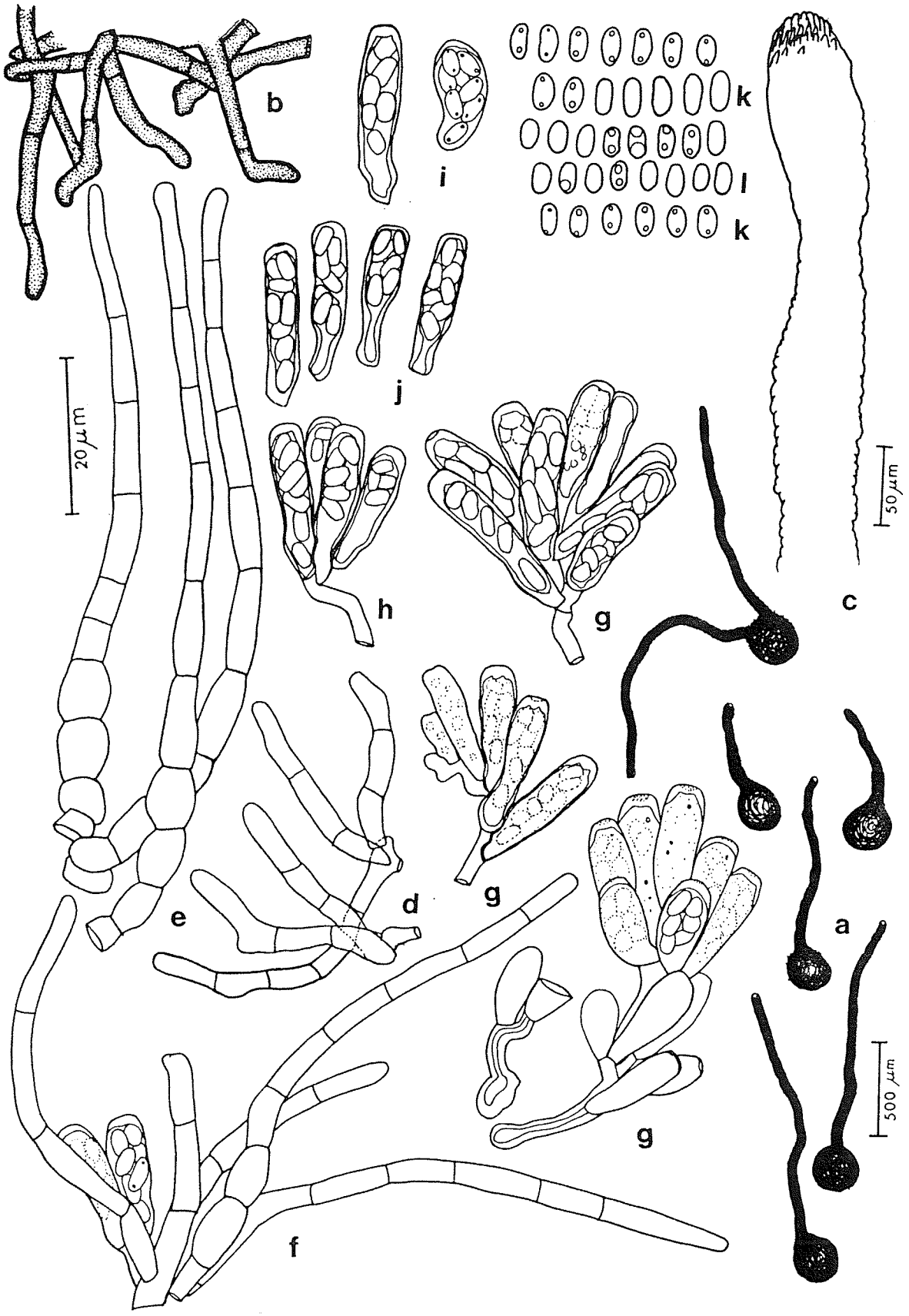
f. Paraphyses and young asci.

g-h. Asci arranged spicately on the generative hyphae; note the inflated bases of the generative hyphae.

i-j. Dehiscent asci.

k-l. Ascospores.

Isolates as illustrated: 105aii: e, h, j, l.
113bi: a, b, c, d, f, g, i, k.


b
i
k
l
k
j
20 µm
h
g
c
50 µm
g
e
d
g
a
500 µm
g
f

present as small clear drops. Hyphae hyaline to brown; smooth to verruculose; 1.5 - 4.0(4.8) μm in diameter; when funiculose, strands are 5 - 18 μm in diameter and comprised of 1.7 - 3.0 μm wide hyphae. Chlamydospores were not seen. Phialophores micronematous to semi-macronematous; hyaline to brown; when brown the basal elements are more darkly pigmented than those at the apex; smooth to verrucose; 20 - 75 x 2.4 - 2.8 μm; each bears 1 - 2 terminal phialides which are subtended by a stem of 1 - 3 cells, and each such cell may form a lateral adelophialide just below its apical septum (Fig. 14A. c); or the stem is lacking (Fig. 14A. a,b,). Complex, indeterminate, loosely arranged phialophores (Fig. 14B. a), which are hyaline to pale brown at the base, are found in aging cultures. These consist of subulate phialides which have proliferated terminally several times, and sometimes given rise to lateral branches (Fig. 14B. a «-). Conidiogenous cells monophialidic or, rarely, with a lateral locus; hyaline to brown; smooth to verruculose; integrated or discrete. Phialides of three types: (1) adelophialides which are usually cylindrical, but occasionally widest at the base and tapering to the apex, 2.0 - 8.5(12.0) x 1.0 - 2.3 μm, sometimes tapering to 0.9 - 1.7(2.3) μm at the apex (Fig. 14A. a); (2) obclavate to navicular and often curved, but narrowing abruptly to a short neck, 7.5 - 15.5 x 2.2 - 3.0 μm tapering to 1.0 - 1.6 μm at the apex (Fig. 14A. b); (3) subulate or slightly inflated at the base and narrowing gradually to a long neck, 16 - 33 x 1.6 - 2.4 μm tapering gradually to 1.0 - 1.6 μm at the apex (Figs. 14A. c,d; 14B. a). All three types have indistinct collarettes that are 1.0 - 1.8 μm long, and periclinal thickenings that

may make the apex slightly wider than the neck below. Phialoconidia aggregate in slimy drops; 1-celled, hyaline and smooth-walled; most are cylindrical to allantoid and measure 3.5 - 7.5(9.0) x 1.4 - 2.4 μm (Fig. 14A. e); a few are oval to short-elliptical and measure 2.4 - 4.8 x 1.5 - 2.4(2.8) μm (Fig. 14A. e); apex rounded, base indistinctly pedicellate on the thinner conidia but rounded on the broader ones. Larger conidia are formed within the medium; these are broadly oblong-elliptical to reniform, and (5.0)6.0 - 10.5 x 2.4 - 3.2(3.4) μm; they often produce a short adelophialide which develops smaller conidia (Fig. 14A. f).

Perithecia develop singly or in clusters, and the protoperithecia developing into mature perithecia in 4 - 6 weeks. Bases globose to broadly-oval; black; 175 - 265 μm in diameter (Fig. 14C. a); ornamented with short, septate, curved, dark brown, and often fairly thick-walled hyphae (Fig. 14C. b). Necks 1 - 2 per perithecium; black but light brown to hyaline at the apices, and somewhat curved; surface coarsely verrucose (Fig. 14C. c); their apical portion often becoming nodulose upon aging as the neck proliferates terminally; 450 - 1300 μm long, 40 - 65 μm wide at the base tapering to 35 - 45 μm at the apex, but at the nodules up to 65 μm wide. Asci arise from the generative hyphae which produce up to at least 15 asci in acropetal succession, and continued to elongate during ascus formation; the generative hyphae are hyaline, smooth-walled, and 1.8 - 2.5 μm wide, with an irregular, inflated, 2.5 - 4.5 μm wide base (Fig. 14C. g). Paraphyses hyaline, thin-walled, and septate; 60 - 115 x 4.0 - 5.5 μm wide at the base, tapering to 2.0 - 2.8 μm at the apex (Fig. 14C. e,f). The paraphyses

originate from the same pseudoparenchymatous tissue as the generative hyphae which produce the asci. Paraphyses dispersed amongst the young asci but, as the asci mature, they tend to collapse and become inconspicuous. Asci 8-spored; narrowly-clavate with nearly truncate apices and sides that are usually straight and tapered only in the lower portion to a truncate base; base often appearing lateral as one side is often sharply curved; 15.5 - 24 x 4.7 - 5.5(6.5) μm, but 2.3 - 4.0 μm at the base (Fig. 14C. g,h). The apical complex is 0.7 - 1.8 μm thick, but its structure is indistinct. The asci appear to be dehiscent from the generative hyphae when mature (Fig. 14C. i,j). Ascospores extruded from the ostiole in slimy masses; 1-celled, hyaline and smooth-walled; elliptical to oblong-elliptical; 3.8 - 5.6 x (1.8)2.2 - 2.6 μm; biguttulate during late stages of development but the oily droplets may be absent from the mature spores (Fig. 14C. k,l).

HOLOTYPE: **New Zealand:** Dried culture of isolate 113bi, isolated from C. macrocarpa, Compartment 14, Woodhill State Forest, Auckland, collected by J. Reid, 25 May 1982.

HOSTS: Cupressus macrocarpa Hartw., Pinus radiata.

CULTURES EXAMINED: **New Zealand:** 113bi, isolated from C. macrocarpa, Compartment 14, Woodhill State Forest, Auckland, collected 25 May 1982; 116c', isolated from P. radiata, Compartment 24, Woodhill State Forest, Auckland, collected 25 May 1982; 89bi, isolated from P. radiata, off

Road 41, Whangapoua State Forest, Coromandel, collected 19 May 1982; 105aii, isolated from P. radiata, off Highway 25, Whangapoua State Forest, Coromandel, collected 19 May 1982.

Initially, prior to the development of the teleomorph in culture, it was difficult to find a genus that would accommodate all the morphological features expressed by the anamorph.

Based on cultural characteristics and phialide shape, E. novae-zelandiae does resemble some species of the genus Phialophora Medler, but the lack of distinct collarettes on any of the phialide types makes assignment to this genus unwarranted; the presence of phialide collarettes are deemed a key character of Phialophora species. Gams & McGinnis (1983) reintroduced the genus Lecythophora Nannfeldt (Melin & Nannfeldt 1934) for Phialophora species with adelophialides, but the characteristics they cited for such adelophialides are not found in the anamorph of E. novae-zelandiae, thus Lecythophora is also an unsuitable choice. The anamorph of E. novae-zelandiae is also excluded from Acremonium Link (section Gliomastix) because the colonies become darkly pigmented, but are not difficult to cut through. Gams & McGinnis (1983) erected Phialemonium W. Gams & McGinnis for species intermediate between the genera Acremonium and Phialophora, and the anamorphic state of E. novae-zelandiae also seems to belong somewhere between those same two genera. However, this fungus, differs from any described Phialemonium species in having broader hyphae, adelophialides with collarettes and distinct periclinal thickenings, and producing a large number of

discrete phialides which may proliferate secondarily. Thus, the anamorph of E. novae-zelandiae may represent another line of intermediate forms between Acremonium and Phialophora.

The long necked, black perithecia superficially resemble those of some members of the genus Ceratocystis Ellis & Halst. sensu lato. However, they differ significantly from those of any described Ceratocystis species in the development, arrangement, and persistence of the asci. Asci of Ceratocystis species are evanescent, and develop in an irregularly scattered manner inside the perithecial base (Upadhyay 1981). They are usually subglobose, thin-walled, and lack any apical specialization; paraphyses are also lacking. But as noted, the asci of E. novae-zelandiae develop in acropetal succession forming clusters of asci arranged apically on short hyphae; the latter arise between long paraphyses. The asci are clearly not evanescent in the sense of Ceratocystis species, but although they possess thickened apices the exact nature of spore release is still uncertain. Mounts of gently squashed perithecia revealed asci containing mature spores were dehisced intact from their locus of formation, and floated freely in the mountant; those with immature spores remained attached to the generative hyphae. It is possible the ascal walls do eventually disintegrate to a degree, since spores in groups of eight with some adherent material, but no walls, were often found in preparations made from older perithecia.

The overall surface of the perithecial necks in members of the genus Ceratocystis is generally relatively smooth when compared to the coarsely verrucose necks of E. novae-zelandiae (Fig. 14C. c).

This organism resembles Calosphaeria fraxinopennsylvanica (Hinds) Upadhyay (≡Ceratocystis fraxinopennsylvanica Hinds in Hinds & Davidson, 1975). However, examination of culture ATCC 26664, derived from the type collection of Cer. fraxinopennsylvanica, showed clearly that while Cer. fraxinopennsylvanica and E. novae-zelandiae are congeneric, they represent different species. E. novae-zelandiae is more darkly pigmented and slower growing than E. fraxinopennsylvanica. Further, the former has oblong-elliptical ascospores, broader asci (4.7 - 5.5 μm), and shorter perithecial hairs than the latter whose asci are 4.0 - 4.8 μm wide and contain allantoid ascospores. Both species produce conidia by phialides which range from short adelophialides to longer subulate phialides. Both also produce conidia submerged in the medium which often swell and may germinate into adelophialides which secondarily produce smaller conidia (microcyclic conidiogenesis).

Isolate 89bi differs somewhat from the species description provided above. It is faster growing (50 mm in 21 days), forms fewer dark sectors, and the colonies are not yellowish when grown in darkness. It also seems to need conditions different from those of the other isolates to form perithecia. Indeed, it produced perithecia very infrequently, but those that did form were identical to those of the other isolates.

Light exposure stimulates perithecial production, with protoperithecia developing from aggregations of brown superficial hyphae in 5 to 7-week old colonies. The centra of the developing perithecia consist of short, thin-walled, hyaline, 2.5 - 3.2 μm wide hyphae (Fig. 14C. d) which elongate apically to form the paraphyses (Fig. 14C. e,f). Thus,

the paraphyses are present before the asci start to develop, and it is only when the perithecial necks begin to elongate that the first asci are found developing amongst the paraphyses.

Although E. novae-zelandiae grows relatively slowly in culture, when paired with other species it often overgrows the other fungus. The perithecia formed in such paired cultures have longer necks and appear slightly more robust than most perithecia formed in pure culture. Such was the case when it was paired with four different fungi, Sclerotium hydrophilum Sacc., Epicoccum nigrum Link, a Cladosporium sp., and isolate 113d which produced abundant brown mycelium but remained sterile. Thus, E. novae-zelandiae may either be partially dependant on chemicals produced by the host fungus, or it might be actively parasitic on the other species.

Gliocladium Corda, Icon. Fung. 4:30. 1840

[including members of Clonostachys Corda, Pracht-fl. 31. 1839]

Type species: Gliocladium penicillioides Corda, the anamorph of Sphaerostilbella aureonitens (Tul. & C. Tul.) Seifert et al. (≡Hypomyces aureo-nitens Tul. & C. Tul.)

Teleomorphic genera: Hypocrea Fr., Nectria Fr., ?Nectriopsis Maire, Roumegueriella Speg., Sphaerostilbella Sacc.

Members of the genus are quite variable. Colonies grow at medium to fast rates, phialophores are mononematous or occasionally synnematous (determinate), erect and often verrucose, and branch apically to form a penicillus. In addition to the penicillate phialophores, some species form simple verticillate phialophores; then, the former bear relatively short phialides, but the latter longer, often subulate phialides. Conidiogenous cells are phialidic and cylindrical to subulate. Phialoconidia aggregate in slimy drops, masses, or columns, all of which may be white, pinkish, yellowish, or green, while individual conidia are 1-celled, hyaline or green, and sometimes asymmetrical.

The verticillate phialophores bearing the long phialides have been referred to as primary conidiophores, while those which are penicillately branched bearing the shorter phialides are referred to as secondary conidiophores (Domsch et al. 1980). The primary conidiophores are relatively simple consisting of a few long phialides and few short lateral branches. The secondary conidiophores usually branch more

often, and may become quite complex consisting of many short phialides and numerous lateral branches.

Many of the species presently assigned to the genus Gliocladium are anamorphs of members of different genera of the Hypocreales, and thus may not have been provided with a specific name under Gliocladium. Other species of the genus have never been connected to a teleomorph.

This group of fungi has never been monographed, but individual species, or groups of species, have been treated either as anamorphs or with their teleomorphs (Booth 1959; Dingley 1957; Doi 1966, 1972; Domsch et al. 1980; Gams & van Zaayen 1982; Gilman 1957; Matsushima 1971, 1975; Morquer et al. 1963; Petch 1939; Pinkerton 1936; Raper & Thom 1949; Samuels 1976a; Seifert 1985; Webster 1964).

A heterogeneous assemblage of species, Gliocladium consists of two, or perhaps three, major groups which might be better accommodated in separate genera that would more accurately reflect the natural relationships amongst these fungi (Seifert 1985; Samuels & Seifert 1987; Samuels & Rossman 1979). If a two group separation were followed, one group would contain the anamorphs of Hypomyces, Sphaerostilbella, and Hypocrea species, while a second would contain the anamorphs of Nectria species. One consequence of this would be that the type G. penicillioides and those other species which also possess erect, penicillate, often verrucose phialophores and symmetric conidia, would remain circumscribed within Gliocladium. However, species such as G. roseum Bainier and similar anamorphs of members of the Nectria ochroleuca-group, all of which produce asymmetrical conidia that adhere in imbricate chains or in

columns, would be placed in Clonostachys Corda. To date, however, the correct names for the species, and other details which would result from such changes, remain unsettled (W. Gams pers. comm.) and it was thus elected not to treat G. roseum as a Clonostachys species until all matters related to such a change are fully clarified.

Samuels & Seifert (1987) noted the relationship of G. viride Matr. with both G. penicillioides and G. virens Miller et al.; with the former it shares the general morphology of the conidiophores, but with the latter the green pigmentation and shape of the conidia. G. virens resembles species of Trichoderma Pers. in fast growth rates, green pigmentation of the conidia, and inflated phialides. However, it resembles many Gliocladium species in producing the conidia in large, slimy drops, one drop on each whorl of phialides. Many Trichoderma species have Hypocrea teleomorphs, and some Hypocrea species have anamorphs which are morphologically identical to G. virens and G. viride. Thus, Hypocrea teleomorphs, green conidia, and fast growth rates are found in fungi presently accommodated in the genera Gliocladium and Trichoderma. It has been proposed that these green spored Gliocladium species might be assigned to either Trichoderma or to a separate genus (Samuels & Seifert 1987), a change which would further split the genus Gliocladium and result in three smaller, more homogeneous groups. However, it has been questioned whether such change would be practical (Seifert 1985).

At the moment there is in fact a number of genera which one must consider in attempting to identify Gliocladium-like fungi in culture.

For example there are the above mentioned Clonostachys species which produce their conidia in columns and have verticillate and penicillate phialophores. And in some Gliocladium species, the basic structure of the phialophores does resemble those found in species of the genus Penicillium Link: Fr., but true species of the latter produce conidia in dry chains, often with connectives but never in slimy drops. A few Gliocladium species form verticillate phialophores typical of species of Verticillium Nees, but their asymmetrical conidia separate them from true species of Verticillium. Another genus, Sarocladium W. Gams & Hawksworth, is characterized by species with very irregularly arranged phialides and is apparently intermediate between Verticillium and Gliocladium. Species of Dendrodochium Bonord. are sporodochial and develop individual phialophores which strongly resemble those found in Gliocladium species. In culture, when the normal stroma produced on natural substrata is lacking, Dendrodochium species can be easily mistaken for those of the genus Gliocladium. The same problem applies to species of Myrothecium Tode and some Gliocladium species with green conidia.

Gliocladium species are generally saprophytes, found on bark, wood, fruiting bodies of larger fungi, soil etc. Some species are mycoparasites. Hawksworth et al. (1983) list the number of Gliocladium species at 13, i.e. those treated by Morquer et al. (1963). In the literature it was found that at least 44 species have been described within Gliocladium but, subsequently, some of these have been reduced to synonymy with other species; the estimated number of species being close

to 30. This number does not include Gliocladium anamorphs described with their teleomorphs when the anamorph was not assigned a specific epithet.

Gliocladium kaingaroae spec. nov. prop. Fig. 15. a-f.

ETYMOLOGY: Derived from the name of Kaingaroa State Forest, Taupo, New Zealand, where the collections were obtained from which the cultures of this species were isolated.

Colonies attaining a diameter of 16 - 18 mm in 12 days at 20°C in darkness on MEA.YE. When young, colonies are yellow (2.5Y $^{8}/_{6}$ to $^{8}/_{8}$) and nematogenous to plectonematogenous in the centre, phalacrogenous at the edge, but with a light reflecting surface; colonies finally become olive (5Y $^{5}/_{3}$, $^{4}/_{3}$, $^{4}/_{4}$), and the surfaces of the colonies are then covered with simple phialophores and conidia aggregated in small slimy droplets at the apex of the individual phialides. On further aging, colonies develop more complex, larger, acrotonously branched phialophores, each bearing a single medium-sized, hyaline to yellow (5Y $^{7}/_{8}$) slimy drop containing conidia; later such drops may fuse thus forming larger, yellow conidial masses. In light, these slimy drops containing the conidia appear pink (5YR $^{8}/_{4}$). In reverse, when young, colonies are yellow (2.5Y $^{7}/_{8}$), but become olive (5Y $^{5}/_{6}$) on aging with occasional yellow (5Y 7/8) areas. When isolates are grown on cellulose and RFA medium, the larger phialophores arise from submerged hyphae. Odour indistinct. Exudate present as small clear drops on the hyphae. A yellow to greenish pigment diffuses into the medium and may surround the periphery of the colonies, but it is usually more abundant amongst the submerged hyphae where it is deposited as minute, densely aggregated

Fig. 15. Gliocladium kaingaroae sp. nov. prop.
(isolates: 415A, 457A'')

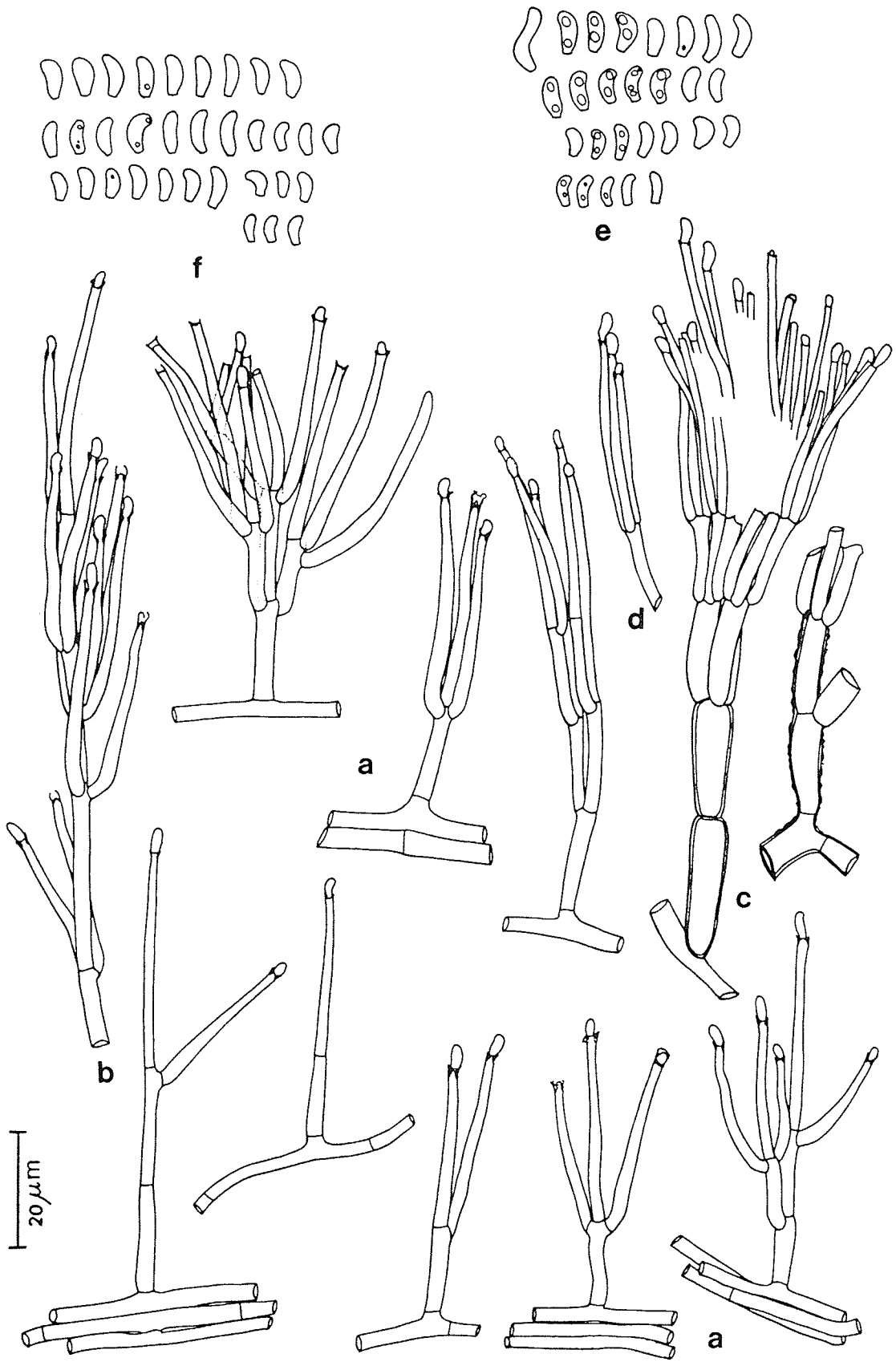
a-b. Micronematous to semi-macronematous phialophores.

c. A detailed illustration of a macronematous phialophores and the lower portion of a second phialophore which illustrates the verrucose nature of the cell walls.

d. Convergent phialides arising from a metula.

e-f. Phialoconidia.

Isolates as illustrated: 415A: b, f.
457A'': a, c, d, e.


f
e
d
a
b
c
a
20 µm

drops of a yellow, oily-appearing substance; beneath very old colonies brown crystals are present in the medium. Hyphae hyaline to strongly yellow; 1.6 - 5.5 μm in diameter; smooth-walled or rarely finely encrusted with yellow deposits; when funiculose, strands are 8 - 40 μm in diameter and comprised of fairly wide individual hyphae. Chlamydospores were not seen. Phialophores of two types: (1) micronematous to semi-macronematous; hyaline to yellow and smooth-walled; branching basitonously, each branch bearing 1 - 4 terminal phialides which are divergent when 3 or less in number, but parallel or convergent otherwise; 50 - 145 x 2.5 - 6.5 μm, with a 12 - 20 x 2.5 - 6.5 μm basal cell and 0 - 6 series of branches subtending the terminal phialides (Fig. 15. a,b); (2) macronematous, mononematous, and arising primarily from the aerial mycelium; hyaline; with broad basal cells that sometimes branch into 2 - 3 major stems each of which also branches. This results in the formation of a compact apex consisting of thin metulae that give rise to 3 - 5 parallel to convergent phialides. Such phialophores are 75 - 175 x 4.5 - 8.0 μm overall, with a 0 - 5 septate stem which is often verrucose, particularly the basal cells thereof, and constricted at the septa. Verticillate branching of the phialophore stem starts with the formation of 2 - 4 short cells. These are the first of 2 - 7 series of short compact branches which form a penicillus, but the phialides only originate from the apical 1 - 2 series of branches (Fig. 15. c). On aging, new conidiophores may arise from the middle branches of the phialophores. Conidiogenous cells monophialidic and discrete or integrated; hyaline and smooth-walled; of two types. (1) Those arising from

simple phialophores are subulate and often wavy in outline below the apex, 20 - 55 x (1.7)2.0 - 2.5 μm tapering to 1.4 - 1.8 μm at the apex (Fig. 15. a,b); and (2) those arising from complex phialophores are subulate to cylindrical, 25 - 33 x 1.6 - 1.8 μm tapering gradually to 1.1 - 1.5 μm at the apex (Fig. 15. c,d); collarette indistinct, but 0.5 - 1.7 μm long. The phialoconidia which coalesce in slimy drops are 1-celled, hyaline and smooth-walled, but often become yellowish and verrucose on aging; often subcylindrical, but usually unequally curved, with most of the curvature being in the slightly wider apical half of each conidium; 4.4 - 7.5(8.0) x 1.7 - 2.6(3.2) μm; apex rounded, base truncate (Fig. 15. e,f). No differences exist between the conidia formed on simple and complex phialophores.

HOSTS: Pinus nigra Arnold, P. radiata

CULTURES EXAMINED: **New Zealand:** 415A, isolated from P. nigra, Compartment 1082, Kaingaroa State Forest, Taupo, 29 February 1988; 457A'', isolated from P. radiata, Compartment 2, Kaingaroa State Forest, Taupo, collected 28 February 1988.

G. kaingaroae has simple phialophores that are often verticillate and more complex penicillate phialophore forms; such a combination of characters could place this species in the genus Clonostachys Corda. However, one of the main characteristics of that genus is that its species produce conidia that adhere in columns. No columns or chains

were observed in these isolates. Therefore this species is assigned to Gliocladium sensu lato while awaiting clarification of the generic concept of Clonostachys. The strong yellow pigment that may become olive coloured in aging colonies and is present in both the hyphae and the medium, together with the curved conidia, suggest a relationship to members of the genus Nectria (W. Gams pers. comm.), although no teleomorph was observed in culture.

The stem of each penicillate phialophore is broad but relatively short, and bears a penicillus which increases in width with the formation of each successive series of smaller branches; this results in the formation of a dense layer of parallel phialides at the apex of each phialophore. Therefore, the phialophores are tapered gradually from the broad apex supporting the conidial drop, down to the stem, and may resemble a small synnema arising from a single hyphal element. Both types of phialophores developed in cultures derived from a single conidium proving the pleoanamorphic nature of the fungus. No difference was noted between conidia formed on the different phialophores.

The yellow to olive colouration of the colonies on MEA.YE, the simpler, often verticillate phialophores, the curved, asymmetrical conidia, and the rather short, broad stem separate G. kaingaroae from other species of Gliocladium sensu lato. Before the penicillate phialophores are produced, G. kaingaroae resembles the darkly pigmented species of Acremonium section Nectrioidea. It resembles Verticillium olivaceum and A. berkeleyanum in the coloration of the colonies, but does not have the constricted phialidic apices of the former and grows

more slowly than A. berkeleyanum which also has more divergent phialophores. It is the presence of the large, penicillate phialophores that most clearly separates G. kaingaroae from these two species. The large phialophores of G. kaingaroae are never darkly pigmented and the phialides have indistinct collarettes. This species is thus easily distinguished from species of the genus Phialocephala Kendrick, which is a genus comprised of dematiaceous species whose conidia are formed within distinct collarettes.

No major differences were noted between the two isolates of this species.

G. kaingaroae was isolated only twice from the New Zealand material available during this study, and therefore cannot be considered a common inhabitant of the bark beetle galleries. In its pleoanamorphic nature it resembles the anamorphs of some Ceratocystis species, where a simple micronematous form often precedes the more complex macronematous form. The pleoanamorphic phialophores of G. kaingaroae may thus be a further adaptation to dispersal of its slimy conidia by beetles.

Gliocladium roseum Bainier, Bull. Soc. Mycol. France 23:111. 1907

Figs. 16A. a-i, 16B. a-d.

Teleomorph: Nectria ochroleuca (Schwein.) Berk., Grevillea 4:16. 1875

Fig. 16A. j-l.

≡Sphaeria ochroleuca Schwein., Trans. Am. Philos. Soc. Phila. II. 4:204. 1834

For synonymy see Isaac (1954), Domsch et al. (1980), and for the teleomorph, Samuels (1976a).

Colonies attaining a diameter of (32)40 - 50 mm in 12 days at 20°C in either darkness, or in alternating light and darkness on MEA.YE. When grown in darkness, colonies are white to pinkish white (2.5Y $^{8}/_{0}$, $^{8}/_{2}$, 5Y $^{8}/_{1}$, 10YR $^{8}/_{2}$ to 7.5YR $^{8}/_{2}$), and sometimes pale yellow (5Y $^{8}/_{4}$) in the centre; finely plectonematogenous or sometimes synnematogenous; conidial production ranging from sparse to abundant, and the conidial masses being white to pale yellow in colour and relatively small in size. In reverse, colonies are very pale brown or pale yellow (10YR $^{8}/_{3}$ or 5Y $^{8}/_{3}$, $^{8}/_{4}$ to $^{8}/_{6}$). Grown in light, colonies become pink to reddish yellow (5YR $^{8}/_{4}$, $^{7}/_{4}$, $^{8}/_{3}$ to 7.5YR $^{7}/_{8}$, $^{8}/_{6}$, 7/6), are usually zonate, and sporulate more abundantly than in darkness; in reverse, they are pink to yellowish red (5YR $^{8}/_{4}$, $^{8}/_{3}$, $^{7}/_{4}$ to 7.5YR $^{7}/_{6}$, $^{7}/_{8}$, $^{8}/_{6}$). All isolates grew well on cellulose medium, with five producing yellowish to orange perithecia either individually or aggregated on a stroma after 3 - 6 weeks in alternating light and darkness. Most of the isolates produced pale-brownish sclerotia on MEA.YE. Odour indistinct. Exudate

Fig. 16A. Gliocladium roseum Bainier and its teleomorph Nectria ochroleuca (Schwein.) Berk.

Gliocladium roseum
(isolates: 50a, 89c, 100b'', 107a, 113a)

a-c. Simple phialophores bearing long phialides.

d-f. Portions of the more complex phialophores bearing short phialides.

g-i. Phialoconidia.

Isolates as illustrated: 50a: f.
89c: a, d, g.
100b'': i.
107a: c.
113a: b, e, h.

Nectria ochroleuca
(isolates: 25a, 105aii'')

j. Cluster of perithecia, habit sketch.

k. Ascus and ascospores.

l. Ascospores and the apical portion of an ascus.

Isolates as illustrated: 25a: j, l.
105aii'': k.

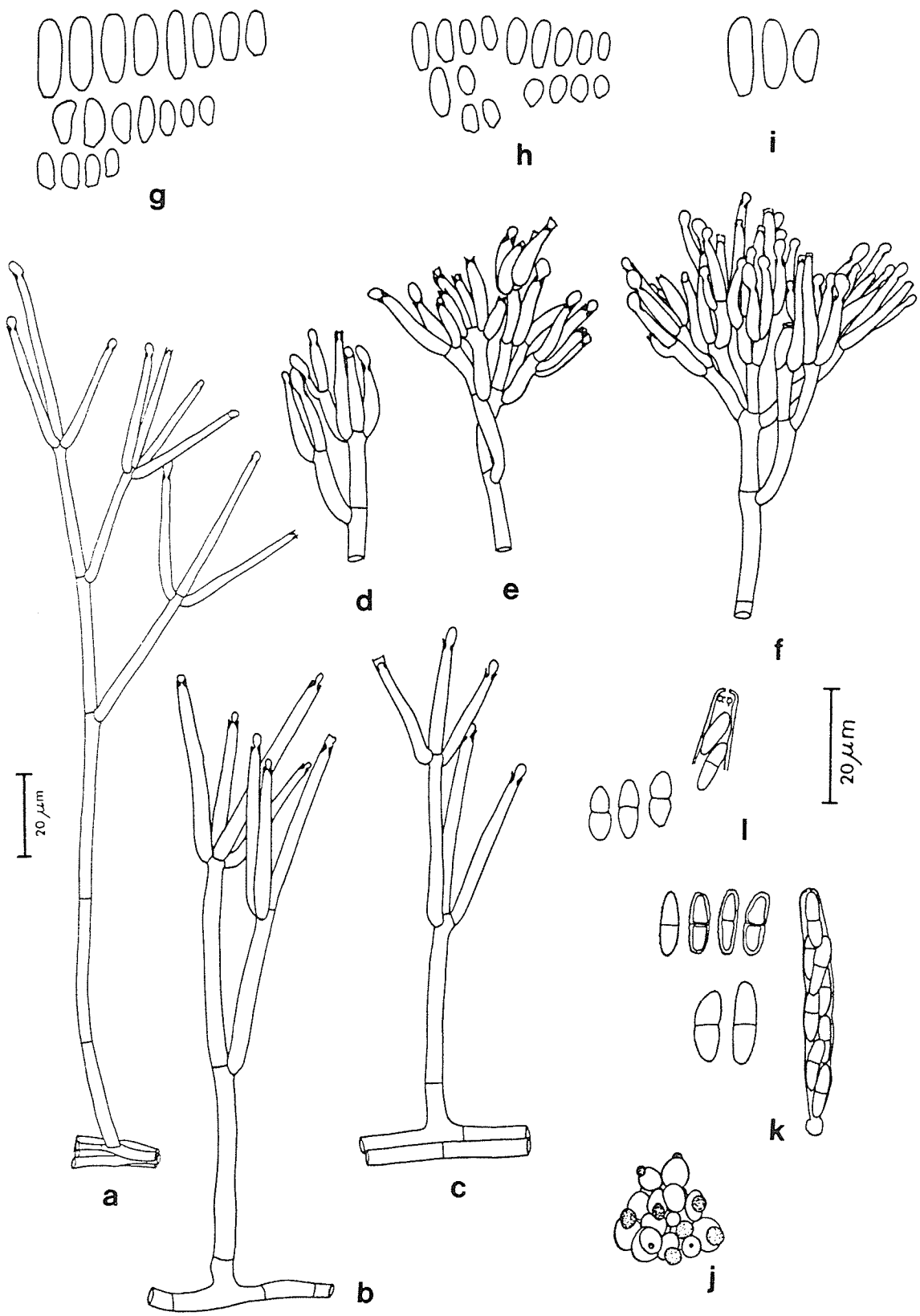

g
h
i
d
e
f
a
b
c
20 µm
l
20 µm
k
j

Fig. 16B. Gliocladium roseum Bainier
(isolate: 165d)

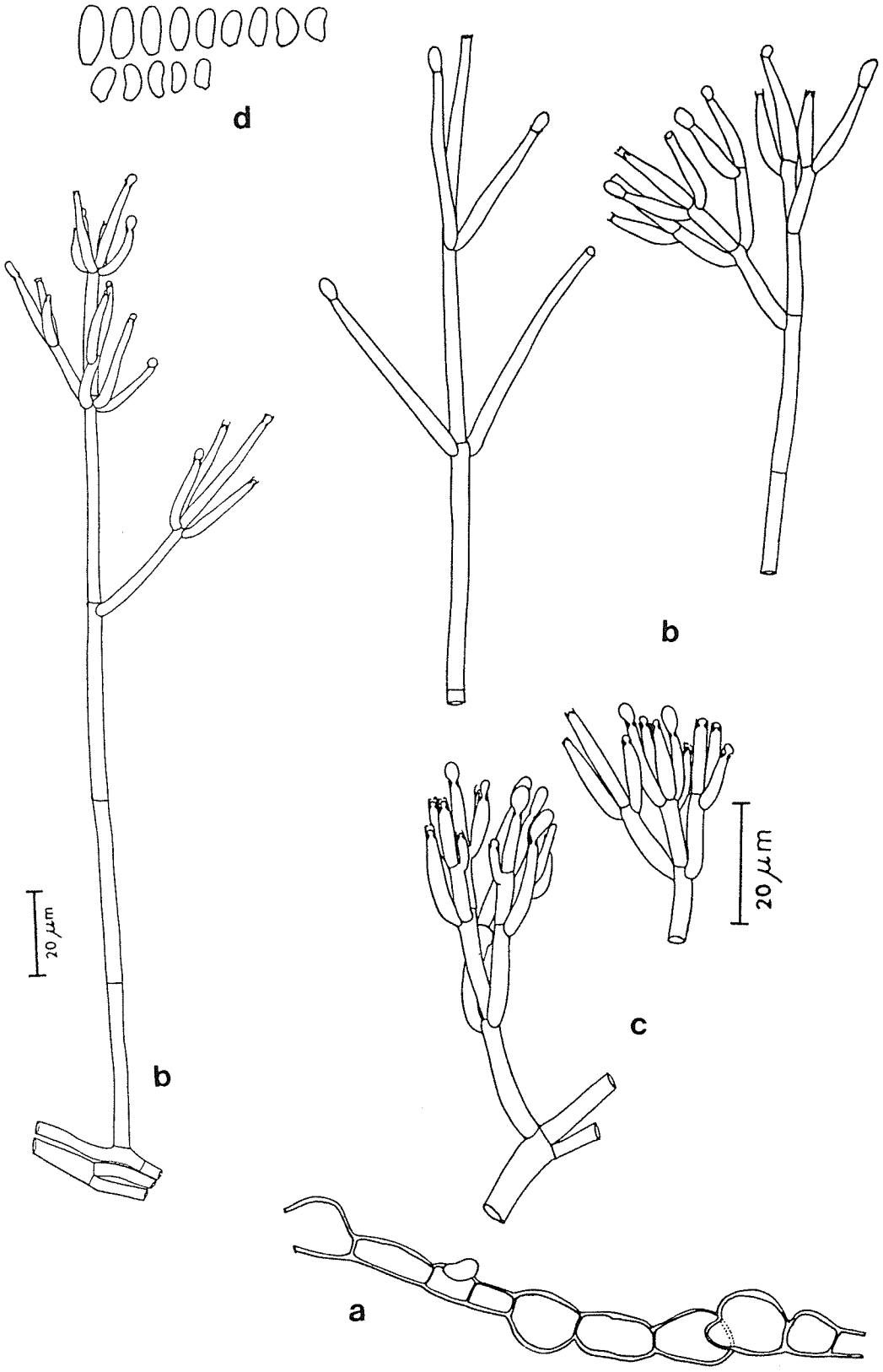
a. Inflated hyphal cells from the submerged mycelium of an aged culture.

b. Simple phialophores bearing long or medium-sized phialides.

c. Complex phialophores bearing short phialides.

d. Phialoconidia.

Isolate as illustrated: 165d: a-d.


d
b
20 µm
b
20 µm
c
a

present as small clear drops. Hyphae hyaline, smooth-walled, and 1.5 - 6.5(7.5) μm in diameter and, when funiculose, strands ranged from 15 - 90 μm wide. Chlamydospores were not seen, but in one isolate some hyphae became excessively septate, and then thick-walled and constricted at the septa, and reached 8.0 - 14.0 μm in diameter (Fig. 16B. a). Phialophores macronematous; hyaline to very pale yellow; walls smooth, often somewhat thickened and occasionally verrucose at the base, and of two types: (1) mononematous, branching in the upper portion, bearing 1 - 3 verticils which each consists of 2 - 5 long, divergent phialides or, occasionally, a branch bearing a whorl of such phialides may substitute for one of these phialides; 80 - 350 μm long, with a 0 - 4 septate stem which is 25 to 200 μm long and is 3.0 - 4.5 μm wide at the base (Figs. 16A. a,b,c; 16B. b); (2) mononematous, acrotonously, mesotonously or, occasionally, basitonously branched, and occurring singly or sometimes aggregated in sporodochia. These phialophores branch several times, and this results in the formation of 3 - 7 series of branches which bear 2 - 7 short phialides on the ultimate and penultimate branches. Such phialophores are 90 - 185 μm long, with a 0 - 3 septate stem which is 15 - 75(130) μm long and 3.5 - 5.0 μm wide at the base (Figs. 16A. d,e,f; 16B. c). Conidiogenous cells monophialidic, hyaline, and smooth-walled; discrete or integrated and of two types; (1) subulate, straight, 20 - 40(50) x (1.8)2.0 - 3.0 μm tapering to 1.5 - 2.0(2.3) μm at the apex; (2) cylindrical to subcylindrical, straight or gently curved, tapering in the upper portion; 9.5 - 16.0(20) x 2.4 - 3.2 μ tapering to 1.6 - 2.0 μm at the apex. Collarette

indistinct; 0.5 - 1.8 μm long; the periclinal thickening is fairly well developed. The phialoconidia aggregate in slimy masses or adhere in columns; 1-celled, hyaline, and smooth-walled; oblong to elliptical, usually asymmetrical, i.e. short-allantoid; (4.5)5.0 - 9.5(13.0) x 2.4 - 3.2(4.0) μm; apex rounded, base short-pedicellate, truncate and often displaced to one side (Figs. 16A. g,h,i; 16B. d). Perithecia are either aggregated on a stroma (Fig. 16A. j) or are single; yellowish-orange coloured; globose to obovate without a perithecial papilla; 260 - 390 μm in diameter; glabrous, with the perithecial wall appearing pseudoparenchymatous in surface view with each cell containing a central, yellow oil drop. Asci unitunicate with a discrete non-amyloid apical ring; narrowly clavate; containing 8 spores which are uniseriate or sometimes biseriate in the upper portion of the ascus; 45 - 60 x 5.0 - 7.0(8.0) μm (Fig. 16A. k). Ascospores 1-septate; hyaline, thick-walled, and verruculose to verrucose; fusiform to ellipsoidal, and sometimes slightly constricted at the septum; 9.5 - 12.0 x 3.5 - 4.7 μm (Fig. 16A. k,l).

HOSTS: Cupressus macrocarpa, Larix sp., Pinus nigra, and P. radiata

CULTURES EXAMINED: **New Zealand:** 49*, 50a, isolated from C. macrocarpa, Compartment 75, Woodhill State Forest, Auckland, collected 14 May 1982; 107a, b, 113a, b, bii, c, isolated from C. macrocarpa, Compartment 14, Woodhill State Forest, Auckland, collected 25 May 1982; 23dii, 25a*, isolated from Larix sp., Compartment 5, Waiotapu, Kaingaroa State

Forest, Taupo, collected 8 May 1982; 165d, isolated from P. nigra, Compartment 1091, Kaingaroa State Forest, Taupo, collected 10 June 1982; 83fi, isolated from P. radiata, near Onemana, Tairua State Forest, Auckland, collected 20 May 1982; 89c*, 100b''*, isolated from P. radiata, off Road 41, Whangapoua State Forest, Coromandel, collected 19 May 1982; 105aii''*, isolated from P. radiata, off Highway 25, Whangapoua State Forest, Coromandel, collected 19 May 1982.

* Isolates which produced the teleomorph in culture.

As treated here, G. roseum is clearly an aggregate species. All of the isolates grouped hereunder produce simple verticillate phialophores, but usually also more complex, penicillately branched phialophores. Both types produce either slimy conidial masses or moist, thick conidial chains which become pink or reddish-yellow in light. So circumscribed, this species could be accommodated within the genus Clonostachys Corda. While some of these isolates formed perithecia in culture, thus confirming their connection with Nectria ochroleuca, others did not, and without a proven teleomorph connection those isolates may represent a distinct species, or even several species, which are morphologically similar, although genetically distinct.

The distribution of G. roseum is worldwide, being frequently reported from soils, plant roots, and from decaying plant parts (Domsch et al. 1980). Members of the Nectria ochroleuca-group are found on bark, wood, fleshy fruits, and herbaceous tissues of various plants and

on fruiting bodies of larger fungi. However, they are more common in tropical and subtropical areas than at temperate latitudes (Domsch et al. 1980; Samuels 1976a). Dingley (1951) reported on the distribution of N. ochroleuca in New Zealand, and later (Dingley 1957) described its anamorph in culture, but her host list did not include pines. G. roseum has also been isolated from soils in New Zealand (Thornton 1958, 1960a, b, 1965; Tubaki 1965).

While N. ochroleuca is rarely reported from pines or other gymnosperms (i.e. none of the numerous collections reported by Samuels (1976a) were from pines), it has been isolated from pine seeds and seedlings, from pine litter, and from stumps of Picea abies L. (Anon 1975; Anon 1987b; Brandsberg 1969; Hallaksela 1977; Hayes 1965; Manoch et al. 1986). It has also been isolated from forest soils, although it is rarer in coniferous forest soils than in soils of other forest types (Bhatt 1970; Domsch et al. 1980).

G. roseum has been found associated with wood inhabiting insects and species of Ceratocystis sensu lato in oaks killed by C. fagacearum (Bretz) Hunt (Shigo 1958), and also in pines infested with cerambycid beetles and the pine wood nematode Bursaphelenchus xylophilus (Steiner & Buhrer) (Wingfield 1987). Moore (1971) listed "Gliocladium spp." as being found in or on Dendroctonus frontalis Zimm. larvae, pupae or adults from infested pines, but considered them nonpathogenic to the insects. However, Balazy (1966) believed G. roseum was capable of killing the weaker larvae of Ips typographus L.

G. roseum is also considered to be an ubiquitous mycophile

(Hawksworth 1981; Tubaki 1955; Udagawa & Horie 1971), and a necrotroph (Rudakov 1978), and has been shown experimentally *in vitro* to be capable of destroying host mycelium (Barnett & Lilly 1962).

As noted earlier under the genus discussion, the taxonomy of *G. roseum* is currently quite confused, and its proper assignment as to genus remains unsettled. In addition, what *G. roseum* actually represents is in doubt! As outlined by Samuels (1976a) the latter problem is related to typification. *Penicillium roseum* Link 1815 was invalidly transferred to *Gliocladium* by Thom in 1910 as *G. roseum* (Link) Thom, nomen provisiorum. *G. roseum* was described by Bainier in 1907 without any reference to Link's fungus. Thom (1930), and Raper & Thom (1949), after examining various collections, but not the type specimen of *P. roseum*, assigned the species to *Gliocladium* as *G. roseum* (Link?) Bainier. Their work left unanswered the question whether Bainier's fungus was identical to that of Link. *P. roseum* Link and *G. roseum* Bainier are based on different types, therefore, even if they were proven to be identical but belonging to the genus *Gliocladium*, *G. roseum* Bainier would be the oldest validly published *Gliocladium* name for this fungus.

Some isolates that produce only simple, verticillate phialophores have previously been assigned to *Verticillium intertextum* Isaac & Davies, but because of their asymmetrical conidia and other characters they are now usually included in *G. roseum*. Furthermore, some *Dendrodochium* anamorphs of the *Nectria ochroleuca*-group may resemble *G. roseum* in culture.

Differences were noted between the New Zealand isolates, especially in the height and the extent of branching of the phialophores. The mycelium of isolate 165d was strongly synnematogenous with most of the phialophores arising from the tapering strands; it also produced a yellow pigment and did not form sporodochia. Isolate 89c produced unusually large conidia which, according to W. Gams (pers. comm.), might indicate a relationship to Nectria byssicola Berk. & Broome. However, this isolate did eventually produce perithecia which were clearly those of N. ochroleuca. The other isolates which formed the teleomorph in culture on cellulose medium, were a rather homogeneous group, producing yellow pigment, more numerous sclerotia (on MEA.YE), and were more effective in stimulating formation of the perithecia of Ceratocystiopsis falcata (Wright & Cain) Upadhyay in vitro than the other isolates.

G. roseum differs from G. viride Matr. and G. virens Miller et al. in its slower growth, hyaline conidia, and pinkish conidial masses. The two types of phialophores which both produce asymmetrical conidia indicate a relationship with the Nectria ochroleuca-group, and intermediate forms exist between G. roseum and Dendrodochium anamorphs of some members of the N. ochroleuca-group. The divergent simple phialophores of G. roseum (fide Domsch et al. 1980) separate it from G. solani (Harting) Petch.

G. roseum was amongst the most commonly encountered species in the bark beetle galleries although, admittedly, these isolates may not belong to a true species, but a small group of closely related species, most likely of the Nectria ochroleuca-group. G. roseum is known from

this habitat, and the teleomorph(s) often occur on bark and wood. It is listed as one of the species capable of causing soft rot of wood (Duncan & Eslyn 1966), can utilize chitin, pectin, break down cellulose, and is a well known mycoparasite (Domsch et al. 1980).

Gliocladium solani (Harting) Petch, Trans. Br. Mycol. Soc. 27:149. 1945

Fig. 17. a-h.

≡Spicaria solani Harting, Niewe Verh. Kon. Inst. Wetensch. Amsterdam 12:226. 1846

Teleomorph: Nectria solani Reinke & Berth., Die Zersetzung der Kartoffel, 39. 1879

Colonies attaining a diameter of 30 - 40 mm in darkness, but 34 - 44 mm in alternating light and darkness in 12 days at 20°C on MEA.YE. Grown in darkness, colonies are white to pale yellow (2.5Y 8/0, 8/2, 10YR 8/2 to 5Y 8/4), nematogenous to finely plectonematogenous, and produce conidia in slimy masses on simple or complex phialophores. At first the conidial masses are white, but may become pale yellow or yellow (5Y 8/4 or 8/6, 8/8) or, in some isolates, very pale brown or light grey (10YR 7/4 or 7/2). In reverse, colonies are yellow to pale yellow (5Y 8/6, 2.5Y 8/6 to 8/4). Colonies grown in alternating light and darkness are zonate, as light clearly stimulates sporulation, with some isolates responding more strongly than others; these conidial masses become reddish yellow to pink (7.5YR 8/6, 7/8, 7/6, 5YR 7/8 to 8/4). In reverse, colonies are reddish yellow to pink (7.5YR 7/8 to 7/4). Odour indistinct to faint, and an exudate is present as small, clear drops. Yellow pigment diffuses into the medium, especially in darkness. Hyphae hyaline to yellow and smooth-walled; 1.4 - 5.0 μm in diameter; when funiculose, strands up to 40 μm in diameter.

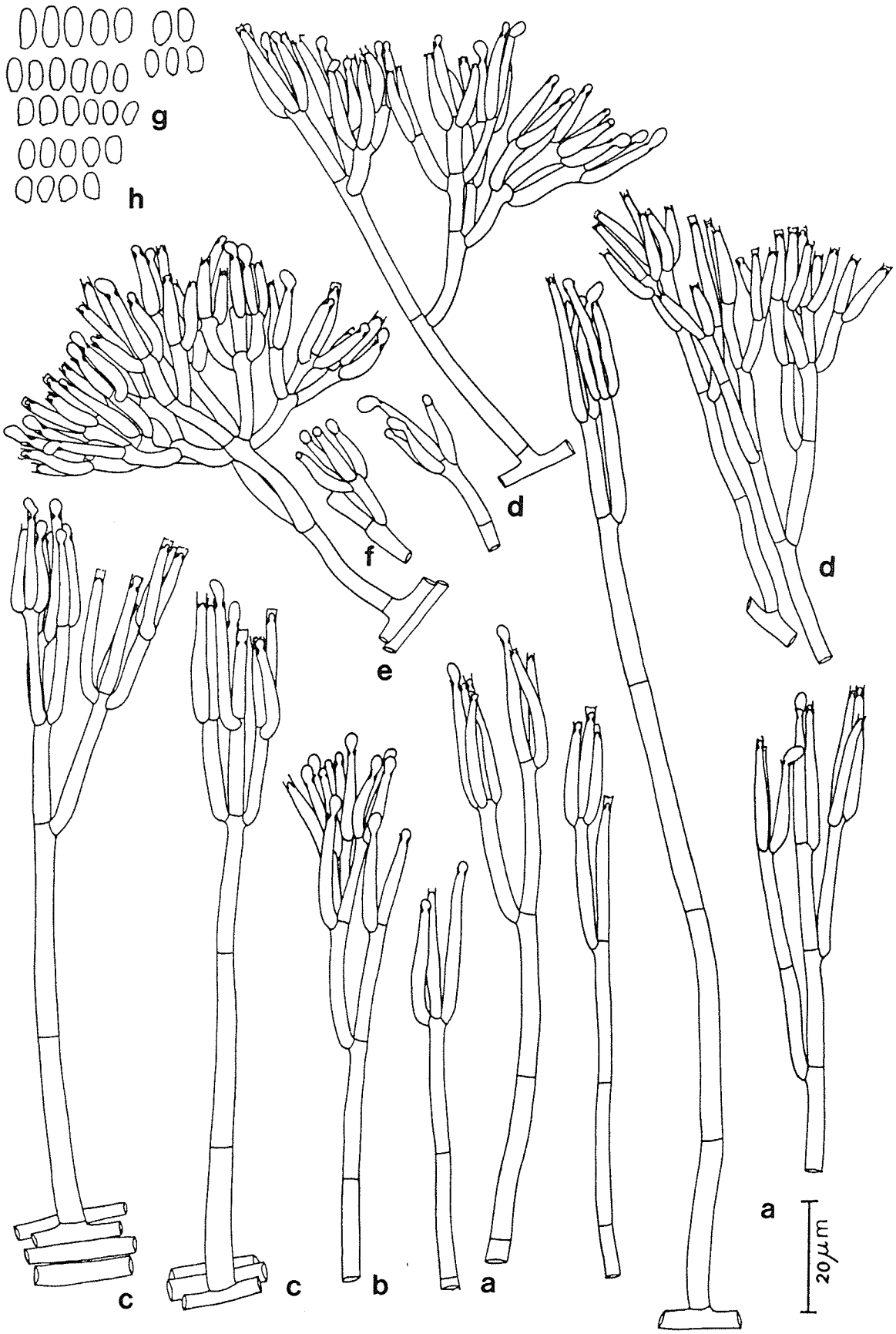
Fig. 17. Gliocladium solani (Harting) Petch
(isolates: 84e, 144a, 144b, 181di, 183fii)

a-c. Apically branching phialophores bearing long subulate to cylindrical, convergent phialides in a penicillate manner.

d-f. Mesotonously branched phialophores bearing short, subcylindrical phialides.

g-h. Phialoconidia.

Isolates as illustrated: 84e: c.
144a: h.
144b: a, d, g.
181di: e.
183fii: b, f.


g
h
d
d
f
e
c
c
b
a
a
20 µm

Chlamydospores and sclerotia were absent. Phialophores macronematous; hyaline to pale yellow and smooth-walled; of two types. (1) Mononematous, branching apically to form a compact penicillus; each of the 1 - 3 branches bears 2 - 5 long phialides which are parallel or convergent (Fig. 17. a,b,c); rarely the phialides are borne at the stem apex. The phialophores are 70 - 250(300) μm long, with a 0 - 4(5) septate stem which is 30 - 210(250) μm long and 3.2 - 5.5 μm wide at the base, tapering to 2.5 - 3.5 μm below the branches, (Fig. 17. a,b,c). (2) Mononematous, but mesotonously branched with 3 - 5(6) series of divergent and often curved branches, with the ultimate branches bearing 2 - 6 short phialides which are parallel or slightly divergent (Fig. 17. d,e); longer phialides originating from the penultimate branches may also be present. These phialophores are 120 - 170 μm long, each with a 15 - 85 μm long stem which is 3.5 - 5.5 μm wide at the base, and they are sometimes aggregated to form discrete sporodochia. Conidiogenous cells monophialidic, hyaline, and smooth-walled; discrete or integrated, and of two types; (1) subulate to cylindrical but tapering gradually in the upper part; usually straight, found mainly on the apically branched phialophores; 20 - 32 x 2.0 - 2.5 μm tapering to 1.5 - 1.8 μm at the apex (Fig. 17. a,b,c); (2) subcylindrical and tapering gradually in the upper portion, usually gently curved but some are straight; 11.0 - 19.0 x 2.3 - 3.2 μm tapering to 1.4 - 1.7 μm at the apex (Fig. 17. d,e,f); collarettes indistinct and 0.7 - 1.8 μm long; periclinal thickenings are well developed. Phialoconidia aggregate in slimy masses; 1-celled, hyaline, and smooth-walled; the larger conidia are oblong to elliptical,

but the smaller are asymmetrical, almost subglobose; 4.5 - 7.3(8.5) x 2.5 - 3.5(4.0) μm; apex curved, base laterally short-pedicellate, truncate (Fig. 17. g,h).

HOSTS: Eucalyptus sp., Pinus radiata, Pinus taeda, Podocarpus spicatus R. Br. ex Mirbel.

CULTURES EXAMINED: **New Zealand:** 181di, isolated from Eucalyptus sp., Waiotapu, Compartment 5, Kaingaroa State Forest, Taupo, collected 9 June 1982; 83a, bi, 84e, isolated from P. radiata, near Onemana, Tairua State Forest, Auckland, collected 20 May 1982; 183fii, isolated from P. taeda, Compartment 21, Riverhead State Forest, Taupo, collected 11 July 1982; 143fi, 144a, b, isolated from P. spicatus, near Minginui, Urewera National Park, Taupo, collected 11 June 1982.

Known primarily from spoiled potatoes, G. solani has also been isolated from cultivated and forest soils. The species is known from Europe, Papua-New Guinea, and Japan (Anon 1987b; Booth 1959; Lindau 1907; Matsushima 1971, 1975; Petch 1944) but this is probably the first record from New Zealand.

The only recent reports of N. solani and its G. solani anamorph in culture, are those of Matsushima (1971, 1975) who grew the species on sterilized banana leaves on corn meal agar. When N. solani was described in 1879, its anamorph, which was derived from ascospore cultures, was considered to be identical to Spicaria solani de Bary, which was, in

fact, an obligate synonym of S. solani Harting fide Petch (1944). The genus Spicaria Harting was erected for S. solani Harting, a species presumably identical to the anamorph of N. solani. Subsequently the generic concept of Spicaria changed, and since it no longer reflects the characteristics of the type, it is now considered confused (Brown & Smith 1957; Hughes 1951). Petch (1944) examined fresh collections of N. solani and an associated conidial fungus he presumed to be the anamorph; based on the latter's conidiophores, he transferred the anamorph to Gliocladium.

The eight New Zealand isolates were clearly divisible into two groups which differed in colony morphology and phialophore branching patterns. Isolates of group one, 83a, bi, and 84e, produced chiefly erect, apically branched phialophores (Fig. 17. c), but in addition to such phialophores the remaining five isolates (group two) also produced abundant, complex, mesotonously branched phialophores. Isolates of the first group have long phialides, but both long and short phialides are produced by members of the latter. No difference was found in the type of conidia produced by members of the two groups.

No general key to species of Gliocladium exists, but using the key in Domsch et al. (1980) these isolates were identified as G. solani based on: (1) the presence of two types of phialophores; (2) the convergent or compact nearly parallel arrangement of the phialides on the simple or primary phialophores; and (3) the conidial masses which were more cream-coloured than green. One culture of group one and four of group two which represented the variation found amongst the eight New

Zealand isolates of this species were examined by Dr. W. Gams who agreed with their identification as G. solani. He commented that the lack of complex phialophores in isolate 83a (the group one representative) set it apart, but he could not offer any alternative to accommodate such a difference. It was therefore decided to include the group one isolates here, even though they lack complex phialophores, because of their otherwise resemblance to the five other isolates; particularly the similarity of their phialophores to the simple phialophores of the other isolates (see Fig. 17. c for group one; and a,b for group two).

In addition to those species formally described within the genus Gliocladium, several species of the Hypocreales have Gliocladium anamorphs. However, none of the New Zealand isolates developed any structures resembling protoperithecia or perithecia, but the possibility of a teleomorph, which may or may not be N. solani, can not be excluded.

The morphology of these isolates resembles that of anamorphs of species of the Nectria ochroleuca-group as outlined by Samuels & Seifert (1987). The main reason for deciding on G. solani was the fact that Domsch et al. (1980) stated that it had "phialides which are appressed even on the primary conidiophores and do not turn pink under light." They did not treat the species further. The conidial masses of the New Zealand isolates do become pinkish in light. Matsushima (1971) illustrates the anamorph of N. solani, but the simple (primary) phialophores are depicted as verticillate, producing the conidia which are white in mass on long, subulate, divergent phialides. Booth (1959) illustrated similar verticillate phialophores as being produced by his

conidial isolate, and the early reports of the species (e.g. Lindau 1907) also seem to suggest verticillate branching. These descriptions appear to contradict the reported presence of appressed primary conidiophores in this species, which is the phialophore character used by Domsch et al. (1980) to distinguish G. solani from G. roseum. However, there is another species, G. caespitosum Petch, (Matsushima 1971, Fig. 139) to which the three isolates producing only simple phialophores might be assigned. This possibility could not be pursued further due to the unavailability of suitable material for study.

In spite of the variation evident between the New Zealand isolates, all produce similar conidia and similar, simple, penicillate phialophores, and the latter are considered to be typical of the genus. The species was found in four different host species and appears to be a fairly common inhabitant of the bark beetle galleries, although no references to G. solani being associated with insects were located.

Gliocladium viride Matr., Bull. Soc. Mycol. France 9:251. 1893

Fig. 18. a-e.

=Gliocladium deliquescens Sopp, Vidensk. Skrifter. I. Mat.-Naturv. Klasse No. 11:89-93. 1912

Teleomorphs: cf. Hypocrea lutea (Tode: Fr.) Petch and cf. Hypocrea gelatinosa (Tode: Fr.) Fr.

Colonies attaining a diameter of 65 - 70 mm in 3 days at 20°C in alternating light and darkness on MEA.YE. Appearing semi-translucent between small, discrete, dark-green spore masses produced in broad, indistinct zones; the masses often most abundant at the edge of the plate, but when sporulating abundantly the surface becomes dark-green; phalacrogenous and nematogenous, a few phialophores often arising together; the conidia aggregate in large, green, slimy drops at the apices of the phialophores, with the masses from adjacent phialophores often coalescing. When colonies are grown in alternating light and darkness, the phialophores develop in 24 hours and the green spore masses after 48 hours. In reverse, the colonies are hyaline with darker shadows below the spore masses. In darkness the colonies remain semi-translucent, and hyaline and appressed, and only produce sparse aerial hyphae with the conidia forming only on aging. Odour indistinct. An exudate is usually present as small to medium-sized, clear drops. Hyphae hyaline and smooth-walled; 2.5 - 12.5 μm in diameter. Chlamydospores develop in aging colonies; hyaline and smooth-walled; intercalary

Fig. 18. Gliocladium viride Matr.
(isolate: 406B)

a. Chlamydospores.

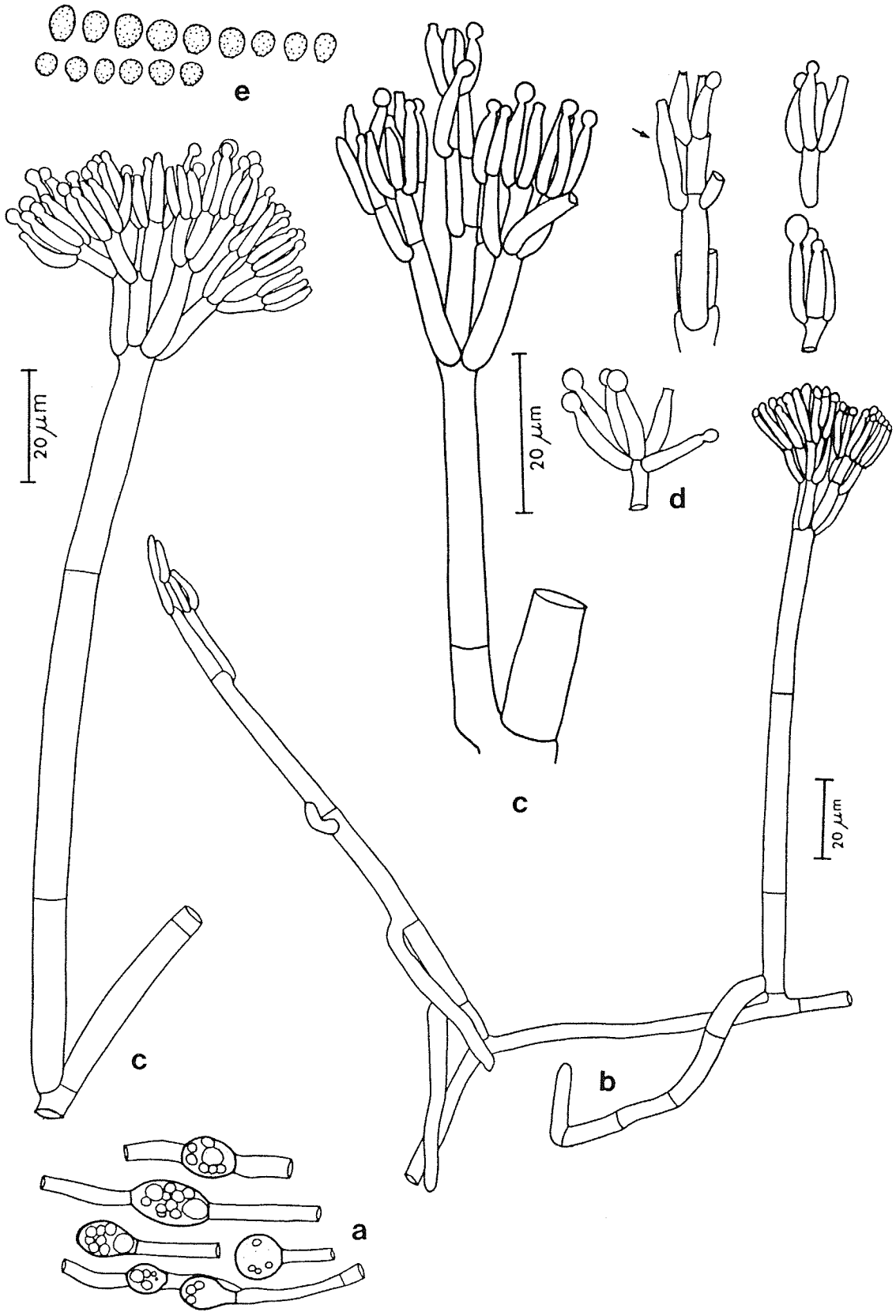
b. Young phialophores illustrating the initial stages in the development of the rhizoid-like basal branches.

c. Phialophores.

d. Phialides; longer phialide («-) arising at the level of the ultimate branches.

e. Phialoconidia.

Isolate as illustrated: 406B: a-e.


e
20 µm
20 µm
d
20 µm
c
c
b
a

or terminal on lateral branches; elliptical with truncate ends or pyriform to globose and measuring 5.5 - 9.5 x 4.0 - 7.5 μm (Fig. 18. a). Phialophores macronematous and mononematous; hyaline; smooth-walled or sparsely verrucose; branching apically to form compact penicilli; 145 - 245 μm long, with a 1 - 3 septate stem which is 95 - 185 μm long, (4.5)6.0 - 9.0 μm wide at the base, and (4.0)5.0 - 8.0 μm at the apex (Fig. 18. b,c). From the lower portion of the stem, branches develop which ultimately resemble rhizoids. These usually arise just above a septum and are 4.0 - 5.5 μm in diameter; they initially grow laterally from the stem, then turn and grow downwards and parallel to it (Fig. 18. b). These rhizoid-like branches undergo further branching, and also anastomose with each other or with adjacent hyphae. The penicilli consist of 2 - 3(4) series of usually nearly parallel branches; the first series consists of 2 - 5 larger branches, the branches in the 2nd and 3rd series becoming progressively smaller and more numerous. A few long phialides arise at the same level as the ultimate branches (Fig. 18. d «-), but most of the phialides are convergent, arising from the ultimate branches in dense groups of 4 - 6. Conidiogenous cells monophialidic, hyaline, and smooth-walled; discrete; cylindrical or sometimes slightly broader in the upper portion just before narrowing to the apex; usually gently curved; 8.0 - 13.0 x 1.6 - 2.3 μm tapering fairly abrubtly to 0.9 - 1.0 μm at the apex (Fig. 18. c,d); collarette lacking. Phialoconidia aggregating in large slimy drops; 1-celled, green, and smooth-walled; globose to subglobose; 2.4 - 4.0(4.5) x 2.4 - 3.2 μm; base indistinctly pedicellate, truncate (Fig. 18. e).

HOST: Pinus sp.

CULTURE EXAMINED: **New Zealand:** 406B, isolated from Pinus sp., Compartment 1027, Kaingaroa State Forest, Taupo, collected 29 February 1988.

G. viride was first described from a rotten Clitocybe fruiting body in France by Matruchot in 1893 (Matruchot 1895), while G. deliquescens was described by Sopp (1912) from Daedalea unicolor (Bull.) Fr. in Norway. Domsch et al. (1980) treated G. deliquescens as a synonym of G. viride, but where G. deliquescens was formally reduced to synonymy with G. viride could not be determined. Matruchot's (1895) description and illustrations of G. viride certainly show great resemblance to the descriptions of G. deliquescens by Gilman (1957), Raper & Thom (1949), and Pinkerton (1936), and thus there is little doubt these species are identical. However, Morquer et al. (1963) studied isolates presumed to represent the two species in culture and reported differences between them did occur.

This fungus is least commonly reported as G. viride, but records from woody hosts or other fungi are usually under this name (Anon 1975; Anon 1987a; Clark & Setliff 1985; Shields 1969). However, isolates from soils, compost, pine leaf litter, organic matter, etc. are more often listed as G. deliquescens (Anon 1975; Baker et al. 1979; Bissett & Parkinson 1979a; Christensen 1969; Christensen et al. 1962; Hodges 1962; Huang & Schmitt 1975; Hubálek et al. 1973; Käärik 1968; Kendrick 1963;

von Klopotek 1962; Komatsu 1976; Matsushima 1975; Park 1972; Raper & Thom 1949; Subramanian 1971; Wallace & Dickinson 1978). Rudakov (1978) considered the species to be necrotrophic on other fungi, and it can cause a greenish grey to buff coloured decay in Picea abies (L.) Karst. stumps within a year of felling (Hallaksela 1977). Domsch et al. (1980) noted it has often been found in woody substrata, where it clearly has the potential to degrade cellulose and inhibit other wood-degrading fungi. It does not appear to be geographically restricted, and it was previously reported from New Zealand soils as G. deliquescens (Tubaki 1965).

Two Hypocrea species, H. gelatinosa (Tode: Fr) Fr. and H. lutea (Tode: Fr.) Petch, have anamorphs which resemble G. viride. The anamorph of H. lutea which Komatsu (1976) illustrated appears close to the description of G. viride, especially isolate TMI 60064, but the other isolate has somewhat larger conidia and phialides. The anamorph of H. gelatinosa, as described by Webster (1964), also has the same general conidiophore morphology but broader phialides. H. gelatinosa (without any mention of its anamorph) is known from New Zealand (Dingley 1952).

In view of the unsettled taxonomy of the genus Gliocladium as a whole, and the presence of taxa with slight morphological differences, i.e. aggregate species, it is difficult to find a place for a single isolate without a connection to a teleomorph. This isolate has quite homogeneous, globose to subglobose conidia with a flattened base, and therefore differs in the conidial shape reported for most other isolates of this species, i.e. spherical to elliptical, or elliptical. It grows

faster than Domsch et al. (1980) report for G. viride, filling the plate in just four days, not eight. Whether such differences are important cannot be judged without knowing the spectrum of variation that exists in related entities. This isolate has therefore been assigned to G. viride, with the understanding that it may indeed be the anamorph of a Hypocrea species.

This appeares to be the first report of G. viride being isolated from bark beetle galleries. It is one of the species often reported from woody substrata, has the potential to stain wood greyish, and seems to be able to out-compete some other wood-degrading fungi.

Graphium Corda, Icon. Fung. 1:18. 1837

Type species: Graphium penicillioides Corda (lectotype)

Teleomorphic genera: Ceratocystis Ellis & Halst. sensu lato, Petriella Curzi, Pseudallescheria Negroni & I. Fischer, and Kernia Nieuwl.

Ellis (1971) clarified the generic concept of Graphium and redescribed the genus as follows. The conidiophores are macronematous, and synnematous, and the individual hyphae of the synnemata are narrow, straight or flexuous, olivaceous brown, smooth-walled and branching. As this branching is more frequent towards the synnematal apex, the individual synnemata are either broadest at the apex or cylindrical to clavate in outline. The conidiogenous cells are monoblastic, percurrent, integrated or discrete, and subulate or cylindrical. The conidia aggregate in a slimy head at the apex of each of the synnemata, with those produced from the same annellide often adhering in chains. The conidia are 1-celled; hyaline or pale olivaceous brown and smooth-walled; cylindrical or allantoid and rounded at the apex, cuneiform or ellipsoidal, but all usually have a flattened base.

Before the mode of conidiogenesis was considered as an important character in delimitation of genera, species which were to be assigned to the genus Graphium had the following characteristics. They produced synnemata with brown to black, cylindrical or clavate stems, which were often lighter in colour at their apices, and were composed of parallel-arranged hyphae. The conidiogenous cells at the apex of the synnemata

were somewhat flared and bore their conidia in a slimy mass. The conidia which formed at the apices of the conidiogenous cells were 1-celled, hyaline, and oval to oblong or cylindrical (Lindau 1910; Morris 1963; Saccardo 1886).

From the two species originally described by Corda (1837), Hughes (1958) selected G. penicillioides Corda to be the lectotype of the genus. Sutton & Laut (1970) examined the type specimen of G. penicillioides and determined that its mode of conidiogenesis is primarily annellidic, but occasionally sympodial ontogeny does occur. Ellis (1971) defined the genus as having "monoblastic, percurrent, integrated or discrete, subulate or cylindrical" conidiogenous cells. For those species previously assigned to Graphium in which conidiogenesis appeared to be strictly sympodial, Crane & Schoknecht (1973) established the genus Pesotum Crane & Schoknecht, thereby reducing the heterogeneity previously present in Graphium. The genus Graphilbum Upadhyay & Kendrick was subsequently erected for hyaline or lightly pigmented Graphium-like species.

Graphium species are usually found on wood, rotten wood, dead herbaceous stems, or in soils, but since no modern treatment is available for Graphium as a whole, the actual number of species is not known. Hawksworth et al. (1983) consider there are at least three, but at least two additional species have been described since then. Most species of Petriella have a Graphium state (fide Barron et al. 1961), as do at least one, and possibly two, Ceratocystis species; Graphium states have also been reported in some members of Pseudallescheria and Kernia.

Graphium calicioides (Fr.) Cooke & Massee, Grevillea 16:11. 1887

Figs. 19. a-f.

≡Sporocybe calicioides Fr., Syst. mycol. 3:342. 1832

≡Calicium haustellare Achar., Kongl. Vetenskaps Academiens Handlingar 122. 1816

≡Periconia calicioides (Fr.) Berk., Outl. Br. Fung. 343. 1860

=Sporocybe flexuosa (Massee) Mason, Mycol. Pap. 5:127. 1941

≡Stilbum flexuosum Massee, J. Roy. Microscopical Soc. ser. 2, 5:758. 1875

Colonies attaining a diameter of 10 - 11 mm in 12 days or 20 - 22 mm in 31 days at 20°C in darkness on MEA.YE. Colonies dark grey (5YR $^{4}/_{1}$, 10YR $^{4}/_{1}$); usually raised in the centre, and of darkly pigmented, fine, dry hyphae without any evident conidial production; margin appressed and very dark grey (10YR $^{3}/_{1}$). Mononematous conidiophores producing very dark grey (10YR $^{3}/_{1}$) conidial masses develop randomly or associated with disturbed areas on the surface of the colonies. Single or loosely aggregated synnemata, bearing brown conidial masses at their apices, also arise in the same areas. In reverse, colonies are very dark grey (10YR $^{3}/_{1}$). Colonies are tough to cut through. Odour and exudate lacking. Hyphae light to dark-brown; walls are smooth, distinct but not thick, and often slightly undulate; 1.5 - 4.0 µm in diameter and guttulate. Inflated hyphal cells which are up to 7.5 µm wide are occasionally present. These occur singly, in short chains, or in small clusters (Fig. 19. a). Chlamydospores were not seen. Conidiophores are

Fig. 19. Graphium calicioides (Fr.) Cooke & Massee (isolate: 16')

a. Inflated hyphal cells.

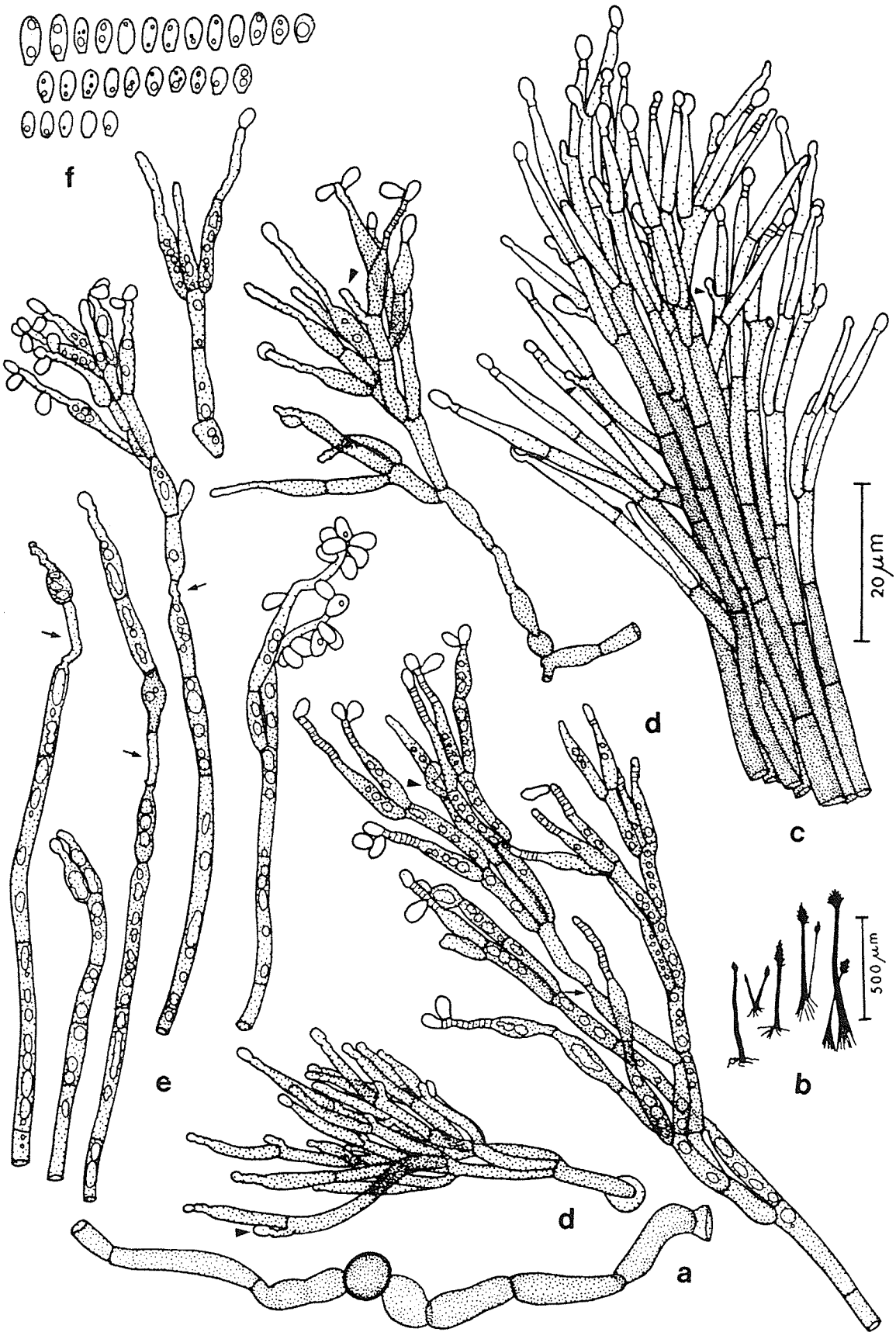
b. Synnemata.

c. The apex of a smaller synnema showing cylindrical to short-subulate annellides subtended by annellidic pegs («).

d-e. Mononematous conidiophores bearing obclavate or oval to naviculate annellides, which sometimes proliferate apically to produce further annellides («-), the annellides are often subtended by annellidic pegs («); (d) mononematous conidiophores which branch several times; (e) mononematous conidiophores which do not branch, or branch only once at their apex.

f. Annelloconidia.

Isolate as illustrated: 16': a-f.


f
d
20 µm
c
d
500 µm
b
e
d
a

annellidic, macronematous and of two types. 1. Synnematous, determinate, erect, and very dark brown; the stem is mostly cylindrical, but often broader at the base where the individual hyphae are looser and somewhat divergent, while the apex is usually highest in the centre; the latter results in pyriform-shaped heads (Fig. 19. b). The stem is composed of very dark brown, smooth-walled, parallel hyphae, 1.8 - 2.5(3.0) µm in diameter. The synnemata which develop in culture are 220 - 750 µm long, and the stem is 165 - 665 x 10 - 35 µm wide, but up to 45 µm in diameter at the base. The apex consists of cylindrical annellides which are usually subtended by annellidic pegs (Fig. 19. c «). 2. Mononematous or semi-macronematous, brown and smooth-walled; the stem originates from the vegetative mycelium as short lateral branches which usually branch several times, and then give rise to multiple series of short branches and conidiogenous cells (Fig. 19. d). The conidiogenous cells are often inflated and may proliferate apically to form branches or new conidiogenous cells (Fig. 19. d,e «-). Such conidiophores range from simple ones with a single apical cell (Fig. 19. e) to those which branch numerous times forming long conidiophores (Fig. 19. d). Conidiogenous cells annellidic, but sometimes the mode of conidiogenesis may appear sympodial although neither scars nor denticles could be distinguished; brown to pale brown, and smooth-walled; integrated or discrete, and of two types, (1) cylindrical to short subulate (more common on synnemata), and measuring 9.0 - 13.5 x 1.3 - 1.8 µm, but tapering at the apex to 0.9 - 1.1 µm which is the diameter of the annellated area; (2) obclavate or oval to naviculate (more common on mononematous conidiophores) and

measuring 6.0 - 11.5 x 1.6 - 2.5 μm but tapering, often abruptly, to 0.8 - 1.3 μm at the apices. The annellides frequently proliferate through the apex (Fig. 19. d,e «-) and the cells subtending the annellides usually produce short conidiogenous pegs (Fig. 19. c,d «). Annelloconidia aggregate in slimy masses; 1-celled; subhyaline or very pale brown, and smooth-walled; obovate, short-oblong-elliptical to subglobose; (2.5)3.0 - 4.2(5.0) x 1.6 - 2.2(2.5) μm; with rounded apex and indistinctly pedicellate, truncate base (Fig. 19. f).

HOST: Picea sp.

CULTURES EXAMINED: Canada: 16', isolated from Picea sp., Rogers Pass Summit, Hwy. 1, Alberta, collected 25 September 1987.

This species is fairly commonly reported on old wood and bark in Britain, and has been found throughout Europe and in New Zealand (Anon 1987b; Ellis 1971; Hughes 1978; Mason & Ellis 1953). Rayner (1977) recovered it from residual stumps of beech, birch, and oak in Scotland within two years of felling. However, it was not one of the more abundant species on the stumps. No records of G. calicioides being found in North America were located.

Mason & Ellis (1953) outlined the history of the species and clarified the confusion which existed between it and some similar species, i.e. Graphium rigidum (Pers.: Fr.) Sacc. and two species of the genus Caliciopsis Peck. G. rigidum differs from G. calicioides in that

its synnemata have lighter coloured heads than the latter, and Caliciopsis nigra (Schrad.) Fitzpatrick and C. ellisii Sacc. are Ascomycetes of the order Coryneliales whose perithecia superficially resemble the synnemata produced by G. calicioides.

The species was described as Sporocybe calicioides by Fries (1832) based on a collection on rotten wood of Fagus. It had been previously described from the same specimen by Acharius in 1816 under the name Calicium haustellare Achar. (Mason & Ellis 1953). That specimen was located by them and designated as the type. Berkeley (1860) transferred the species to the genus Periconia Tode and later Cooke & Massee in Cooke (1887) placed it in Graphium.

G. calicioides differs from other Graphium species in its small conidia and long synnemata. It grows very slowly in culture, forming synnemata on aging or in cut colonies, but the synanamorph, resembling members of Exophiala J. W. Carmichael and Rhinocladiella Nannf., often appears earlier. No differences were noted between conidia formed on the different conidiophores.

As G. calicioides is a wood-inhabiting species, its presence in bark beetle galleries can be expected. It is a slow-growing organism and was isolated from a mixed culture of the faster growing Leptodontidium elatius (Mangenot) de Hoog var. elatius. No reports of this species being associated with bark beetles were located; although Rayner (1977) who was investigating the discolouration of the wood of tree stumps by a community of fungal species, did note G. calicioides was one of the organisms present.

Graphium penicillioides Corda, Icon. Fung. 1:18. 1837

Figs. 20A. a-h, 20B. a-l.

=Stilbum basitruncatum Matsushima, Microfungi of the Solomon Islands and Papua-New Guinea, 62. 1971

Colonies attaining a diameter of 26 - 34 mm in 12 days at 20°C in alternating light and darkness on MEA.YE. When young, colonies are light brownish grey to dark greyish brown (2.5Y $^{6}/_{2}$ to $^{4}/_{2}$) in the centre, and phalacrogenous. The black synnemata bearing brown, greyish, or black conidial masses at the apex arise from appressed surface hyphae. Irregular white (10YR $^{8}/_{2}$) sectors and tufts of moist aerial hyphae are usually present, but the colonies are usually hyaline towards their margins. On aging, colonies become light brownish grey (10YR $^{6}/_{2}$) with very dark greyish brown (10YR $^{4}/_{2}$) sectors and zones which are covered with small, black conidial masses. In reverse, young colonies are very pale brown (10YR $^{7}/_{3}$) in the centre, but white (10YR $^{8}/_{2}$) towards the margin. On aging, the reverse is light brownish grey, grey, olive grey, or greyish brown to dark greyish brown (2.5Y $^{6}/_{2}$, 5Y $^{5}/_{1}$, $^{5}/_{2}$ or 10YR $^{5}/_{2}$ to 2.5Y $^{4}/_{2}$), usually with irregular darker and lighter coloured areas. This species sporulates more readily on OA than MEA.YE, and even young colonies become very dark grey (2.5Y $^{3}/_{0}$) and punctate when the black synnemata are abundant. When grown in alternating light and dark, colonies are zonate. Odour distinct and fairly strong. Small crystals are present on the surface of the submerged hyphae. Exudate lacking. Hyphae hyaline, smooth-walled, and 1.2 - 4.0 μm in diameter.

Fig. 20A. Graphium penicillioides Corda
(isolate: 23div)

a. Small synnema.

b. Annellides from synnemata.

c-d. Micronematous to semi-macronematous conidiophores; (c) annellides arising from basal cells; (d) annellides from aging colonies producing thick-walled, brown conidia.

e. Short-clavate annelloconidia.

f. Secondary conidia developing from pegs on primary conidia.

g. Brown, thick-walled conidia found in aged colonies.

h. Conidia bearing short frills.

Isolates as illustrated: 23div: a-h.

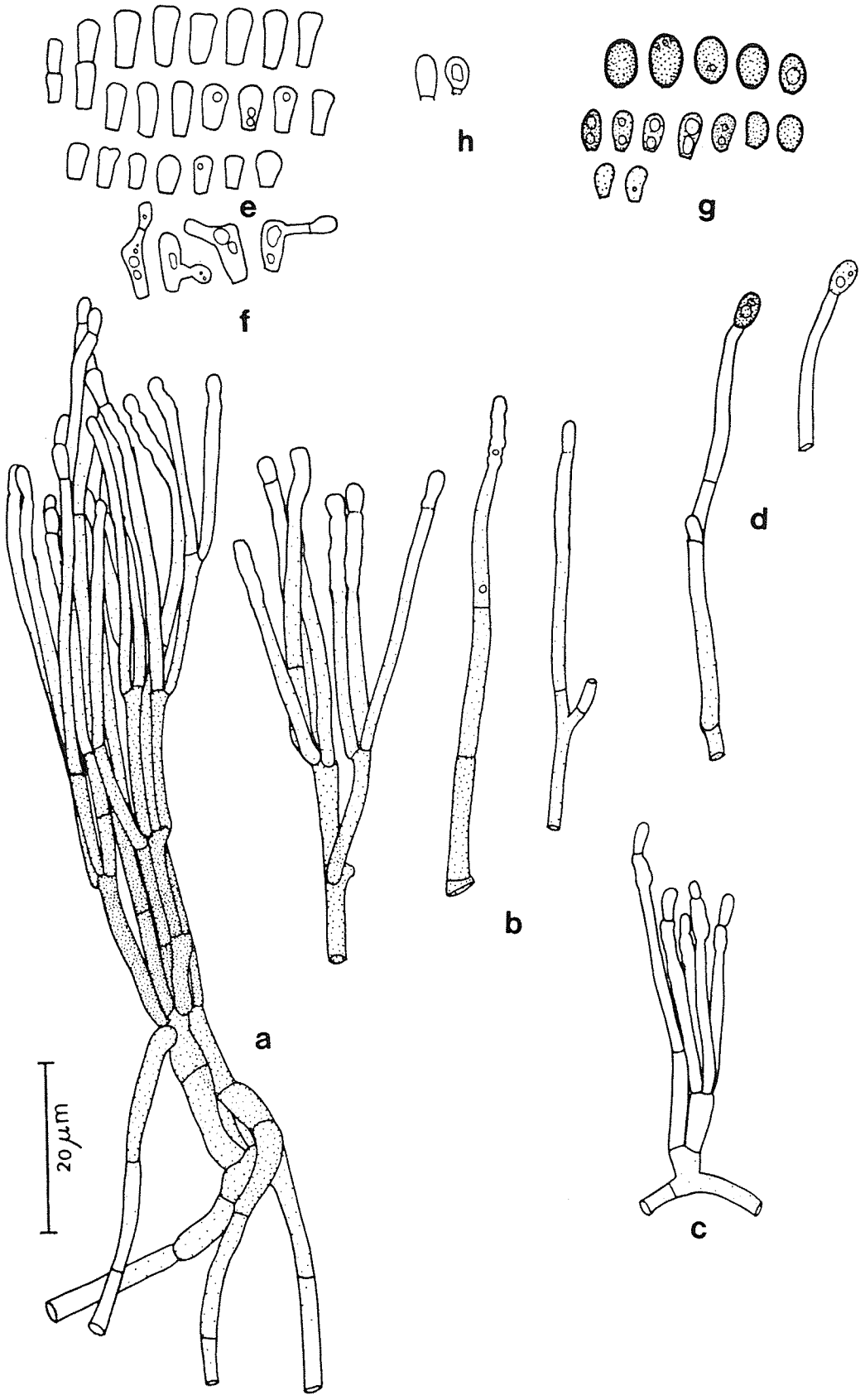

a
b
c
d
e
f
g
h
20 µm

Fig. 20B. Graphium penicillioides Corda
(isolates: 319A', 457A')

a. Synnemata.

b. Synnematal base.

c. A portion of the apex of a synnema.

d-e. Micronematous to semi-macronematous conidiophores.

f. Annellides producing allantoid conidia bearing short frills.

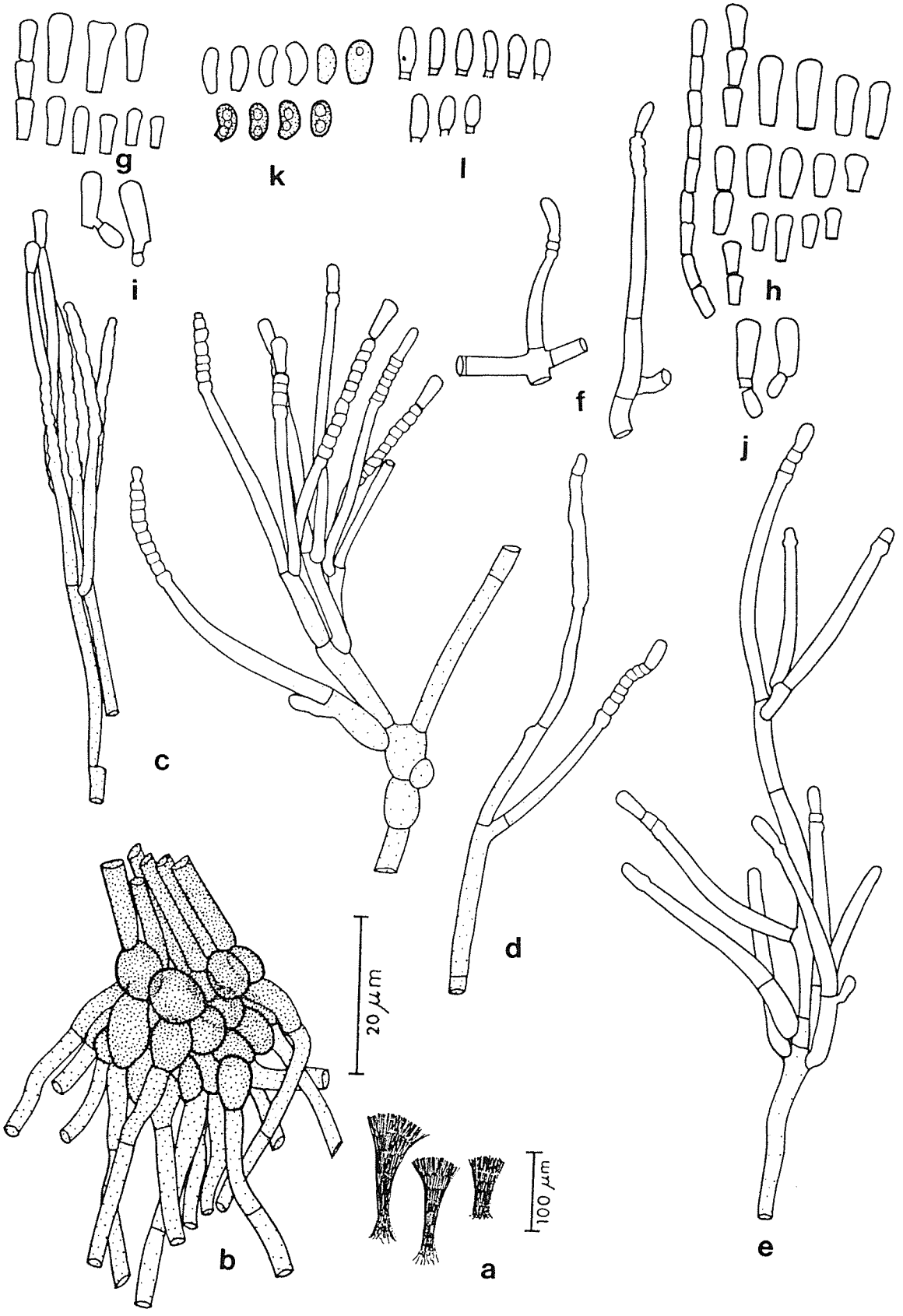
g-h. Short-clavate annelloconidia.

i-j. Secondary conidia developing from pegs on primary conidia.

k. Allantoid conidia (lacking frills), which are initially hyaline and thin-walled, but gradually become reniform, brown and thick-walled.

l. Allantoid conidia bearing short frills.

Isolates as illustrated: 319A': e, f, h, j, l.
457A': a, b, c, d, g, i, k.


g
k
l
i
h
f
j
c
d
e
b
a
20 µm
100 µm

Chlamydospores were not seen. Conidiophores annellidic, macronematous and synnematous; dark-brown to black, but becoming hyaline at the apex; narrowly clavate as the stem gradually increases in width from the base to the rather flat apex (Fig. 20B. a). The stem is composed of dark-brown, smooth-walled, or finely verruculose parallel hyphae which have broad, short cells at the base, but thinner and longer cells towards the apex where the hyphae branch and the stem increases in width (Figs. 20A. a, 20B. b). The annellides arise from the ultimate branches, but there is no clear separation between the stem and the layer of conidiogenous cells. Synnemata are 70 - 205 x 8 - 23 μm wide at the base and 15 - 100 μm wide at the apex. Very variable micronematous to semi-macronematous annellidic conidiophores are also present. Their structure ranges from single annellides arising from the vegetative hyphae to 1 - 3 annellides arising from a basal cell, or from structures which resemble portions of the base of the synnemata (Figs. 20A. c,d, 20B. d,e). Conidiogenous cells are annellidic; hyaline to brown at the base but hyaline towards the apex, and cylindrical to subulate; 13 - 25 x 1.5 - 1.7 μm wide at the base, but tapering to 1.4 - 1.6 μm at the apex. As the conidia are produced the conidiogenous cells elongate in small increments, with the result the annellation zone becomes 1.7 - 2.0 μm wide and often longer than the cell. Annelloconidia aggregate in slimy masses; 1-celled, hyaline, and smooth-walled; most are short-clavate with a very slightly curved apex and truncate base which virtually lacks frills; 3.5 - 6.5(9.0) x 1.7 - 3.2(4.0) μm (Figs. 20A. e, 20B. g,h). Occasionally short-allantoid conidia are also present which very rarely may

possess very short frills (Figs. 20A. h, 20B. 1); these are 4.0 - 6.0 x 1.8 - 2.0 μm. On aging the conidial masses blacken, and some of the conidia secondarily become subglobose, elliptical, or reniform in shape (Figs. 20A. g, 20B. k). Such conidia are brown with thick walls, and are 4.5 - 6.0(6.5) x 2.5 - 4.2 μm with truncate or flattened base. Annellidic microcyclic conidiogenesis on swollen conidia is common (Figs. 20A. f, 20B. i,j).

HOSTS: Larix sp., Pinus radiata

CULTURES EXAMINED: **New Zealand:** 23div, isolated from Larix sp., Compartment 5, Waiotapu, Kaingaroa State Forest, Taupo, collected 8 May 1982; 319A', isolated from P. radiata, Compartment 1212, Kaingaroa State Forest, Taupo, collected 17 February 1988; 457A', isolated from P. radiata, Compartment 2, Kaingaroa State Forest, Taupo, collected 28 February 1988.

G. penicillioides is known throughout Europe, from India, Japan, Tunisia, Taiwan, and North America, but this appears to be the first report of its occurrence from New Zealand. It has been found on rotten bark and wood of various deciduous trees, sometimes in association with bark beetles. Other substrata are woody plants, oak leaves and forest soils (Anon 1975; Anon 1987b; Ellis 1971; Lindau 1910; Matsushima 1971, 1975, 1980).

This species was commonly found in the galleries of the bark beetle

Hylurgopinus rufipes (Eichhoff) in the bark of Ulmus americana L., in the provinces of Manitoba and Saskatchewan (Sutton 1973; Sutton & Laut 1970). It has also been isolated from the large elm beetle Scolytus scolytus (F.) in the United Kingdom, and from bore holes of a Xyleborus species in Fagus sylvatica L. (Anon 1975; Anon 1987b).

Crane & Schoknecht (1973) compared G. penicillioides with the synnematous anamorph of Ceratocystis piceae (Münch) Bakshi, and found the two were different. It was therefore shown that G. penicillioides was not the anamorph of C. piceae as some had previously supposed.

The three New Zealand isolates produced the same type of synnemata, grew at approximately the same rate, had annellides which were of the same width as the subtending branches, and on aging produced thick-walled, brown conidia. Isolate 23div produced the least amount of dark pigment when grown on MEA.YE, while isolate 457A' produced the most. However, the shape of the conidia amongst the isolates appears a rather plastic character, but as previous descriptions of this species indicate that conidial shape is variable, the variation noted here was to be expected. Nonetheless, the majority of the conidia are reported to be curved or short-allantoid (Crane & Schoknecht 1973; Ellis 1971; Sutton 1973; Sutton & Laut 1970; Matsushima 1971, 1975), and this was not the majority shape in the isolates studied. In one of Matsushima's (1975) isolates, however, the conidia were predominantly straight. In culture (on MEA.YE), a proportion of the conidia became swollen, and secondary annelloconidia were produced from short pegs (Figs. 20A. f, 20B. i,j). Thus in view of the reported conidium variability in G. penicillioides,

the fact allantoid conidia are less common in these isolates than is normally recorded is discounted, and they assigned to this species.

G. penicillioides has shorter synnemata than the other Graphium species. Their dark pigmentation readily separates the species from any member of the genus Graphilbum.

These isolates appear to represent the first time this species has been obtained from coniferous hosts. However, as was the case with the deciduous tree species, they were associated with bark beetles, being found in their galleries. G. penicillioides seems to be a saprophyte which sometimes occurs in association with the vectors of more harmful fungi.

Graphium taxonomic sp. 1. Fig. 21. a-h.

Colonies attaining a diameter of 26 - 31 mm in 21 days at 20°C in darkness on OA, but growth is usually slower and more restricted on MEA.YE. Young colonies on OA are brown to dark brown (7.5YR $^{4}/_{2}$) punctate, phalacrogenous; little or no aerial mycelium is present between the brown synnemata bearing brown conidial drops, except at the white (10YR $^{8}/_{1}$) appressed margins. On aging, secondary synnemata may arise from the older ones. In reverse, colonies are at first colourless, but become grey to greyish brown (5YR $^{5}/_{1}$ to 2.5Y $^{5}/_{2}$) in the centre. Colonies grown on MEA.YE are light grey (10YR $^{7}/_{2}$) with brown to dark brown (7.5YR $^{4}/_{2}$) areas; phalacrogenous, with pale brown to brown conidial drops borne at the apex of individual, simple conidiophores or synnemata. Fewer synnemata are formed on MEA.YE than on OA, they usually develop late, and are often clustered on reddish-brown stromata (Fig. 21. b). In reverse, colonies are greyish brown (10YR $^{5}/_{2}$) in the centre, but very pale brown (10YR $^{8}/_{3}$) at the margins. Odour indistinct and an exudate is lacking. Hyphae hyaline and smooth-walled; 1.5 - 4.0 μm in diameter. Chlamydospores were not seen. Conidiophores annellidic, macronematous, synnematous, and semi-determinate; brown to pale brown but usually hyaline at the apex. Synnemata are narrowly clavate as the stem gradually increases in width from the base to the rounded apex (Fig. 21. a,b). The stem is composed of brown, smooth-walled, parallel hyphae, which arise as a result of repeated branching from broader, often inflated basal elements; towards the apex

Fig. 21. Graphium taxonomic sp. 1.
(isolate: 3F)

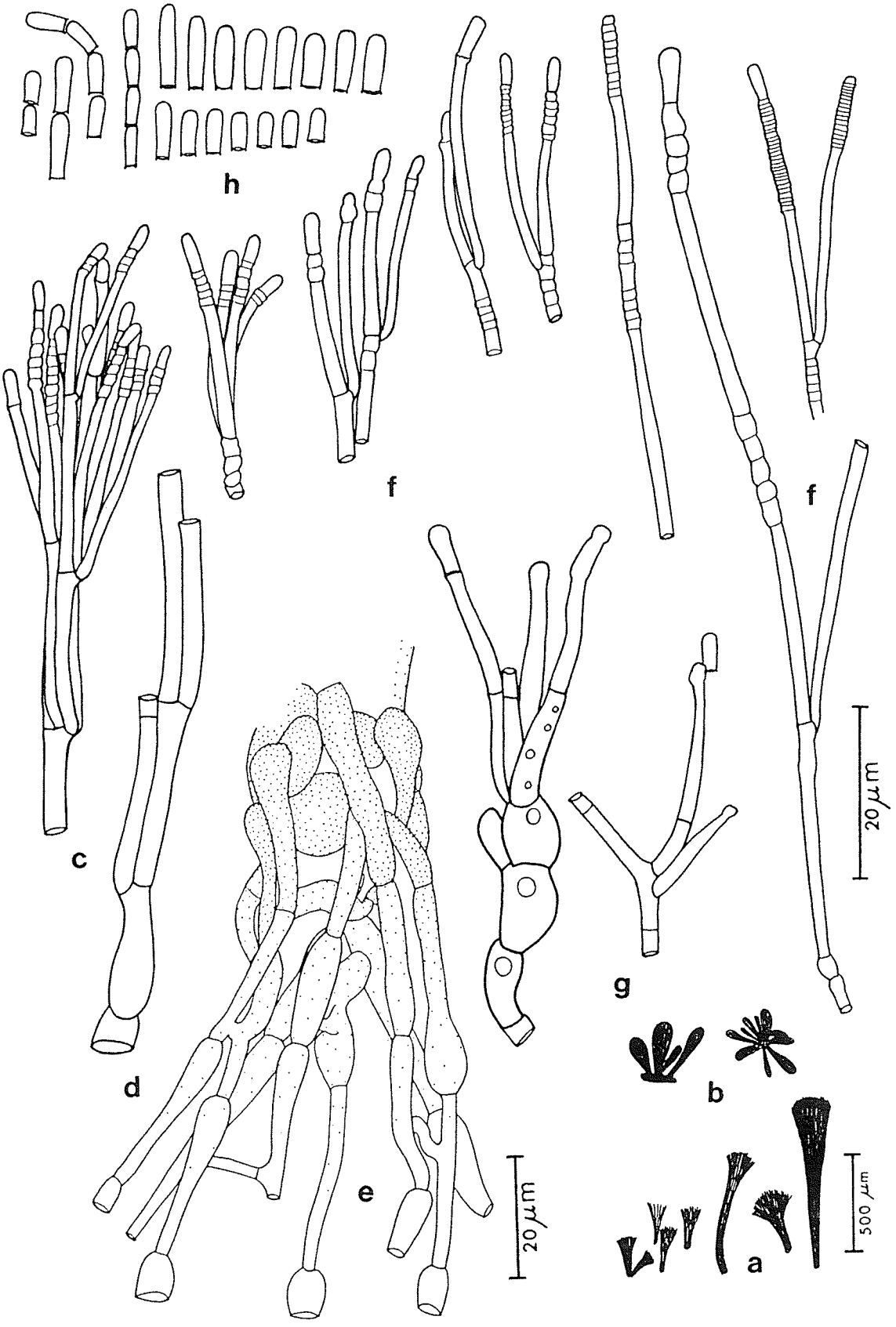
a-b. Synnemata; (b) habit sketch of a synnematal cluster arising from a stromatic mass.

c-f. Details of the synnematal structure: (c) portion of the apex of a young synnema with annellides on the apical branches; (d) branching hyphae of the stem of a synnema; (e) portion of the inflated hyphae anchoring the base of the synnema to the submerged hyphae; (f) annellides arising by proliferation from older annellides.

g. Micronematous to semi-macronematous conidiophores.

h. Annelloconidia.

Isolate as illustrated: 3F: a-h.


h
f
f
c
d
e
g
b
a
20 µm
20 µm
500 µm

the cells are thinner and longer as the hyphae branch repeatedly (Fig. 21. c,d,e), and this in turn causes the stem to increase in width. The annellides arise singly or in clusters of 2 - 3 from the ultimate branches of the stem (Fig. 21. c), or from older conidiogenous cells which may proliferate apically or sometimes branch (Fig. 21. f); the latter causes slight increases in the length of the synnemata. Synnemata are 120 - 1000 x 10 - 40 μm wide at the base, but without a clear separation between the stem and the layer of conidiogenous cells. Brown, clavate hyphal elements may occur between the basal elements of the synnemata and the vegetative hyphae (Fig. 21. e). Mononematous, micronematous to semi-macronematous, annellidic conidiophores are also present. They vary from annellides arising from structures which resemble single elements of the synnemata to those where the annellides arise from 1 - 3 series of branches which in turn develop from inflated, hyaline to pale brown basal cells borne singly or in chains; the basal cells measure 10.0 - 15.5 x 7.5 - 10.0(15) μm (Fig. 21. g). Conidiogenous cells annellidic; hyaline to brown at the base but becoming hyaline towards the apices; smooth-walled; cylindrical; 15 - 25 μm long, those on the synnemata are 1.4 - 1.7(1.9) μm wide at the base, tapering to 1.2 - 1.6 μm at the apex. Those on the smaller conidiophores may be as above, or they may be broader and then measure 1.8 - 2.4 μm in diameter at the base and 1.5 - 1.8 μm at the apex. As the conidia are produced, the conidiogenous cells elongate in small increments, and the annellation zone is 1.7 - 2.0 μm wide on the narrower cells and 2.0 - 2.4 μm wide on the broader ones; the zone is

often as long as or longer than the cell. The conidiogenous cells frequently proliferate and branch thereby giving rise to new conidiogenous cells (Fig. 21. f). Annelloconidia aggregate in slimy masses; 1-celled, hyaline, and smooth-walled; they are narrowly-clavate to cylindrical and measure (3.5)4.0 - 8.5(9.5) x 1.7 - 2.4 μm with rounded apices, truncate bases, and 0.7 - 1.0 μm long frills (Fig. 21. h).

HOST: Pinus contorta Dougl. ex Loud.

CULTURE EXAMINED: **Canada:** 3F, isolated from P. contorta, Hwy. 14, 15 km west of Sooke, Vancouver Island, British Columbia, collected 17 September 1987.

This isolate resembles Graphium penicillioides Corda in basic synnematal morphology, but it differs in: (1) having larger, brown or pale reddish-brown synnemata; (2) producing straight conidia which all have the same shape; and (3) producing annellides which frequently proliferate apically and if the synnemata develop abundantly, the colonies become reddish brown due to the colour of the synnemata. However, the hyphae are mostly hyaline, although some brown hyphae are present in the stromatic aggregations which occasionally develop in cultures on MEA.YE. G. putredinis (Corda) S. J. Hughes is the species which would be closest to isolate 3F in the height of the synnemata and their colour, but the conidia produced by this isolate are smaller than the 5 - 11 x 2 - 4 μm conidia reported for that species, and the shape

of the synnemata also differ.

This isolate is placed in Graphium based on the brown pigmentation of the synnemata, which although much lighter than the olivaceous pigmentation found in most other Graphium species, is sufficient to exclude it from Graphilbum whose species are strictly hyaline. Graphilbum was erected for the synnematal state of Ceratocystis sparsa R. W. Davidson (Upadhyay & Kendrick 1975) to emphasise the differences between that state and species of Graphium. Subsequently, species which form hyaline or very pale coloured synnemata, and produce conidia on annellides have been assigned to Graphilbum.

In describing Graphilbum pleomorphum, Okada & Tubaki (1984) commented on the presence of a brownish-orange pigment in the synnemata of that fungus on natural substrata, while the pigment was either absent, or only very pale structures were formed in culture. They therefore considered G. pleomorphum to be sufficiently distinct from Graphium species to warrant placement in a different genus. Since in culture the synnemata were hyaline, they selected Graphilbum. Isolate 3F may also produce palely pigmented synnemata in culture, but under other cultural conditions, fairly strongly pigmented synnemata developed. It can thus be considered an intermediate between Graphilbum and Graphium as those genera are currently defined.

Neither protoperithecia nor perithecia were produced in culture so no teleomorph connection was uncovered.

Hyalodendron Diddens, Zentbl. Bakt. ParasitKde. Abt. II, 90:316. 1934

Type species: Hyalodendron lignicola Diddens

Teleomorphs unknown or wanting.

This genus is characterized by fairly slow-growing colonies, and hyaline, smooth-walled hyphae in which thick-walled, pale olivaceous, saturnoid, chlamydospore-like structures may be present. Conidiophores may be micronematous or semi-macronematous, with each semi-macronematous conidiophore consisting of a short, simple or branched stem bearing terminal conidiogenous cells. Each micronematous conidiophore consists of a conidiogenous cell which arises laterally from hypha. The conidiogenous cells are discrete or integrated, hyaline, smooth-walled, and cylindrical with 1 - 3 short and rather flat, apical denticles; the latter may be considered indistinct, raised secession scars. The holoblastic conidia are 1-celled, hyaline and smooth-walled, and are produced acropetally in simple or sparsely branched chains. Although the conidia are longer in the lower portion of each chain, all conidia are cylindrical-elliptical, and taper at each end to a short, truncate pedicel. Polyblastic ramoconidia are to be found at the bases of the branches, and in aging colonies some conidia produce secondary conidia.

This genus was erected to accommodate both H. lignicola, which was originally described as being polymorphic, and H. album (Dowson) Diddens, a white species that was transferred from the genus Cladosporium Link (Diddens 1934). The latter has subsequently been

equated with Ramularia deusta (Fuckel) Karakulin. Morphologically, species of the genus have been considered to be hyaline but rather delicate counterparts of Cladosporium. Several species have been formally assigned to this genus (Diddens 1934; Hansford 1947; Reddy & Bilgrami 1971), while other possible members have been briefly described without being formally named (Barron 1968; Matsushima 1975; Meyer 1959). Approximately nine Ceratocystis species are reported to have Hyalodendron anamorphs or synanamorphs (Hutchison & Reid 1988a; Kowalski & Butin 1989; Upadhyay 1981), as well as Endomyces cortinarii Redhead & Malloch (Redhead & Malloch 1977).

Based on morphological, physiological, and ultrastructural criteria (de Hoog 1979; Martinez 1979; Martinez et al. 1979), that unlike all other species assigned to Hyalodendron, H. lignicola unquestionably has basidiomycetous affinities; the genus is therefore clearly monotypic, but its actual taxonomic position remains unresolved.

Diddens (1934) compared the two species of Hyalodendron she accepted with species of Monilia Bonord., but noted that although the latter also produce their conidia in branched chains, their conidia were broader and of different shape than those produced by the Hyalodendron species. H. lignicola is distinguished from the somewhat similar species of Candida Berkhout, Moniliella Stolk & Dakin, and Trichosporonoides Haskins & Spencer since it does not produce bud cells, nor does it become pigmented on aging, as do species of the latter two genera. Species of Sporothrix Hekt. & Perkins are also distinct; here conidiogenous cells are well defined, with distinct denticles, and only

short, acropetal conidial chains. Species of Ramularia Unger are restricted to higher plant leaves, and those hyaline Cladosporium-like entities described by Barron (1968) are considered to be merely Cladosporium mutants by de Hoog (1979).

H. lignicola is now the only species recognized in this genus (de Hoog 1979). Anamorphs or synanamorphs of Ceratocystis species which have been assigned either to the genus Hyalodendron, or considered intermediate between Sporothrix and Hyalodendron, can probably all be accommodated in Sporothrix. This genus, as presently circumscribed by de Hoog & Constantinescu (1981), includes species which produce conidia in short acropetal chains in a manner defined as "Hyalodendron-like".

Hyalodendron lignicola Diddens, Zentbl. Bakt. ParasitKde. Abt. II, 90:317. 1934 Fig. 22. a-d.

=Hyalodendron lignicola Diddens f. undulatum Diddens, Zentbl. Bakt. ParasitKde. Abt. II, 90:318. 1934

=Hyalodendron lignicola Diddens f. simplex Diddens, Zentbl. Bakt. ParasitKde. Abt. II, 90:318. 1934

Colonies attaining a diameter of 12 - 19 mm in 12 days at 20°C on MEA.YE. White (between 2.5Y $^{8}/_{0}$ and $^{8}/_{2}$) but sometimes with light grey (10YR $^{7}/_{1}$) sectors; mostly phalacrogenous or nematogenous, with the conidiophores which cover the surface of the medium consisting of short stems bearing branching chains of conidia. In reverse, colonies are yellowish brown, brown or dark grey (10YR $^{5}/_{4}$, $^{5}/_{3}$ or $^{4}/_{1}$) in the centre but light yellowish brown or pale brown (10YR $^{6}/_{4}$ or $^{6}/_{3}$) towards the very pale brown or light grey (10YR $^{8}/_{3}$, $^{7}/_{3}$ or 2.5Y $^{7}/_{2}$) margins. On aging, in reverse, the colonies may become brown or strong brown to dark grey (7.5YR $^{4}/_{5}$ or $^{5}/_{6}$ to 10YR $^{4}/_{1}$). Odour indistinct. Exudate present as small to large, clear drops. Globose, hyaline to very pale yellow crystals which measure 4.8 - 6.5 µm in diameter (Fig. 22. a) are often present in the medium within the colonies. Hyphae hyaline; smooth-walled and 1.5 - 2.5 µm in diameter; often containing yellowish oil droplets and, on aging, some surface hyphae may become brown and verruculose. Chlamydospores were not seen. Conidiophores semi-macronematous or micronematous, hyaline and smooth-walled; when semi-macronematous, consisting of 1 to 6-celled, unbranched stems each bearing a terminal

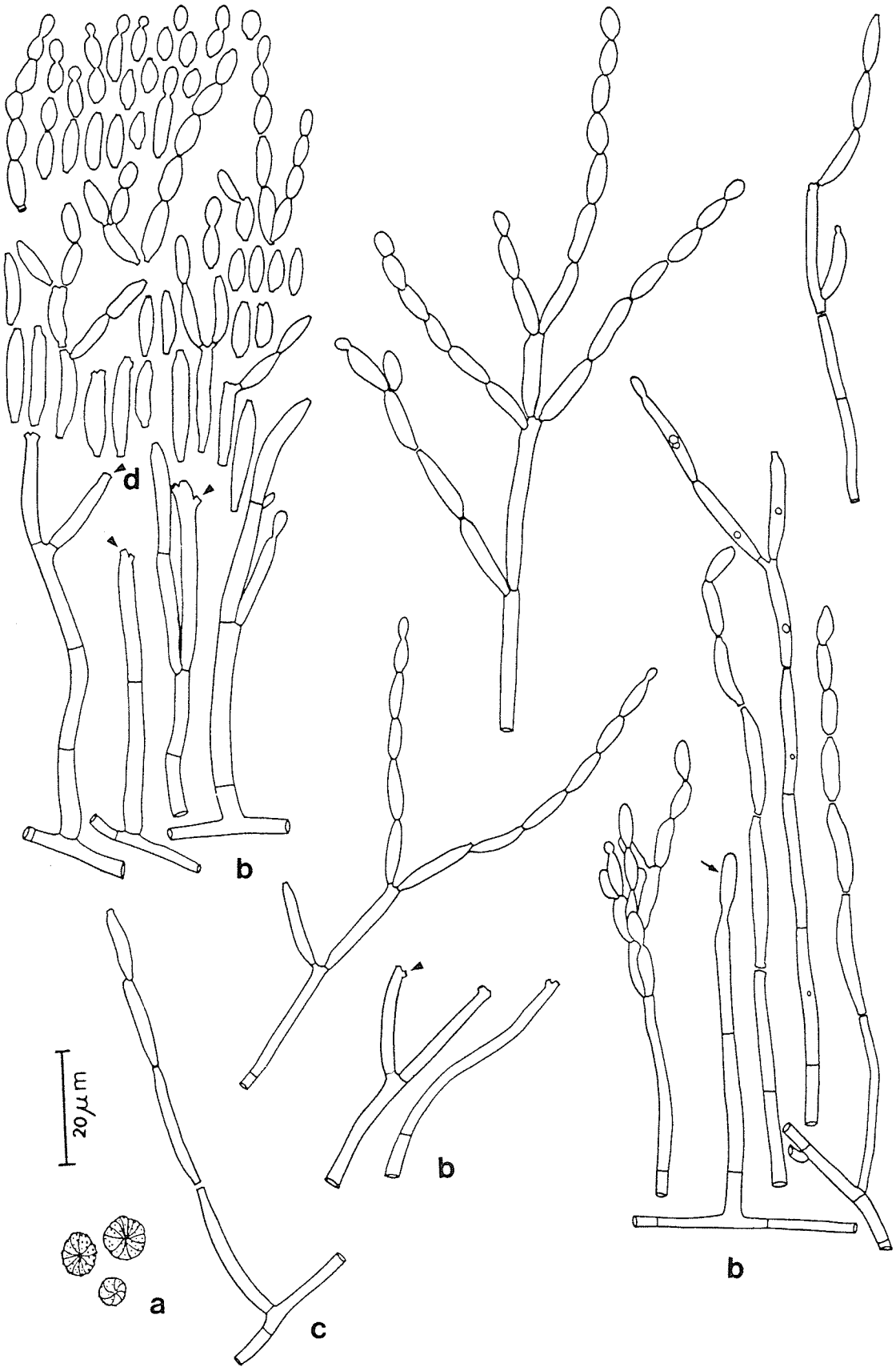
Fig. 22. Hyalodendron lignicola Diddens
(isolates: 98c, 105ai)

a. Crystals (stylized drawing).

b-c. Conidiophores, the conidiogenous cells producing catenate conidia on short, flat denticles («); a first-formed conidium («-).

d. Conidia, long, short and polyblastic.

Isolates as illustrated: 98c: c.
105ai: a, b, d.


d
b
b
b
c
a
20 µm

conidiogenous cell or, when micronematous, the stem is lacking. Each conidiogenous cell has 1 - 3 apical conidiogenous loci (Fig. 22. b «) from which the first conidia arise holoblastically (Fig. 22. b «-). The conidiophores, measured to the apices of the conidiogenous cells, are 20 - 95 x 1.7 - 3.2 μm (Fig. 22. b,c) and apically bear 1 - 3 chains of conidia which may branch; the conidia in the basal portion of the main chains are usually the longest. The holoblastic conidiogenous cells are discrete or integrated, hyaline, smooth-walled, and nearly cylindrical; 18 - 25 x 2.0 - 3.0 μm, with 1 - 3 short and flat cylindrical, apical denticles which are truncate and not thickened at their apices (Fig. 22. b «). Conidia produced acropetally in long, dry, branched chains; 1-celled, hyaline and smooth-walled; shape ranging from elliptical-oval with short, truncate pedicels on each end, to cylindrical but tapering at the ends to short, truncate pedicels; the shorter, elliptical-oval conidia predominate. The polyblastic conidia from which branches develop are not tapered at the bi-pedicellate apices. The size range for all the conidia is 4.5 - 16(20) x (2.0)2.4 - 3.2 μm (Fig. 22. d). Some conidia may produce secondary conidia.

HOST: Pinus radiata

CULTURES EXAMINED: **New Zealand:** 98c, isolated from P. radiata, off road 41, Whangapoua State Forest, Coromandel, collected 19 May 1982; 105ai, isolated from P. radiata, off Highway 25, Whangapoua State Forest, Coromandel, collected 19 May 1982.

H. lignicola, which was first isolated from ground pulp in Sweden, reduced the amount of staining caused by certain blue stain fungi when the organisms were grown in paired cultures on pulp wood under laboratory conditions (Diddens 1934; Melin & Nannfeldt 1934). It has also been found in leaf litter, as one of the rarer endophytes of Pinus sylvestris L. and Fagus sylvatica L., and in beer pipes in a brewery (de Hoog 1979; Petrini & Fisher 1988; Tubaki & Yokoyama 1971). It is known from Sweden, the Netherlands, Britain, and Japan but has not been previously reported from New Zealand.

De Hoog (1979), based on his examination of the cultures of the three formae erected by Diddens, decided the characters used to separate them, i.e. undulating hyphae for f. undulatum and simple conidial chains for f. simplex, were actually present in all of them, hence the now accepted synonymy.

The New Zealand isolates differ only slightly in colony characteristics and growth rates; isolate 98c being somewhat faster growing and its colonies are more lightly pigmented in reverse than those of isolate 105ai. The small, globose bodies (Fig. 22. a) present in the medium beneath the colonies were first thought to be chlamydospores. However, since they were not connected to the hyphae, and their content appeared more crystalline than oily, these bodies are considered to be crystals.

Although the New Zealand isolates agree quite well with Diddens (1934) description, she did report the conidia were somewhat shorter; the conidial measurements being closer to those of de Hoog (1979).

Neither the conidial scars nor the denticles on the conidiogenous cells were thickened, and the conidial chains were rather sparsely branched and quite long. The illustrations of Diddens (1934) and de Hoog (1979) suggest relatively short chains compared to those observed, but the illustrations may not accurately reflect their actual observations. Nonetheless, in spite of the minor differences noted, these isolates certainly represent H. lignicola.

Although Hyalodendron as now understood is monotypic, H. lignicola does resemble the Hyalodendron-like fungus (MFC-4608) described and illustrated by Matsushima (1975); and if the latter organism is not an isolate of H. lignicola, it may actually represent a second Hyalodendron species.

H. lignicola is chiefly isolated from woody substrata, and has been found in association with blue stain fungi (Melin & Nannfeldt 1934). It appears to be of relatively rare occurrence, at least judging from the number of times it has been mentioned in the literature.

Hyalopesotum Upadhyay & Kendrick, Mycologia 67: 801. 1975

Type species: Hyalopesotum introcitrina Upadhyay & Kendrick, the anamorph of Ceratocystis introcitrina Olchowecki & J. Reid

Teleomorphic genera: Ceratocystis Ellis & Halst. sensu lato & Ceratocystiopsis Upadhyay & Kendrick

The genus is characterized by hyaline colonies growing at moderate rates. Conidiophores are sympodial, macronematous, and synnematous; hyaline; erect to lax; the stem consisting of simple or branched hyphae bearing the sympodulae penicillately arranged at the apex. The conidiogenous cells are sympodial, hyaline, and cylindrical to subulate, and produce 1-celled sympodioconidia which aggregate in slimy masses.

Hyalopesotum was erected for hyaline counterparts of the genus Pesotum Crane & Schoknecht. Typically, species of the latter produce darkly pigmented synnemata and, usually, dark coloured colonies. It was one of four new genera proposed for different anamorphs of Ceratocystis and Ceratocystiopsis species by Upadhyay & Kendrick (1975) and was based on the Hyalopesotum state of Ceratocystis introcitrina Olchowecki & J. Reid. In contrast to the generic concept of Pesotum, when Hyalopesotum was erected reference was made only to the synnematous state, and not to any monomematous or micronematous states which might occur with the synnemata. However in practice these different states of a single species are usually referred to as separate synanamorphs. Hyalopesotum species differ from those of Pesotum only in the lack of dark pigmentation, but

as noted by Hutchison & Reid (1988b), some species may produce small amounts of pigments, and thus the stems of synnemata produced in aging colonies may become pale brown or brown. The existence of intermediate forms certainly raises the question of how reliable pigmentation is as a major character in delimiting genera. The mode of conidiogenesis is another important character, and this together with the presence or absence of pigmentation serves as the basis for separating the synnematous anamorphs of Ceratocystis into six different genera. On the whole this group of organisms is very plastic in their mode of conidiogenesis and may produce conidia on phialides, sympodulae, or annellides, and often more than one kind of conidiogenous cells is present on the same conidiophore.

There are three Ceratocystis species reported as having Hyalopesotum anamorphs or synanamorphs, and one species, H. pini Hutchison & J. Reid, has not been connected to a teleomorph. All are associated with bark beetles or their galleries.

Hyalorhinocladiella Upadhyay & Kendrick, Mycologia 67: 800. 1975

Type species: Hyalorhinocladiella minuta-bicolor Upadhyay & Kendrick, the anamorph of Ceratocystiopsis minuta-bicolor (R. W. Davidson) Upadhyay & Kendrick

Teleomorphic genera: Ceratocystiopsis Upadhyay & Kendrick and Ceratocystis Ellis & Halst. sensu lato

This genus was originally simply described as "Rhinocladiella-like but lacking pigmentation" (Upadhyay & Kendrick 1975), and with reference to the description of Davidson (1966).

Colonies grow at slow to moderate rates, are whitish in colour, and often appear slimy or moist. The conidiophores are micronematous to semi-macronematous, hyaline, usually simple or sparsely branched, but occasionally they are penicillately branched. They bear integrated, cylindrical to subulate sympodulae at the apex. The conidiogenous cells are sympodial and produce the conidia directly on irregular, proliferating rachises with indistinct secession scars. The sympodioconidia aggregate in slimy masses, are 1-celled, hyaline and smooth-walled, and are clavate to oblong-oval with a truncate base.

Hyalorhinocladiella was one of four new genera proposed by Upadhyay & Kendrick (1975) to accommodate anamorphs of various Ceratocystis and Ceratocystiopsis species, and was based on the anamorph of Ceratocystiopsis minuta-bicolor.

Hyalorhinocladiella species differ from those of Sporothrix Hekt. &

Perkins by producing the conidia directly on the rachises, but not on distinct denticles as do species of the latter. The conidiophores are not aggregated into sporodochia, nor do the colonies become darkly pigmented as do most species of the genus Raffaelea von Arx & Hennebert.

Upadhyay (1981) lists eleven species of Ceratocystis and seven species of Ceratocystiopsis as having Hyalorhinocladiella anamorphs or synanamorphs. All the Hyalorhinocladiella species described to date are associated with their teleomorphs and are found in association with bark beetles and their galleries.

Hyalopesotum taxonomic sp. 1. Fig. 23. a-l.

Synanamorph: Hyalorhinocladiella sp.

Teleomorph affinities: Ceratocystiopsis spp.

Colonies attaining a diameter of 28 - 32 mm in 12 days at 20°C in darkness on MEA.YE. White (5Y 8/1) and mostly nematogenous; the colony surface is flat, with irregular patches being covered with white, slimy conidial masses, but the central area is sometimes plectonematogenous to synnematogenous with long thin hyphal strands. On aging, shorter, often clustered, moist appearing, lanceolate to cylindrical synnemata develop. In reverse, colonies are white (10YR 8/2). Colonies grown in alternating light and darkness are zonate. Numerous conidia are produced submerged in the medium. Odour indistinct and an exudate is lacking. Occasionally small darkly pigmented bodies were produced in these cultures, but it was in cultures maintained at 4°C for several months that numerous sterile perithecia developed. Hyphae are hyaline, smooth-walled, and 1.5 - 4.0 µm in diameter; when funiculose, the strands are 7 - 80 µm wide, the thinner strands consisting of 2.0 - 3.5 µm wide hyphae, but the broader strands are formed of hyphae about 1.5 µm wide. Chlamydospores were not seen. Conidiophores sympodial, macronematous, semi-macronematous, and micronematous; hyaline and smooth-walled except for some branches which are irregularly verrucose. Macronematous conidiophores are synnematous; indeterminate; usually lanceolate or cylindrical but then tapering to a pointed apex; their base consists of a series of inflated, thick-walled cells (Fig. 23. g), while in the

Fig. 23. Hyalopesotum taxonomic sp. 1., synanamorph: Hyalorhinocladiella sp. (isolate: 110N (UM74-110))

a. Sterile Ceratocystiopsis-like perithecia.

b-c. Ostiolar hyphae; (b) at a perithecial neck apex; (c) a single hypha.

d-f. Micronematous conidiophores; (d) young conidiophores with sympodulae and pegs («-); (e) sympodulae, some arising from inflated, thick-walled basal cells; (f) older conidiophores with both sympodulae and pegs («-) producing long rachises.

g. Inflated, thick-walled cells from the base of a synnema.

h. Upper portions of synnemata illustrating sympodulae and numerous short branches.

i. Cylindrical sympodulae from synnemata.

j-k. Sympodioconidia; (j) clavate; (k) oval.

l. Inflated conidia with short pegs.

Isolate as illustrated: 110N (UM74-110): a-l.


a
100 µm
b
20 µm
c
d
e
f
g
h
i
j
k
l
20 µm

upper portion the hyphae branch repeatedly producing short branches and sympodulae (Fig. 23. h). Each branch produces 2 - 3 new branches and/or sympodulae, and at the apex are the youngest sympodulae and growing branches. The sympodulae borne on the synnemata are cylindrical, and arise from thin hyphal branches. Semi-macronematous conidiophores are usually aggregated on aerial hyphae or thin hyphal strands, are 25 - 90 µm long and consist of a short stem or a basal cell which may be thick-walled. These bear conidiogenous cells directly, or a penicillate cluster of 1 - 3(7) series of short branches and sympodulae. The primary branches are often short-clavate and sometimes thick-walled, and 2.5 - 5.5 µm wide, while subsequent series are usually shorter and thinner (Fig. 23. e,f). The sympodulae, which are sometimes reduced to short pegs (Fig. 23. d,f «-), arise amongst the branches at any level, and are usually somewhat divergent and thinner than the subtending branches; each branch produces 2 - 5 branches and/or sympodulae (Fig. 23. e,f). Micronematous conidiophores consist of a short basal cell bearing 1 - 3 sympodulae, or the sympodulae arise singly from the vegetative hyphae. Conidiogenous cells sympodial, integrated or discrete, hyaline and smooth-walled, cylindrical to subcylindrical and tapering to the apex; the cylindrical sympodulae on the synnemata measure 14.5 - 20(23) x 1.3 - 1.5 µm, and are 0.9 - 1.2 µm wide at the apex (Fig. 23. h,i), but other sympodulae measure 6.0 - 17.5 x 1.5 - 2.4 µm and taper to 1.0 - 1.4 µm at the apex (Fig. 23. d,e,f). The conidia are produced directly on the 1.0 - 1.5 µm wide, flexuose rachises. The rachises appear irregular and coarsely verrucose because of the

indistinct secession scars. Sympodioconidia aggregate in slimy masses; 1-celled, hyaline, and smooth-walled; short-clavate to short-cylindrical; 3.2 - 4.8(5.5) x 1.5 - 2.4 μm with an obtuse apex and truncate base (Fig. 23. j), but some conidia from the conidial masses are somewhat inflated, appear oval (Fig. 23. k), and are 2.0 - 2.8 μm wide. Rarely, inflated conidia from the slimy masses develop a short peg on one end and are thus presumed to be undergoing secondary conidiogenesis (Fig. 23. l). Sterile perithecia, when formed, occur singly, are black and have a subglobose base; these are 75 - 110 μm in diameter, and have a neck which is 120 - 220 μm long, 30 - 50 μm wide at the base and 20 - 25 μm wide at the apex (Fig. 23. a). Ostiolar hyphae are subhyaline and converge to a point (Fig. 23. b). They are approximately 20 μm long and 2.5 μm wide at the base and taper to a blunt tip (Fig. 23. b,c). Ascospores were not seen.

HOST: Pinus sylvestris L.

CULTURES EXAMINED: **Norway:** 110N (UM74-110), isolated from Ips typographus L. galleries in P. sylvestris, Hwy. 2, near Kongsvinger, Hedmark, collected in October 1973.

Based on the morphology of the mononematous conidiophores, this hyaline isolate was originally assigned to the genus Hyalorhinocladiella. However, in addition to these, it also occasionally produced hyaline synnemata. Although the colonies consist mostly of the

Hyalorhinocladiella synanamorph, some synnemata are usually produced, and these form small patches in aging colonies. Since the most complex synanamorph is usually listed as the principal anamorph, it was decided to report this isolate as a Hyalopesotum based on the presence of synnemata. However, the Hyalorhinocladiella synanamorph is always more abundant, and develops before the synnemata.

The synnemata of this isolate differed from those of other, more typical Hyalopesotum anamorphs of Ceratocystis species. Most obvious was the fact that the synnemata of this Norwegian isolate appear to be indeterminate, and capable of producing up to 20 series of short, relatively thin branches and sympodulae in the upper portion of the synnemata, while actively producing new branches at the apex. The synnemata of the more typical Hyalopesotum species usually consist of a cylindrical stem, and only a few series of branches bearing a discrete layer of sympodulae at the top. The Hyalorhinocladiella anamorphs of some Ceratocystiopsis species have been reported as having penicillately branched, micronematous conidiophores and some species also form short, synnema-like structures (Upadhyay 1981). Such complex structures were not included in the generic concept of Hyalorhinocladiella, but Upadhyay (1981) did not report them as separate synanamorphs either. If such structures, which perhaps are only produced occasionally, are included in the generic concept of Hyalorhinocladiella, this new species could be assigned to that genus, without assigning a separate name to the synnemata.

In culture, this isolate produced sterile perithecia which were

morphologically similar to those found in the genus Ceratocystiopsis, a genus in which several species are known to have Hyalorhinocladiella anamorphs. Although these sterile perithecia may not accurately reflect the size of mature perithecia, the shape of the rather short neck and the ostiolar hyphae converging to a point certainly resemble the perithecia of Ceratocystiopsis species. When the size and shape of the sterile perithecia and the branching pattern of the conidiophores were compared with the Ceratocystiopsis species reported as having Hyalorhinocladiella states (Upadhyay 1981), it appeared closest to C. minuta (Siemaszko) Upadhyay & Kendrick. That species, like this isolate, has penicillate conidiophores with 1 - 3 series of branches which occasionally appear synnematous and up to 120 μm long. However, Upadhyay considers these synnemata-like structures as aggregated conidiophores, not true synnemata. The perithecial necks found in the Norwegian isolate were longer (up to 220 μm) and somewhat broader than those of C. minuta which are reported to be 45 - 150 μm long.

Until either methods are found to induce maturation of the perithecia, or the affinities of this isolate are determined by other techniques, e. g. restriction fragment analysis of the ribosomal or mitochondrial DNA, the actual affinities of this organism cannot be determined. Therefore, for now, no final decision has been made as to its status.

Leptodontidium de Hoog, Taxon 28:348. 1979

≡Leptodontium de Hoog, Stud. Mycol. 15:122. 1977 (non Leptodontium (C. Mueller) Hampe ex Lindb. 1864 (Musci))

Type species: Leptodontidium elatius (Mangenot) de Hoog

Teleomorphs unknown or wanting.

This genus is characterized by relatively slow growing species, producing grey to black, often plectonematogenous colonies, whose submerged hyphae are often hyaline and thin-walled, but may become brown and compact; chlamydospores are often common in many species. In young colonies the conidiophores are micronematous or semi-macronematous with relatively thin, light-coloured walls, and the conidiogenous cells are hyaline, thin-walled, and often occur in groups or clusters; however, on aging, the conidiophores may become dark-brown and thick-walled while the septa remain thin. The conidia are produced in a sympodial manner directly on elongating rachises and do not leave thickened secession scars. They are 1-celled, hyaline or occasionally brown, smooth-walled, cylindrical, allantoid, navicular to globose, and sometimes produce secondary conidia.

Leptodontidium species have often been isolated from wood, especially that of conifers where they are often found associated with rotten areas. Other substrata, although rarer, include forest soil and other fungi (de Hoog 1977).

The original generic name Leptodontium de Hoog (1977), was

subsequently found to be a later homonym of the moss genus Leptodontium (C. Mueller) Hampe ex Lindb., and was thus renamed Leptodontidium (de Hoog 1979). Its type species had originally been placed in Rhinocladiella Nannf. but, during a study of the black yeasts, de Hoog (1977) decided L. elatius (Mangenot) de Hoog differed sufficiently from those species he felt properly belonged in Rhinocladiella to warrant generic separation. At that time he assigned five species and one variety to the genus, and at least one species has been added since.

Morphologically Leptodontidium species do closely resemble Rhinocladiella species, but differ therefrom in lacking pigmentation in both the young colonies and conidiogenous cells, and in possessing proliferating rachises which lack any distinct scars or denticles. The lack of denticles also separates Leptodontidium species from those of Sporothrix Hekt. & Perkins, and from species of Acrodontium de Hoog sect. Acrodontium, although the latter may superficially resemble some darkly pigmented Leptodontidium species.

Leptodontidium elatius (Mangenot) de Hoog var. elatius, Taxon 28:348. 1979 Figs. 24A. a-d, 24B. a-d.

≡Rhinocladiella elatior Mangenot, Revue gen. Bot. 59:57. 1952

≡Leptodontium elatius (Mangenot) de Hoog var. elatius, Stud. Mycol. 15:47. 1977

Colonies attaining a diameter of 15 - 19 mm in 12 days and 22 - 30 mm in 21 days, at 20°C in darkness on MEA.YE. At first grey (5Y $^{6}/_{1}$, 2.5Y $^{6}/_{0}$), but becoming light grey (5Y $^{7}/_{1}$) at the margins; nematogenous to finely plectonematogenous and tufted, producing dry conidia apically on thin conidiophores which later resemble minute bottle-brushes. The conidial production varies between isolates, and thus as the colonies age they become either grey or dark grey to olive grey (5Y $^{5}/_{2}$ or $^{4}/_{1}$ to $^{5}/_{2}$), and appear mealy in texture due to abundant conidial production on hyphal strands. Sometimes the colonies may be light grey to olive or olive grey (5Y $^{7}/_{2}$ to $^{4}/_{3}$ or $^{4}/_{2}$), depending on the pigmentation of the submerged hyphae, with the conidiophores being sparse on the tufted surface, but more abundant towards the surface of the medium. In reverse, colonies are at first grey to light olive grey (5Y $^{5}/_{1}$ to $^{6}/_{2}$) in the centre and white (2.5Y $^{8}/_{2}$ to 5Y $^{8}/_{2}$) at the margins, but become grey or dark grey to olive grey (2.5Y $^{5}/_{0}$ or $^{4}/_{0}$ to 5Y $^{5}/_{2}$) on aging. Odour and crystals are lacking, but an exudate may be present as small to medium sized, clear drops. Hyphae hyaline to brown, smooth-walled, and 1.5 - 5.0 µm wide, the aerial hyphae only up to 3.5 µm in diameter; submerged hyphae are often constricted at the septa and irregularly

Fig. 24A. Leptodontidium elatius (Mangenot) de Hoog var. elatius (isolate: 16'')

a. Conidiophores with cylindrical sympodulae, several of which illustrate secondary proliferation through the rachises («-), others branching («).

b. Conidiophores bearing the shorter (naviculate) sympodulae.

c. Sympodioconidia.

d. An allantoid conidium being produced at the apex of a conidiophore, and below which an earlier produced conidium has undergone secondary changes to become oblong-elliptical in shape.

Isolate as illustrated: 16'': a-d.

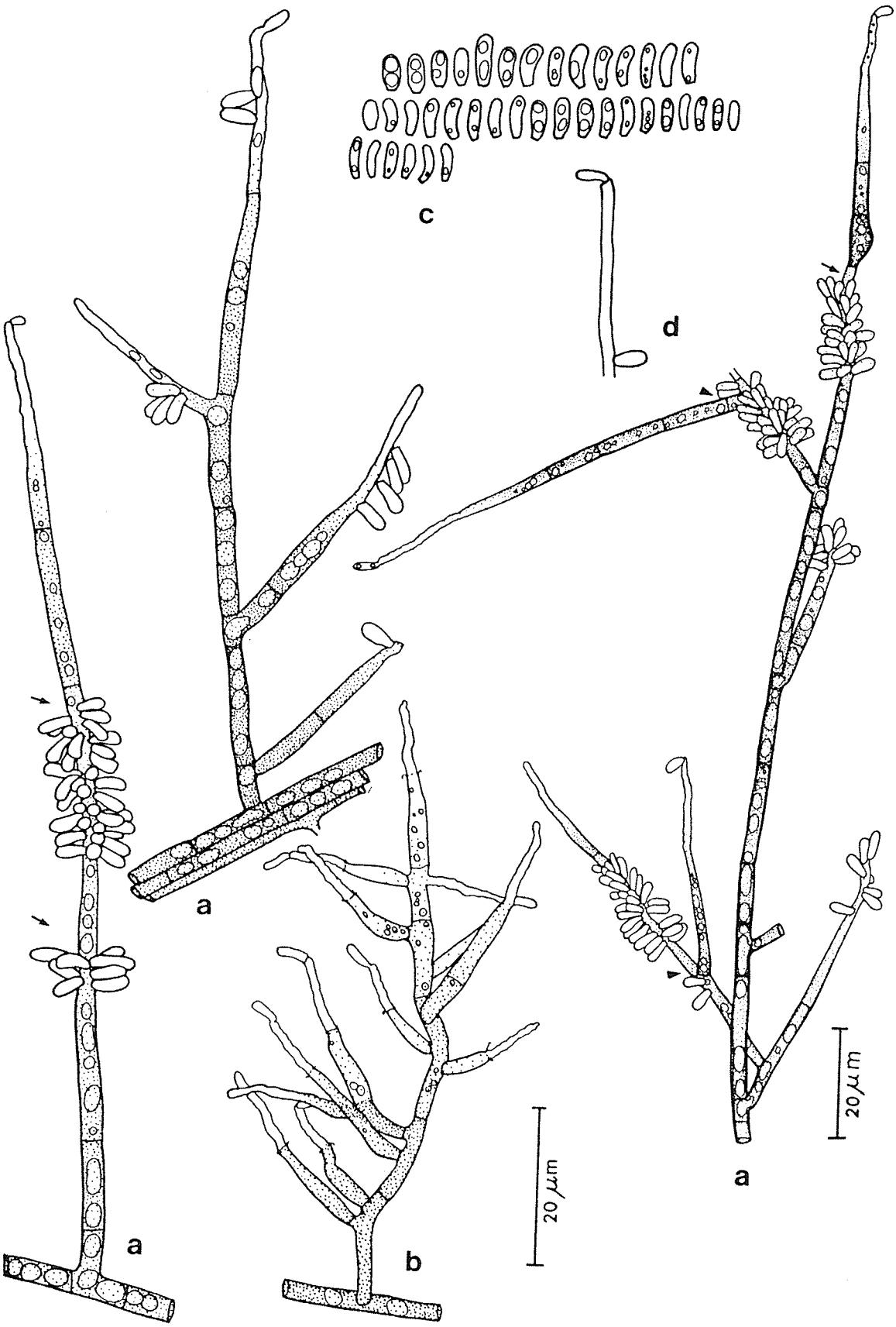

c
d
a
a
b
a
20 µm
20 µm

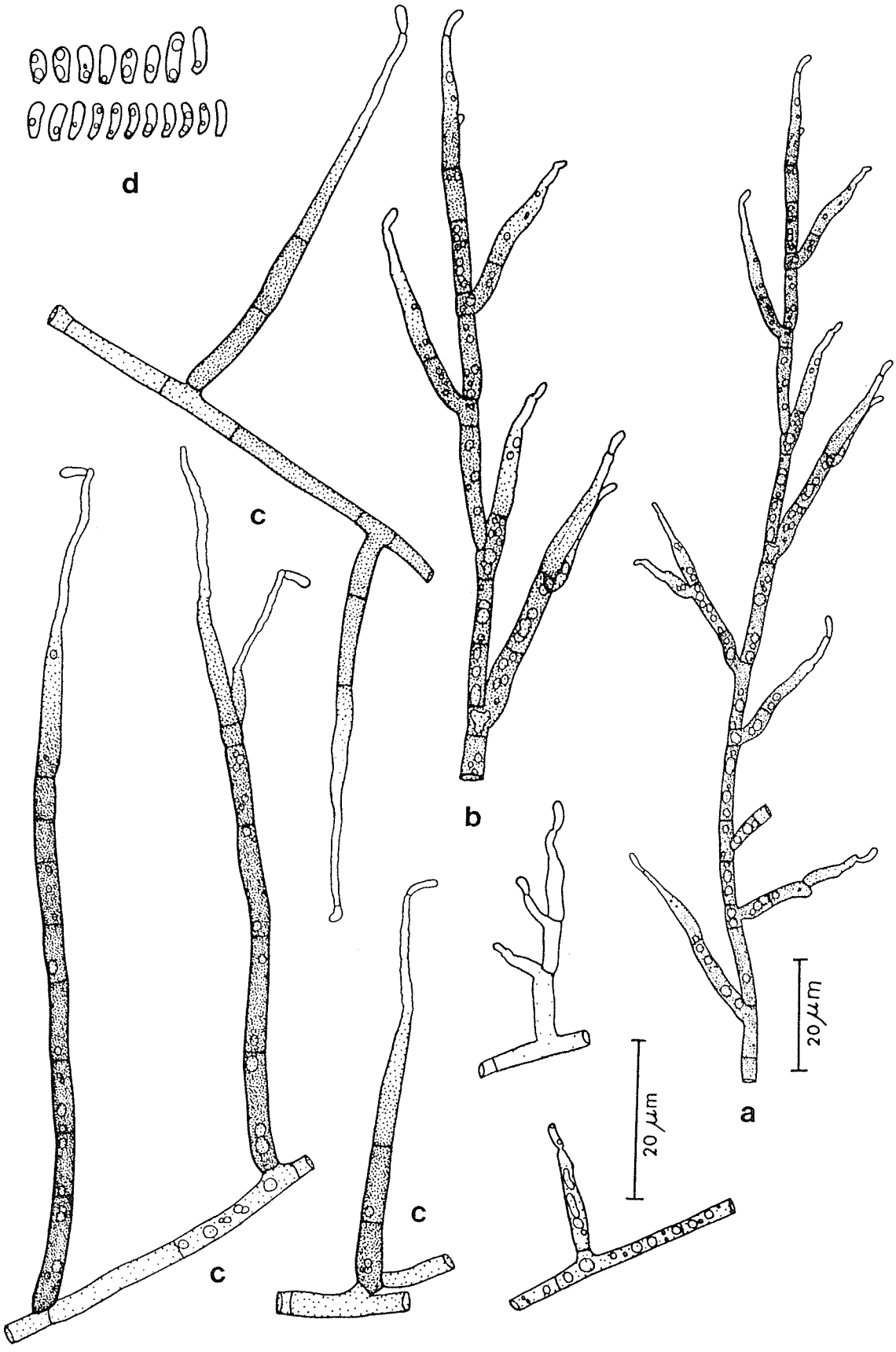
Fig. 24B. Leptodontidium elatius (Mangenot) de Hoog var. elatius (isolate: 9C)

a-b. Conidiophores with short sympodulae and pegs; (b) details of the apex of (a).

c. Subulate sympodulae, some on long stems.

d. Sympodioconidia.

Isolate as illustrated: 9C: a-d.


d
c
b
a
c
c
20 µm
20 µm

inflated; when funiculose, strands are 6 - 15 μm in diameter. Chlamydospores were not seen. Conidiophores sympodial and micronematous to semi-macronematous; hyaline to dark-brown, but when brown usually more lightly pigmented towards the apices. The conidiophore walls are smooth, distinct, and sometimes thickened in the lower portion. Semi-macronematous conidiophores are simple and consist of 1 - 5 celled stems bearing 1 - 2 apical sympodulae (Fig. 24A. a, 24B. c), and often bear lateral pegs, or sympodulae which may lack basal septa. The erect, brown conidiophores, including rachises, are 40 - 115 μm long and their stems measure 15 - 95 x 2.0 - 3.2 μm (Fig. 24A. a, 24B. c). On aging the conidiophores may proliferate either terminally or laterally (branching) through the rachises, either as a short stem segment with a terminal sympodula or as a secondary sympodula, the conidiophores thus becoming up to about 150 μm long (Fig. 24A. a «- (terminal), « (branching)). Micronematous conidiophores are usually hyaline to light brown and often curved; they consist of 1 - 2 celled stems bearing 1 - 2 rather short, curved, apical sympodulae, and lateral pegs or sympodulae (Fig. 24A. b, 24B. a,b), or the stem may be lacking. Conidiogenous cells sympodial, integrated or discrete; hyaline in young colonies, but those produced subsequently are often brown, although more lightly pigmented towards the apices; walls smooth, usually thin, sometimes distinct in the lower portion; cylindrical, but tapering at the apices, to subulate; straight, 13 - 25 x 2.0 - 3.2 μm wide at the base tapering to 1.4 - 2.2 μm at the apices (Fig. 24A. a, 24B. c); or shorter, slightly curved, sometimes broadest above the base (naviculate), 7.5 - 13.0 x

1.7 - 2.5 μm wide and tapering in the upper portion to 1.1 - 1.5 μm (Fig. 24A. b, 24B. a,b). Pegs are common. All produce crowded conidia directly on the hyaline, 1.0 - 1.5 μm wide rachises. The rachises appear irregular and almost coarsely verrucose because of the indistinct secession scars. Sympodioconidia dry, 1-celled, hyaline to subhyaline, and smooth-walled; the newly produced conidia are allantoid or occasionally cylindrical with rounded apices and truncate bases, but those produced earlier which have matured on the rachises are oblong-elliptical with round apices and taper slightly to truncate bases; 3.2 - 5.5(6.5) x 1.0 - 2.0(2.4) μm, usually containing oil droplets (Fig. 24A. c,d, 24B. d).

HOSTS: Picea sp., Tsuga heterophylla (Raf.) Sarg.

CULTURES EXAMINED: Canada: 16'', isolated from Picea sp., Rogers Pass Summit, Hwy. 1, Alberta, collected 25 September 1987; 9C, isolated from T. heterophylla, Hwy. 1, Annis Mountain, near Salmon Arm, British Columbia, collected 21 September 1987.

First described as Rhinocladiella elatior by Mangenot in 1952 from Betula sp. in France (de Hoog 1977), this species is frequently isolated from various conifers, especially from rot zones, but has also been recovered from species of Populus, Betula, Prunus, and Acer, and from Theobroma cacao. It has also been isolated from peat and soil, from a wood-inhabiting basidiomycete, and from stored wood chips (de Hoog 1977;

Shields 1969; Wallace & Dickinson 1978). The only report of this species being directly associated with insects in coniferous wood is that of Wingfield (1987) who isolated it from cerambycid pupal chambers in Pinus resinosa Ait. and P. banksiana Lamb where it was one of the fungi associated with the pine wood nematode, Bursaphelenchus xylophilus (Steiner & Buhrer).

This species was transferred to the new genus Leptodontidium (de Hoog 1977, 1979) because it lacked distinct scars or denticles on the rachises, and the hyphae and sympodulae in young colonies were not pigmented.

Although Schol-Schwarz (1968) reported R. elatior was a pleomorphic species with budding cells, phialides, and multiple scars, de Hoog (1977) stated the culture on which she had based her description was mixed with Exophiala pisciphila McGinnis & Ajello, a species which produces phialide-like conidiogenous cells. Since then, there has been no further evidence that this is a pleomorphic species. However de Hoog (1977) did find some phialide-like cells producing slimy conidia amongst the typical L. elatius var. elatius conidiophores in some dried cultures he examined. However as he could neither determine the purity of the cultures, nor the mode of conidiogenesis, he excluded them from the species description. He found no such cells in living cultures.

De Hoog (1977, 1979) considered isolates which produced obovate-elliptical conidia and dark-brown chlamydospores as a separate variety, L. elatius var. ovalisporum (de Hoog) de Hoog, although he noted intermediate forms existed between it and the var. elatius. Such

intermediate forms would be considered representative of the var. ovalisporum if they produced cylindrical conidia, as well as obovate-elliptical conidia and chlamydospores. However it was noted that in older colonies of the var. elatius, the most recently formed conidia were curved and slender, while those produced earlier and often still adherent to the lower portion of the rachises, differed (Fig. 24A. d). The latter were only slightly curved, and were straighter and broader than the more recently formed conidia. Clearly, the conidia undergo degrees of morphological change as they mature, and this results in some variation in their shape; but since the broader conidia are oblong-elliptical, not obovate, the conidial shape reported for var. elatius still differs from that of var. ovalisporum.

As noted above, Wingfield (1987) recently reported this species under the name R. elatior. Whether this author was unaware of de Hoog's treatment, and thus the use of the older name, or is making a taxonomic statement, i.e. suggesting de Hoog's treatment was wrong, is impossible to know. Hutchison & Reid (1988b) reported this species from New Zealand, but further examination of their isolates indicates they belong to Phaeoisaria clematidis (Fuckel) Hughes, and not L. elatius var. elatius.

These British Columbia isolates differ in degree of conidial production. Throughout the colonies, isolate 16''(Fig. 24A) produced numerous conidiophores with elongating rachises and dry conidia, while isolate 9C (Fig. 24B) produced more aerial hyphae but significantly fewer conidiophores. The latter produced only a few distinct pigmented

conidiophores with elongating rachises, and most of the conidia were aggregated in small moist drops at the apices of individual sympodulae. However, in isolate 16'', such micronematous conidiophores were greatly outnumbered by the longer ones.

The grey colour of young colonies readily separated these isolates from members of Rhinocladiella atrovirens Nannf. which have olive grey colonies. L. elatius var. elatius differs from other Leptodontidium species and the var. ovalisporum in producing cylindrical to allantoid conidia on cylindrical to subulate sympodulae, and in lacking chlamydospores. In lacking synanamorphs it also differs from Rhinocladiella species which often have Exophiala states and budding cells. It has shorter rachises than Acrodontium crateriforme (van Beyma) de Hoog, and after a long time in culture and the loss of pigmentation, it may resemble species of Hyalorhinocladiella Upadhyay & Kendrick except it possesses shorter and more flexuose sympodulae.

De Hoog (1977) states this species is quite common in coniferous trees in Canada, and the two varieties often occur in the same locality. However, L. elatius var. elatius does not appear to have been previously reported in association with bark beetles, although Wingfield (1987) did list it amongst several species including six Ceratocystis and one Ceratocystiopsis species isolated from cerambycid pupal chambers in two pine species, thus associating it with staining fungi and wood-inhabiting insects.

Leptodontidium elatius (Mangenot) de Hoog var. ovalisporum (de Hoog) de Hoog, Taxon 28:348. 1979 Fig. 25. a-e.

≡Leptodontium elatius (Mangenot) de Hoog var. ovalisporum de Hoog, Stud. Mycol. 15:47. 1977

Colonies attaining a diameter of 20 mm in 12 days and 40 mm in 21 days at 20°C in darkness on MEA.YE. At first light grey (5Y $^{7}/_{2}$) with dark, undulating hyphae or thin hyphal strands on the surface; phalacrogenous at the margin but nematogenous to plectonematogenous in the central area. Colonies are relatively flat and sparsely covered with hyphae bearing hyaline, moist, terminal spore-drops on short conidiophores; these are most abundant at the surface of the medium. On aging the colonies become light grey (5Y $^{6}/_{1}$) in the centre, but the rest of the colony remains olive grey (5Y $^{4}/_{2}$). In reverse, colonies are at first light grey to light olive grey (5Y $^{7}/_{2}$ to $^{6}/_{2}$), later grey to olive brown (2.5Y $^{5}/_{0}$ to $^{4}/_{4}$) with hyaline margins; colonies show strong zonation when grown in alternating light and darkness. Odour indistinct; exudate and crystals lacking. Hyphae chiefly hyaline to brown, smooth-walled and 1.5 - 4.0 µm wide; but some submerged hyphae are brown to very dark brown, and often thick-walled but slightly constricted at the septa, and 3.5 - 5.0 µm wide; when funiculose, strands are 5 - 45 µm in diameter. The chlamydospores are catenate, brown to very dark brown, and have thick, smooth walls; they are globose to ellipsoid, measure 6.5 - 10.5 x 5.0 - 8.0 µm, and contain one or more large oil drops; the chlamydospores develop in both the submerged and aerial hyphae

Fig. 25. Leptodontidium elatius (Mangenot) de Hoog var. ovalisporum (de Hoog) de Hoog
(isolate: 34N (UM74-101))

a. Chlamydospores.

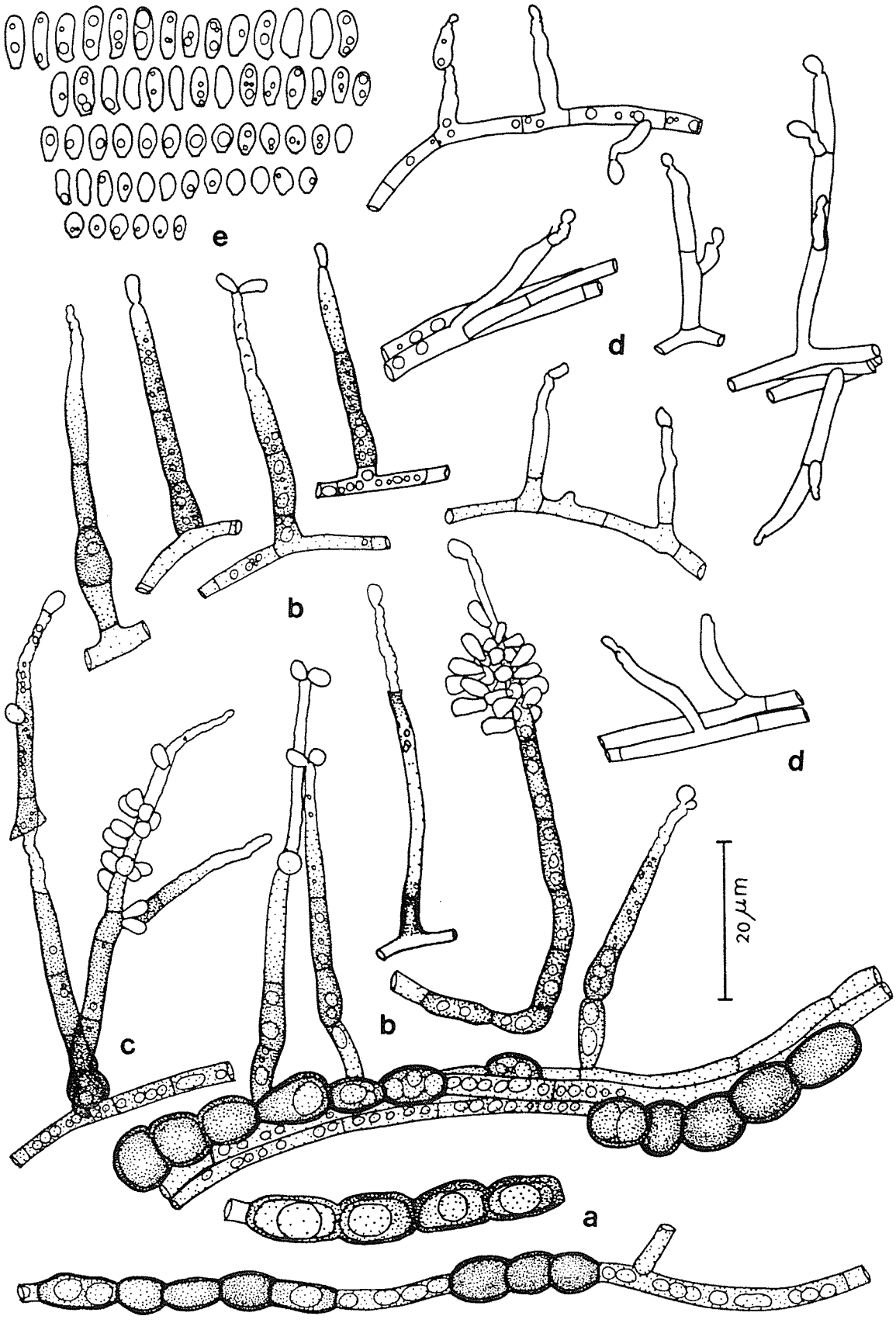
b. Simple, pigmented conidiophores.

c. Conidiophore with an inflated basal cell and secondary sympodulae.

d. Micronematous conidiophores produced by young colonies.

e. Sympodioconidia.

Isolate as illustrated: 34N (UM74-101): a-e.


e
d
b
d
c
b
20 µm
a

(Fig. 25. a). Conidiophores are sympodial and micronematous to semi-macronematous, usually hyaline in young colonies but, on aging, brown conidiophores which are paler towards their apices develop; wall smooth, often slightly thickened in the lower portion. Semi-macronematous conidiophores are usually simple, consisting of 1 - 4 celled stems each bearing a single terminal sympodula; they measure 25 - 75 x 2.0 - 4.8 μm; their base may be somewhat inflated and have thickened walls (Fig. 25. b,c). On aging, the sympodulae may proliferate terminally or laterally (branching) through the rachises and produce either a short stem segment with a terminal sympodula or only the secondary sympodulae (Fig. 25. c). Micronematous conidiophores are flexuous and bear an apical sympodula on a short, 1 - 2 celled stem which also may have lateral pegs, or the stem is lacking (Fig. 25. d). Conidiogenous cells sympodial and integrated or discrete; hyaline and thin-walled in young colonies; those produced later are often brown, but sometimes paler at their apices; walls smooth, usually thin, but sometimes slightly thickened in the lower portion; chiefly cylindrical but tapering somewhat abruptly at the apices, fewer tapering gradually in the upper portion; 8.0 - 18.0 x 2.2 - 3.0 μm tapering to 1.5 - 1.8 μm. Pegs are common on the conidiophore stems in young colonies. All produce crowded conidia directly on the hyaline, 1.3 - 1.6 μm wide rachises. The rachises appear irregular and almost coarsely verrucose because of the indistinct secession scars. Sympodioconidia dry, 1-celled, hyaline to pale brown and smooth-walled; cylindrical and straight to slightly curved at the base to oval-elliptical; all with round apices and bases with indistinct

pedicels, truncate; 3.2 - 7.3 x 1.8 - 2.5(3.2) μm, with one or more oil droplets (Fig. 25. e).

HOST: Pinus sylvestris

CULTURE EXAMINED: **Norway:** 34N (UM74-101), isolated from P. sylvestris, near Tangen, Hwy. 21, Akershus, collected in June 1974.

De Hoog (1977) states this variety is common on living trees, mainly coniferous species in the northern temperate zone. He studied isolates from conifers, species of Betula, Fagus, Acer and Sorbus, rotten wood, soil, a basidiomycete, and a culture contaminant. Most were from Canada, but several were from Europe and one was from the U.S.A. Other reports on the occurrence of L. elatius do not specify varieties and, consequently, are presumed to refer to var. elatius. No previous reports of this fungus from Norway were found.

De Hoog (1977) stated var. ovalisporum differed from var. elatius in the obovate-elliptical shape of its conidia, production of dark-brown chlamydospores, and somewhat longer conidiophores. However, he reported isolates occurred which were intermediate between those of the two varieties, but those with straight conidia were to be considered var. ovalisporum. As in var. elatius, de Hoog (1977) noted the presence of phialide-like cells amongst the typical sympodulae in dried cultures, but again their origin could not be ascertained, and such cells were not found in living cultures; therefore they too were excluded from the

description.

This Norwegian isolate did indeed appear intermediate in conidial shape. They ranged from 3.2 - 4.0 x 2.0 - 2.7 μm for obovate-elliptical conidia to 4.0 - 7.3 x 1.8 - 2.5 μm for those cylindrical in shape; forms intermediate in shape between these two groups were also present. Because of this variability, verification of the identification was obtained from CBS, Baarn. Proliferation of the pigmented sympodulae was a common occurrence in older colonies.

According to de Hoog (1977), this variety resembles Rhinocladiella spinifera (Nielsen & Conant) de Hoog, but differs in colony characteristics and does not have an Exophiala synanamorph. If the rachises were broader, it might also resemble Ramichloridium anceps (Sacc. & Ellis) de Hoog somewhat, but it would still be separated from that species by the hyaline conidia, lack of denticles, and lightly pigmented hyphae.

This may be the first report of L. elatius var. ovalisporum occurring in association with wood-inhabiting insects; however, since it appears to occupy the same habitats as var. elatius, such an association can be expected.

Mariannaea Arnaud ex Samson, Stud. Mycol. 6:74. 1974

=Mariannaea Arnaud, Bull. trimest. Soc. mycol. Fr. 58:196. 1952 (nom. inval.).

Type species: Mariannaea elegans (Corda) R. A. Samson

Teleomorphs are unknown or wanting.

This genus is characterized by verticillately branched conidiophores bearing terminal whorls of slender, flask-shaped phialides. The latter produce 1-celled, hyaline, and smooth-walled conidia in imbricate chains or slimy drops. The described species grow moderately fast on artificial media, and may produce chlamydospores. No teleomorphs have been reported to date.

The genus was originally proposed, without the required latin description, to accommodate the single species M. elegans, which Arnaud said resembled Penicillium elegans Corda; it differed therefrom in producing conidia in imbricate chains. Hughes (1951) states that neither Corda's illustrations nor descriptions indicate his fungus produced its conidia in imbricate chains, but that examination of Corda's material showed such chains were indeed present. Based on this, Hughes transferred P. elegans to Paecilomyces as P. elegans (Corda) Mason & S. J. Hughes. Samson (1974) examined both the Corda material and the type of Mariannaea elegans Arnaud, and he concluded P. elegans was quite different from other members of the genus Paecilomyces Bainier. Therefore he validated Arnaud's generic name Mariannaea by

providing a latin diagnosis, and designated Mariannaea elegans (Corda) R. A. Samson as the type species.

Species of the genus Mariannaea differ from Paecilomyces species in producing their conidia in imbricate chains from rather gradually tapering, slender phialides. However, both produce erect phialophores which often branch verticillately in the upper portion, and bear metulae and phialides, which may be basally inflated, in whorls or penicilli, and produce the conidia in chains. Species of Sesquicillium W. Gams also produce conidia in chains reminiscent of those found in Mariannaea species, but the former differ in having an adelophialide below each phialide.

The genus Mariannaea presently consists of 3 species and 1 variety that are most often found in soils and on decaying wood or bark (Domsch et al. 1980).

Mariannaea elegans (Corda) R. A. Samson var. elegans, Stud. Mycol. 6:75. 1974 Figs. 26A. a-j, 26B. a-c.

≡Penicillium elegans Corda, Icon. fung. 2:17. 1838

≡Paecilomyces elegans (Corda) Mason & S. J. Hughes apud Hughes, Mycol. Pap. 45:27. 1951

≡Spicaria elegans (Corda) Harz, Bull. Soc. imp. Nat. Moscou 44:238. 1871

=Mariannaea elegans Arnaud, Bull. trimest. Soc. mycol. Fr. 68:196. 1952 (nom. inval.)

For further synonymy see Samson (1974).

Colonies attaining a diameter of 28 - 40 mm in 12 days at 20°C in darkness on MEA.YE. In areas of abundant conidiogenesis, colonies are white (2.5Y $^{8}/_{0}$), phalacrogenous to nematogenous, and mealy in texture, but yellowish brown to dark yellowish brown (10YR $^{5}/_{6}$ to $^{4}/_{4}$) in areas where the yellowish brown tinted surface of the medium is sparsely covered with hyphae. Colonies finally become pale brown (10YR $^{7}/_{4}$ to $^{8}/_{4}$) and covered with slimy conidial masses in the centre, but remain white with a mealy texture at the margins except in areas sparsely covered with aerial hyphae; the latter become dark reddish brown (5YR $^{2}/_{2}$ to $^{3}/_{2}$). In reverse, colonies are dark reddish brown (5YR $^{3}/_{4}$) in the centre, becoming reddish brown (5YR $^{5}/_{4}$) and fading to white (10YR $^{8}/_{2}$) at the margins; later becoming dark reddish brown to dark reddish grey (5YR $^{3}/_{2}$, $^{3}/_{3}$ to $^{4}/_{2}$). Grown in alternating light and darkness, the colonies are strongly zonate, each zone being approximately 2 mm

Fig. 26A. Mariannaea elegans (Corda) R. A. Samson var. elegans (isolates: 152a, 280A)

a. Habit sketch of an erect phialophore bearing dry conidial chains, and a bushy phialophore bearing tiny conidial drops on each phialide.

b-c. Chlamydospores.

d. Inflated hyphal cells.

e-h. Erect phialophores; (e) one such phialophore, note the thicker walls in the lower portion of the stem; (f) portion of a verrucose stem; (g,h) whorls of phialides, some on short branches, produced at the apices of the erect phialophores.

i-j. Phialoconidia, including a chain.

Isolates as illustrated: 152a: b, f, g, i.
280A: c, d, e, h, j.

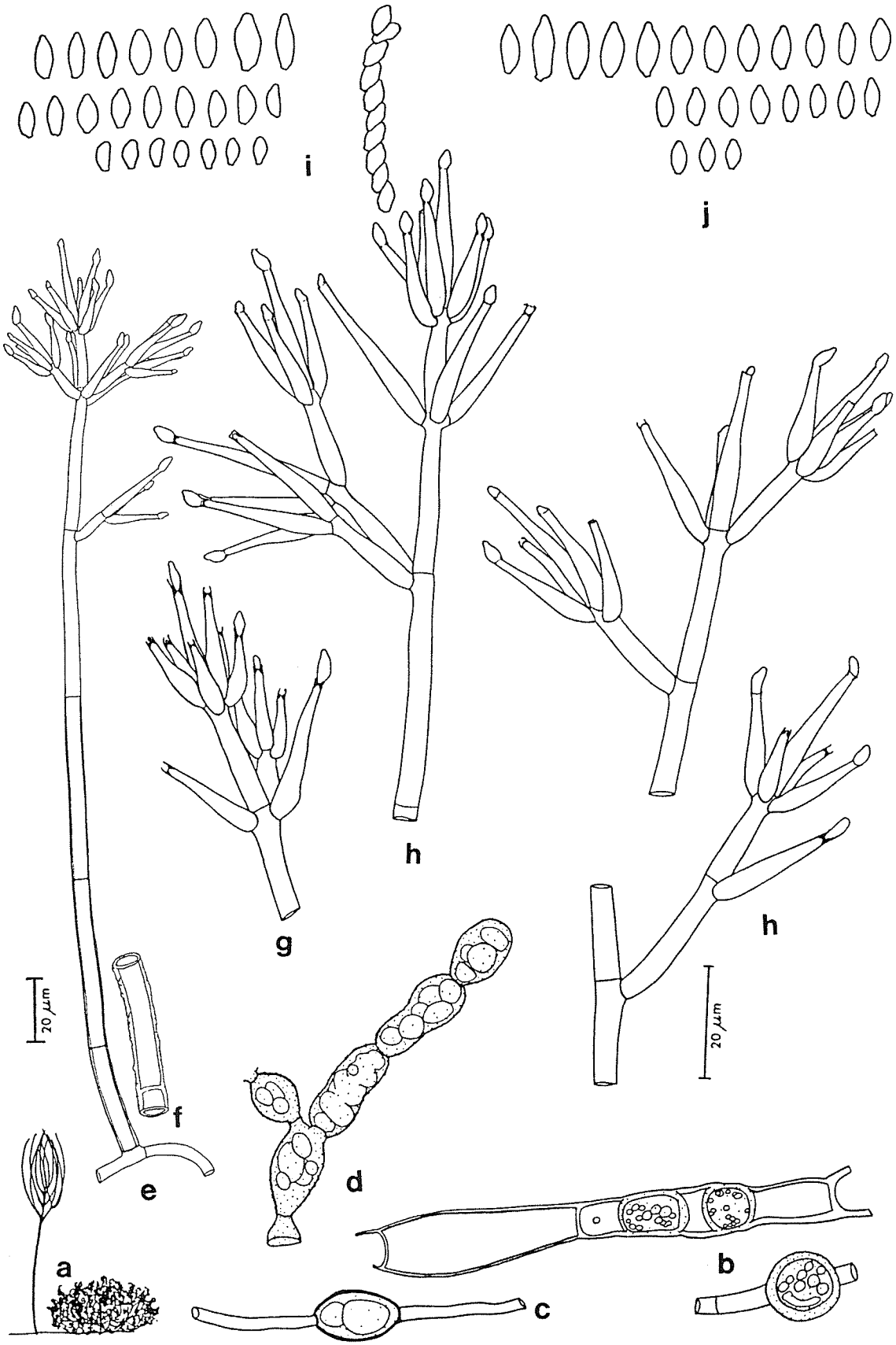
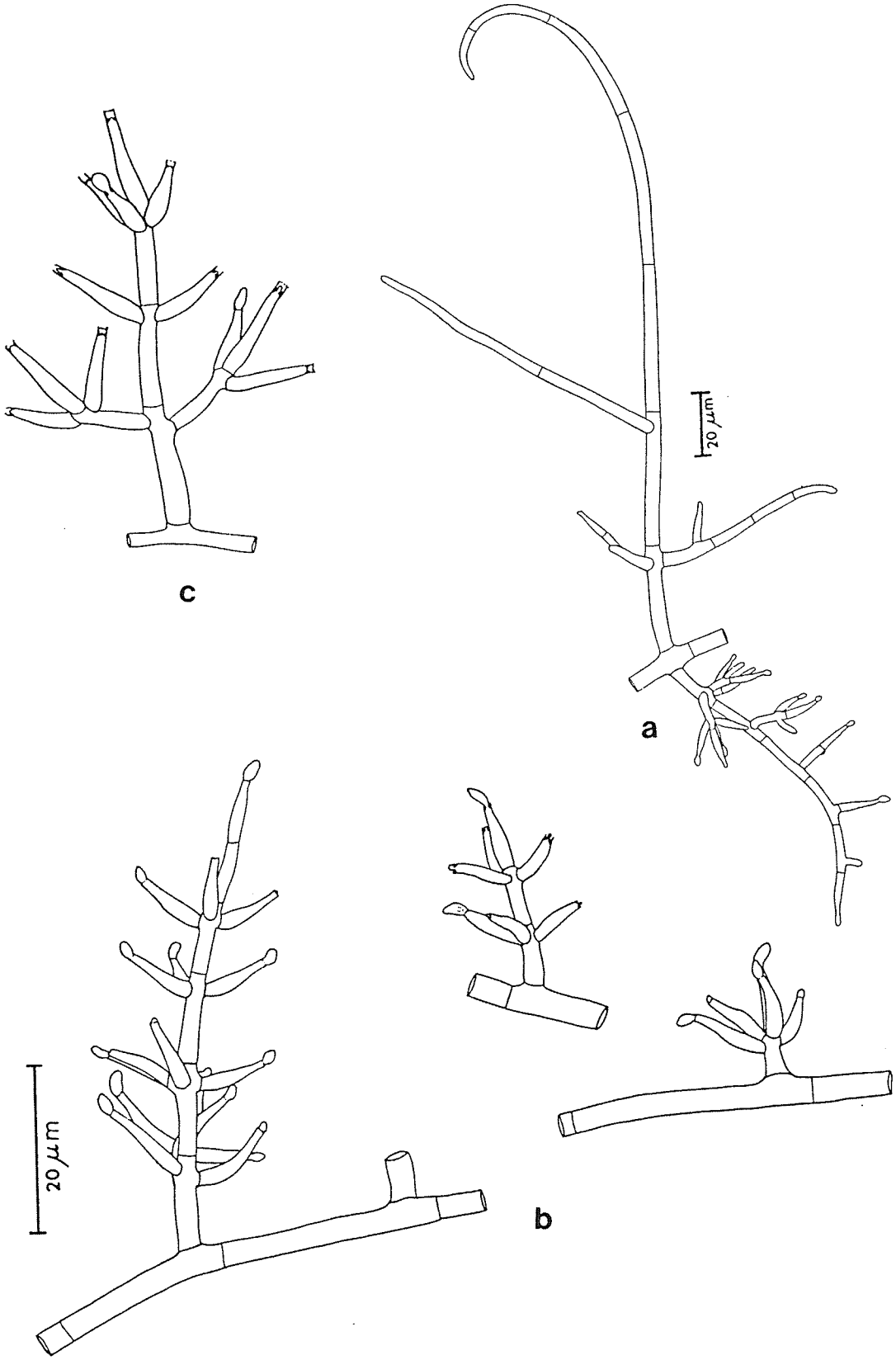

i
j
h
g
h
h
20 µm
20 µm
f
e
d
a
b
c

Fig. 26B. Mariannaea elegans (Corda) R. A. Samson var. elegans (isolates: 152a, 280A)

a-c. Bushy phialophores: (a) a portion of a phialophore; from a main hyphal branch, a secondary branch with a curved apex has developed opposite another secondary branch which has already formed phialides; (b,c) secondary branches bearing short divergent phialides, the longest such branches are produced by the primary branch close to the stem (or branches of higher order) and the shorter ones towards their apices.

Isolates as illustrated: 152a: a, b.
280A: c.


20 µm
a
20 µm
b
c

wide and densely covered with phialophores; white (10YR $^{8}/_{2}$ to 2.5Y $^{8}/_{0}$) and mealy in texture, but becoming pinkish grey (7.5YR $^{7}/_{2}$) and slimy in the centre. In reverse, colonies are very pale brown (10YR $^{7}/_{4}$ to $^{8}/_{4}$) in the centre, becoming white (2.5Y $^{8}/_{2}$) towards the margins; on aging, the centre often becomes light yellowish brown to light brown (10YR $^{6}/_{4}$ to 7.5YR $^{6}/_{4}$). Odour indistinct and an exudate is present as small to medium sized clear drops. A yellowish-brown pigment diffuses gradually into the medium amongst the submerged hyphae. Hyphae hyaline to yellowish-brown; smooth to verruculose; but occasionally with irregularly swollen cells (Fig. 26A. d); 2.5 - 16.0 μm in diameter. Chlamydospores, when present, are hyaline to yellowish brown, fairly thick-walled, and smooth to verruculose; intercalary and produced singly or in short chains; globose, oval, or elliptical; 7.5 - 20.0 x 7.5 - 12.0 μm (Fig. 26A. b,c). Phialophores macronematous and of two types: (1) mononematous; erect (Fig. 26A. a,e); either all hyaline and smooth-walled, or pale yellow, thick-walled, and sometimes verrucose below, but becoming hyaline with thin and smooth walls in the upper portion; verticillately branched in 1 - 3 series at the apex; the first series usually consists of 1 - 2 branches, the second series is of branches and phialides or phialides only, and the third is a terminal verticil of 5 - 9 phialides (Fig. 26A. e,g,h); 130 - 760 μm long, 5.5 - 11.0 μm wide at the base, tapering to 3.5 - 5.0(7.3) μm below the branches; conidia produced in long, often entangled chains; (2) complex branched phialophores which are bushy in appearance and relatively short (Fig. 26A. a); their main stem and its primary branches are often pale yellow basally, but they

are hyaline towards the tips which may consist of either sterile appendages or a whorl of 2 - 4 phialides; smooth-walled to finely verruculose; the primary lateral branches arise in opposite pairs almost at right angles to the stem. The primary branches (Fig. 26B. a) are 300 - 600 μm long, 4.0 - 9.5 μm wide at the base, and have up to 15 septa. Each such branch bears several whorls of up to 3 secondary branches which may be of different lengths, and from these the phialides arise; the secondary branches are 20 - 150 x 3.2 - 4.7 μm and 0 - 6 septate, usually longest at the base, but shorter towards the end of the primary branches (Fig. 26B. b,c). Conidiogenous cells monophialidic; hyaline and smooth-walled; discrete or rarely integrated; of two types: (1) those produced by the erect phialophores straight, and usually somewhat inflated at the base, and either narrow gradually to form the neck or, when shorter, narrow more abruptly; 10.5 - 28(31) x 2.5 - 4.0 μm wide at the base and 1.4 - 1.7 μm at the apex (Fig. 26A. g,h); (2) those produced by the bushy phialophores subcylindrical or rarely slightly inflated in the lower portion, often gently curved, tapering gradually to the apex; 9.0 - 14.5(20.0) x 2.4 - 3.2 μm wide at the base, tapering to 1.1 - 1.6 μm at the apex (Fig. 26B. b,c). Both types have 0.6 - 1.2 μm long, indistinct collarettes and form the conidia obliquely at the apex. Phialoconidia produced by the erect phialophores adhere in imbricate chains, but those produced by the bushy type aggregate in moist drops; 1-celled, hyaline, and smooth-walled; broadly fusiform to fusiform-elliptical or oval; (4.2)4.5 - 7.5 (11.0) x 2.1 - 3.6(4.0) μm; apex often papillate; base distinctively pedicellate, often curved to the

side, or truncate (Fig. 26A. i,j).

HOSTS: Pinus sp., Pseudotsuga menziesii (Mirb.) Franco.

CULTURES EXAMINED: **New Zealand:** 152a, isolated from P. menziesii, Compartment 1097, Kaingaroa State Forest, Taupo, collected 19 June 1982; 280A, isolated from Pinus sp., Compartment 3, Kaingaroa State Forest, Taupo, collected 18 February 1988.

Corda (1838) based his description on a collection on the inner surface of loose bark of rotten trunks of fir-trees in Brezina, Czechoslovakia, but the fungus is now known to be of wide distribution. It is common on decaying coniferous bark and wood in various countries (Brown & Smith 1957; Holubová-Jechová 1973; Hughes 1951; Samson 1974), and from decaying wood of deciduous trees (Holubová-Jechová 1973; Hughes 1951; Matsushima 1975; Samson 1974). However, the only report of it ever having been isolated from stained wood is that of Sasaki & Yoshida (1971); they isolated it from stained birch wood in Japan.

M. elegans grows in association with other fungi (Hughes 1951; Samson 1974; Tubaki 1955), often, apparently, as a ubiquitous saprophyte on decaying fruiting bodies of members of the Hymenomycetes (Hawksworth 1981), although Rudakov (1978) considered it a facultative biotroph. It is regularly isolated from forest soils and litter (Bhatt 1970; Brandsberg 1969; Eicker 1969; Gochenaur 1978; Hering 1965; Huang & Schmitt 1975; Manoch et al. 1986; Tubaki & Yokoyama 1971), including washed

pieces of decaying pine needles (Widden & Parkinson 1973). It was also isolated from collembola and soybean nematode cysts (Carris et al. 1989; Visser et al. 1987). Further information on the distribution and occurrence of this cosmopolitan species is recorded in Domsch et al. (1980).

Hughes (1978) recorded M. elegans from dead wood of two unidentified hosts and Podocarpus spicatus; this was the only previous report found of this fungus from New Zealand.

Hughes (1951) detailed description of the species, based on a range of material including the type specimen of Corda's P. elegans, included his finding of a "curious lax growth" of some phialophores which he described on page 25, line 35 as follows: "These lax conidiophores have a stipe tapering to a flexuose sterile apex and along its length are widely spaced, long primary branches....."; these are seen in his Fig.6c (p.26) and correspond to what are called bushy phialophores herein.

Instead of stressing the sharply defined dimorphic nature of the phialophores as had Hughes, Brown & Smith (1957) suggested there was a continuous range of variation between the two forms. Their description and illustration (text-fig.6, 2 p.48) does not appear to have been based on the main stem with several attendant major or primary lateral branches, but solely upon a single primary branch with its secondary lateral branches bearing whorls of phialides and short branches terminated by phialides. They appear to have overlooked that what they considered the main stem was only a unit (i.e. a primary branch) of the complex branching system of a bushy phialophore. Hughes (1951) description of the lax

conidiophores was based on such units, but he added that the phialophores could be produced together in large numbers resulting in "fluffy colonies". Samson (1974), on the other hand, emphasized the tall phialophores, virtually ignoring the bushy type.

If one only stresses occurrence of the tall phialophores, the dimorphic nature of M. elegans is obscured. When cultures are observed using a dissecting microscope and one sees the two phialophore types occurring together, one forming chains of conidia, the other bearing drops of conidia on slightly curved, divergent phialides, their contrasting appearance is one of the most striking characteristics of the species.

In addition to the branching pattern of the phialophores, the shape and size of the phialides produced by the bushy phialophores are different from those produced by the erect ones. This is clearly seen in the measurements of the New Zealand isolates, and furthermore, the phialides of the erect phialophores are only moderately divergent, usually straight and crowded with up to nine in each whorl on the ultimate branches. Very short phialophores may be produced by either of the two types, and the primary branches of the bushy type sometimes arise from the lower stem cells of the erect type. Each lateral branch, however, could easily be placed in the appropriate category based on the shape and arrangement of the phialides. None of the descriptions cited above have discussed the dimorphic nature of the phialides and how this is associated with the phialophore type.

The phialoconidia produced by the New Zealand isolates were larger

than the measurements given for the species by Brown & Smith (1957) and Samson (1974), but agreed quite well with the measurements of Tubaki (1955) and Matsushima (1975). Most conidia were 2.4 - 3.4 μm wide, and 4.5 - 6.5 μm long, but larger conidia, up to about 11.0 μm and 4.0 μm wide, although fewer in number, were consistently present.

Since M. elegans is a regular inhabitant of decaying coniferous wood, its presence in the bark beetle galleries can be expected. However, it is apparently not common in New Zealand as only two isolates were obtained from the large number of samples examined.

Monocillium S. B. Saksena, Indian Phytopath. 8:9. 1955

Type species: Monocillium indicum S. B. Saksena

Teleomorphic genus: Niesslia Auersw.

This genus is characterized by discrete, subcylindrical phialides whose walls are thickened and highly refractive in the lower portion, but thin-walled and often inflated right above the thick-walled area; the 1-celled, rarely 1-septate phialoconidia are produced in slimy drops or in chains. In culture, many species form characteristic crystals in the supporting medium, and a few species produce pigmented chlamydospores; the latter are usually formed in chains.

While originally the key character of the genus was that species possessed centrally inflated phialides with thickened walls in their lower portion, Gams (1971) widened the generic concept of Monocillium to include species with thickened walls but which lacked the inflated area above. He also emphasised the teleomorphic connection to Niesslia Auersw. (Sphaeriales: Trichosphaeriaceae), and expected these species to represent a natural group of related organisms.

Members of the genus are mainly saprophytes found in soils, on various decaying plant materials, or on dead and decaying wood. On conifers they have been found growing on needles, bark, and wood, while a few species have been recorded growing on other fungi, and one species is known from lichens (Gams 1971; Hawksworth 1979).

Hawksworth et al. (1983) estimated the genus comprises at least 15

species, some of which are known to have teleomorphs in the genus Niesslia. Monocillium and its teleomorphs are currently being monographed, but this work has not yet been published (W. Gams, pers. comm.).

Monocillium pinicola sp. nov. prop. Fig. 27. a-c.

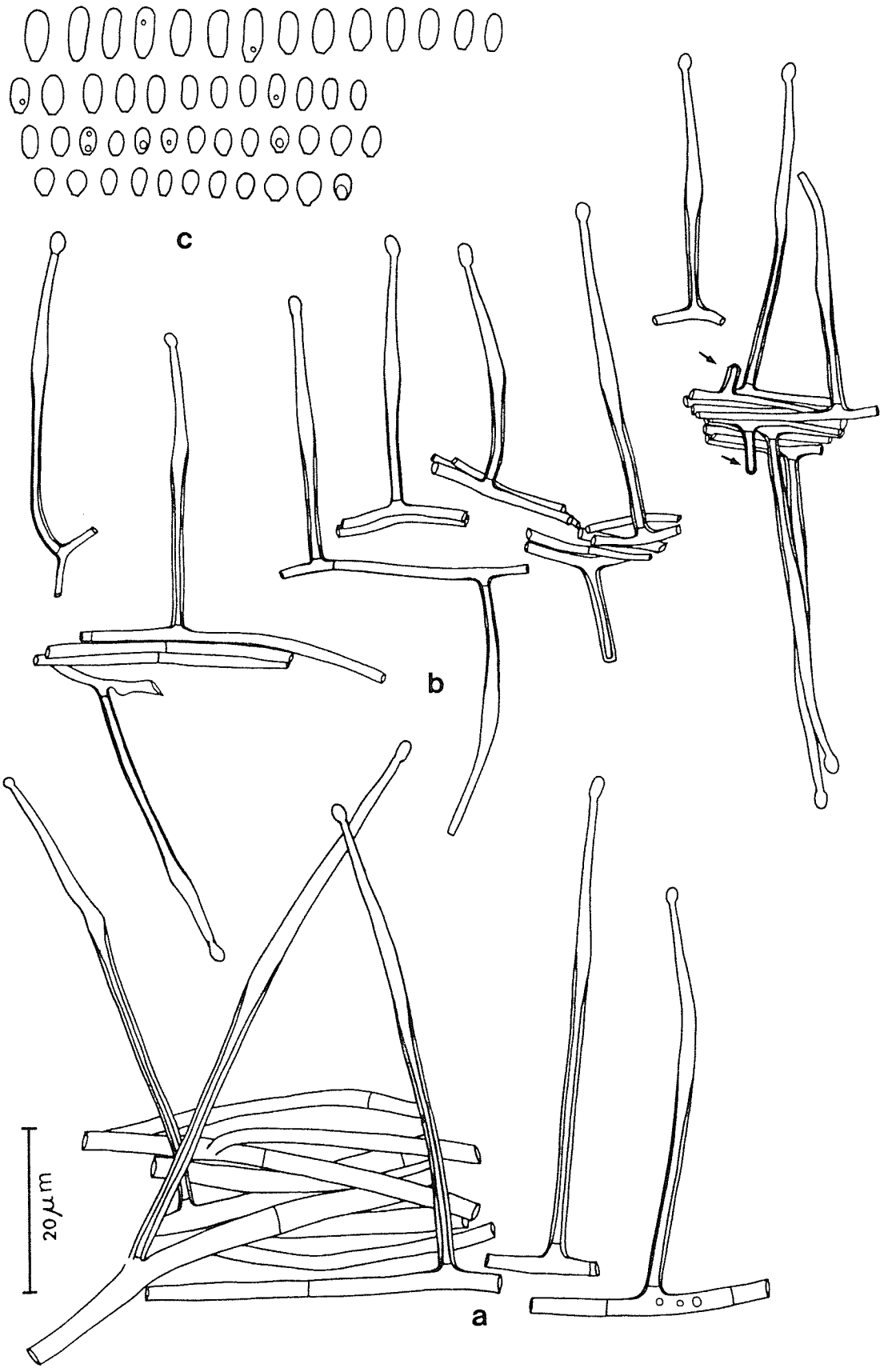
Colonies attaining a diameter of 19 - 21 mm in 12 days at 20°C in darkness on MEA.YE. When young, colonies are white (10YR $^{8}/_{1}$ (centre), 2.5Y $^{8}/_{0}$ (margin)), becoming light grey (10YR $^{7}/_{1}$) on aging; flat to moderately convoluted (radial depressions) in the centre; nematogenous to finely plectonematogenous, except sparsely synnematogenous in the centre, and phalacrogenous at the very margin, which gives the surface a grainy texture. Colonies grown in light become light grey, pinkish grey, to pink (5YR $^{7}/_{1}$, $^{7}/_{2}$ to $^{7}/_{3}$) and, on aging, become pink (7.5YR $^{7}/_{4}$) at the margin, but otherwise resemble dark-grown cultures. The conidia aggregate in clear drops at the apices of individual phialides. In reverse, dark-grown colonies are light grey to light brownish grey (2.5Y $^{7}/_{2}$ to $^{6}/_{2}$, 10YR $^{6}/_{2}$) in the centre, but pale brown to white (10YR $^{8}/_{3}$, $^{8}/_{2}$) towards the margin. In reverse, colonies grown in light are light grey to grey (5YR $^{6}/_{1}$) in the centre, but very pale brown (10YR $^{8}/_{3}$, $^{7}/_{3}$) towards the margin; gradually becoming pink to reddish yellow (7.5YR $^{7}/_{4}$ to $^{8}/_{6}$) on aging. Colonies fairly easy to cut through and exudate lacking. Odour very faint, mildly aromatic, fruity, increasing if the colonies are cut. No crystals were observed. Hyphae hyaline, or very pale brown; smooth-walled to finely verruculose; submerged hyphae forming a densely interwoven layer, and on aging some may become brown and slightly constricted at the septa; 0.8 - 3.2(4.0) µm in diameter; when funiculose, most strands are 3 - 25 µm in diameter except for a few which were 45 - 85 µm wide at the base, and taper gradually to

Fig. 27. Monocillium pinicola sp. nov. prop.
(isolate: 87cii')

a-b. Phialophores; (a) phialophores formed from the surface hyphae at the colony margins; (b) phialophores which originate from the aerial hyphae or hyphal strands. The phialides appear to be brittle and often break close to the base leaving a short piece still attached to the hyphae («-).

c. Phialoconidia.

Isolate as illustrated: 87cii': a-c.


c
b
a
20 µm

a long flexuous apex; all consist of 1.2 - 2.0 μm wide parallel or slightly interwoven hyphae. Chlamydospores were not seen. Phialophores micronematous, hyaline, smooth-walled and consist of a single phialide; these arise from the submerged hyphae at the colony margin (Fig. 27. a), from aerial hyphae, and from hyphal strands (Fig. 27. b); 25 - 55(69) x 1.0 - 1.5(1.6) μm wide at the base. Conidiogenous cells monophialidic; discrete, hyaline; walls are smooth, thick and highly refractive in the lower (approximately) half, thin in the upper portion; straight; cylindrical in the lower half, somewhat inflated as the walls become thinner around the middle then tapering gradually to a cylindrical neck; 25 - 55(69) x 1.0 - 1.5(1.6) μm wide at the base, becoming 1.6 - 2.4 μm wide in the middle, but tapering to 0.8 - 1.1 μm at the apex; collarettes usually lacking (Fig. 27. a,b). Phialoconidia aggregate in slimy drops; 1-celled, hyaline, and smooth-walled; dimorphic (Fig. 27. c), either (1) subglobose to oval; 2.4 - 3.6(4.0) x 1.6 - 2.4 μm with a short, truncate pedicel; or (2) cylindrical to oval-elliptical; 4.0 - 6.4(7.0) x 1.8 - 2.4(2.5) μm, most being 4.0 - 5.0 μm long; apex rounded, base indistinctly pedicellate.

HOST: P. radiata

CULTURE EXAMINED: **New Zealand:** 87cii', isolated from P. radiata, near Onemana, Tairua State Forest, Coromandel, collected 20 May 1982.

This fungus clearly belongs in the genus Monocillium because its

simple phialophores consist of phialides having thick, highly refractive walls in the lower portion and an inflated middle. However, it can not be accommodated in any of the previously described Monocillium species, and is therefore described here as new.

Originally M. pinicola was thought to represent a variant of M. nordinii (Bourchier) W. Gams, but according to Dr. W. Gams (pers. comm.) it differs from M. nordinii in the following characteristics: (1) M. nordinii has shorter phialides and (2) its conidia adhere in rather dry conidial heads, but not in slimy drops. This leaves no repository for this fungus amongst the known species of Monocillium, but Dr. W. Gams believes it is close to the anamorph of Niesslia exilis (Albertini & Schwein.) G. Winter which also produces darkly pigmented submerged hyphae in the centre of its colonies, but has larger, cylindrical, conidia, some of which are 1-septate. N. exilis may also have phialophores that are up to 160 µm long (although 40 - 50 µm long are the most common), and it does have phialides which are not inflated at the middle. These characteristics clearly separate N. exilis from M. pinicola.

M. pinicola produces both subglobose and cylindrical phialoconidia, and colonies which are fairly easy to cut through since there is only a thin layer of densely interwoven hyphae. Its thin phialides appear to be brittle in the lower portion, as short thick-walled stumps are commonly all that is left attached to the hyphae (Fig. 27. b «-).

This fungus was isolated only once from the wood samples collected in New Zealand, and then from a mixed culture. It is possible it was

present more frequently, but masked by other faster growing species. It is rather inconspicuous, being slow growing, consisting of fine hyphae, and lacking distinctive phialophores, and could thus easily have been overlooked during isolation and purification of the fungi from the beetle galleries.

Monocillium tenue W. Gams, Cephalosporium-artige Schimmelpilze (Hyphomycetes) 153. 1971 Fig. 28. a-g.

For synonymy see Gams (1971).

Colonies attaining a diameter of 15 - 25 mm in 12 days at 20°C in darkness on MEA.YE. White (2.5Y $^{8}/_{0}$), nematogenous to synnematogenous except phalacrogenous at the margin. Colonies grown in alternating light and darkness are pink (5YR $^{8}/_{3}$ to $^{8}/_{4}$) with a pinkish white (5YR $^{8}/_{2}$) margin, and usually more strongly synnematogenous than dark-grown cultures. The conidia aggregate in clear droplets at the apices of the individual phialides which cover the surface of the colony. In reverse, dark-grown colonies are very pale brown (10YR $^{8}/_{3}$ to $^{7}/_{4}$), but colonies grown in light are reddish yellow to pink (5YR $^{7}/_{6}$, $^{7}/_{8}$ to $^{8}/_{4}$), often becoming pinkish white (5YR $^{8}/_{2}$) at the margin. Colonies are difficult to cut through, and are usually moderately to strongly convoluted (radial furrows), and may become indistinctly zonate when grown in alternating light and darkness. A marginal exudate is usually present as small clear drops; small or medium sized drops are also sometimes present at the colony centre. Aggregated, needle-shaped crystals are usually present amongst the hyphae, or in the medium within colonies. Hyphae hyaline; most are smooth-walled except some aerial hyphae that become verrucose; inflated in parts, and often thick-walled; submerged hyphae are usually very compact, and sometimes densely interwoven; 0.7 - 2.8 µm in diameter; when funiculose, strands are compact, 5 - 110 µm in diameter, the broader strands often erect, and then up to 2 - 3.5

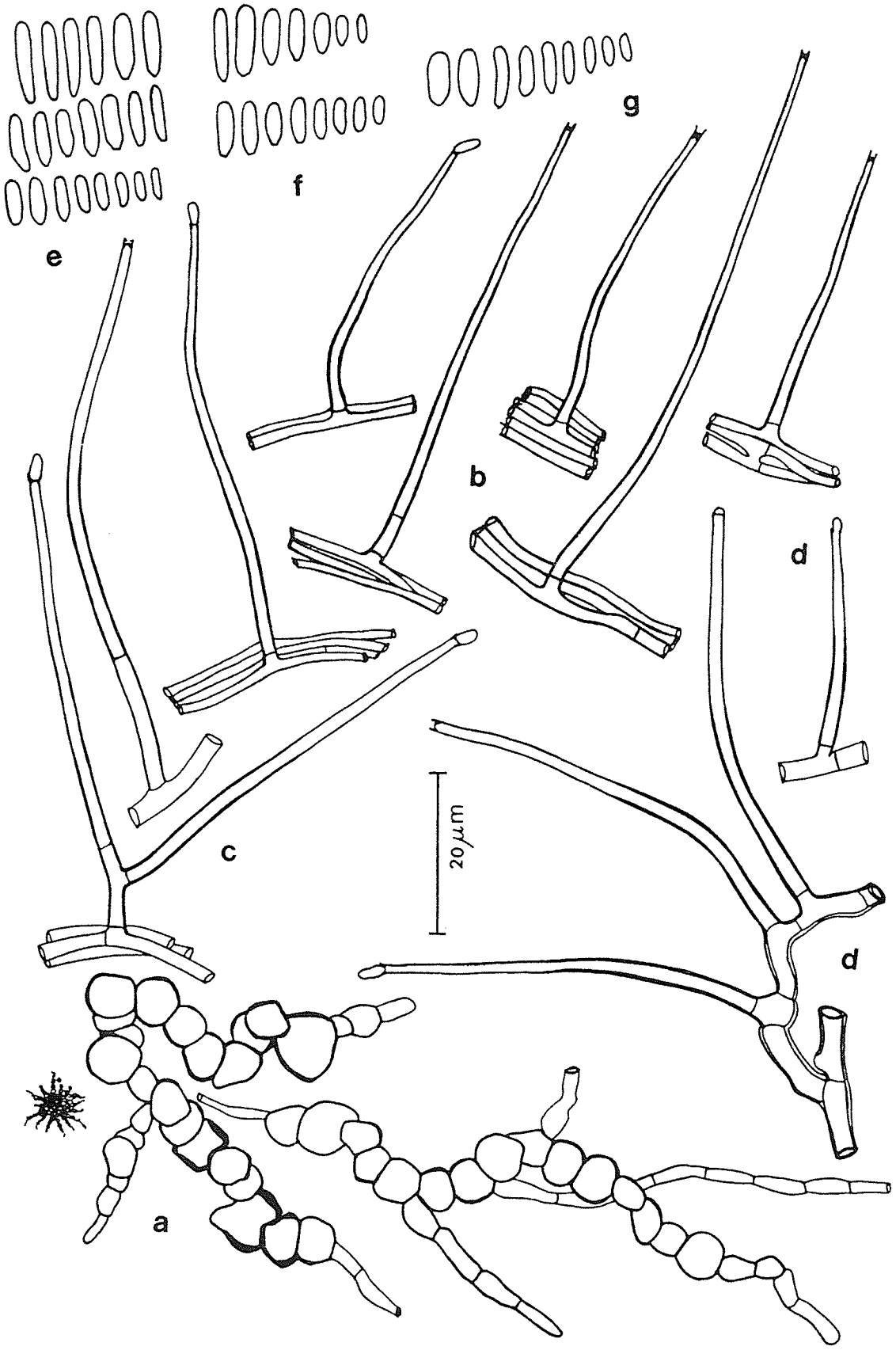
Fig. 28. Monocillium tenue W. Gams
(isolates: 85dii', 88c, 115, 142a)

a. Habit sketch, and details, of star-shaped aggregations of inflated cells produced by aging colonies.

b-d. Phialophores.

e-g. Phialoconidia.

Isolates as illustrated: 85dii': a, c.
88c: b, e.
115: d, f.
142a: g.


a
b
c
d
d
e
f
g
20 µm

mm long, yellowish red in colour and tapered to a point. Typical chlamydospores were not seen, but star-shaped aggregations of hyaline, thick-walled, and inflated hyphal cells which were 4.5 - 9.0 μm in diameter (Fig. 28. a), developed in aged (5 months old) cultures. Phialophores micronematous or rarely semi-macronematous; hyaline; smooth-walled to verruculose in the basal portion; individual phialides arise directly from the hyphae or, occasionally, they are subtended by a 10 - 20 x 1.7 - 2.4 μm basal cell which may rarely produce a second phialide (Fig. 28. b,c,d). Conidiogenous cells monophialidic; discrete or rarely integrated; hyaline; wall smooth, and usually thicker in the lower portion, but much thinner above; acicular to narrowly subulate; 25 - 60(75) x 1.6 - 2.2(2.4) μm, but tapering very gradually to 0.8 - 1.2 μm at the apex (Fig. 28. b,c,d); collarette indistinct and then 0.6 - 0.9 μm long, or lacking. Phialoconidia aggregating in slimy drops; 1-celled, hyaline, and smooth-walled; straight; cylindrical to oblong-elliptical, but sometimes broadest just above the base; (3.2)3.5 - 7.5(9.0) x (1.4)1.5 - 2.0(2.6) μm; apex rounded, base either rounded or indistinctly pedicellate (Fig. 28. e,f,g).

HOSTS: Pinus radiata, Podocarpus spicatus, Podocarpus sp.

CULTURES EXAMINED: **New Zealand:** 54'', isolated from P. radiata, in the south end of Tairua State Forest, Coromandel, collected 21 May 1982; 85dii'', isolated from P. radiata, near Onemana, Tairua State Forest, Coromandel, collected 20 May 1982; 88c, isolated from P. radiata, near

Onemana, Tairua State Forest, Coromandel, collected 20 May 1982; 115, isolated from P. radiata, Compartment 24, Woodhill State Forest, Auckland, collected 25 May 1982; 147e', isolated from P. spicatus, Minginui, Urewera National Park, Taupo, collected 11 June 1982; 142a, isolated from Podocarpus sp., near Minginui, Urewera National Park, Taupo, collected 11 June 1982.

M. tenue has been isolated from a number of wood inhabiting members of the Hymenomycetes and Ascomycotina, as well as from dead leaves of several plants in Europe, and as Cephalosporium rubrobrunneum Benedek ex Nannizzi from a patient infected with Trichophyton gypseum Bodin (Gams 1971). Gams also lists one isolation from fallen needles of P. radiata in southern Australia. This may well be the first report of M. tenue from New Zealand.

Gams (1971) description of M. tenue was based on an isolate from Hypoxylon fragiforme (Pers.: Fr.) Kickx, to which C. rubrobrunneum was doubtfully referred as a synonym. Although predating Gams' name, the culture derived from the type of the latter no longer matched the original description, thereby confusing the identity of that species.

The phialides produced by M. tenue lack the typical inflation found immediately above the thick-walled portion of the phialides in most other species of the genus. Thus except for the thickened walls in the basal portions of the phialides, and the toughness of the colonies which makes them difficult to cut through, M. tenue seems closer to species of Acremonium.

Gams (pers. comm.) now considers M. tenue an aggregate species, since various isolates assigned to it have been shown to have different species of the genus Niesslia as teleomorphs. However, he does not believe he is able yet to distinguish between the probable subgroups within M. tenue. Nonetheless, the non-inflated phialides and small, cylindrical conidia which aggregate in slimy drops at the phialide apices, together with the lack of pigmented chlamydospores, are characters which separate M. tenue from other Monocillium species.

The six New Zealand isolates are all similar microscopically, but differ in growth rate and tendency to form hyphal strands and crystals. Isolates 88c, 115, and 147e', which demonstrate the range of variation found in the New Zealand isolates, were examined by Dr. W. Gams. He considered 115 to be the most typical of M. tenue, as this isolate formed numerous white crystals in the medium amongst the submerged hyphae. Of the three isolates, 147e' was the least typical, but still assignable to this species. Neither protoperithecia nor perithecia were produced by any of these isolates. Of interest was the fact that 5-month-old colonies of all the isolates had produced "star"-shaped aggregations of chlamydospore-like cells in the submerged hyphae. Such structures have not been previously reported for this species.

Although it is quite possible that M. tenue is a fairly common inhabitant of bark beetle galleries in New Zealand, its presence may be obscured by other fungi; three of these isolates were recovered from mixed cultures originally thought to be pure. Previous records of the species show that its habitat is associated with wood and other wood-

inhabiting fungi (often dead) where Gams (1971) considers M. tenue a common species. Finding it associated with other fungi in the bark beetle galleries should therefore not be surprising.

Phaeoisaria Höhn., Sitzungber. Akad. Wiss. Wien, Abt. 1, **118**:329. 1909

=Graphiopsis Bain., Bull. trimest. Soc. mycol. Fr. **23**:19. 1907 (non Trail 1889)

=Hansfordiula E. F. Morris, Am. Midl. Nat. **69**:103. 1963

Type species: Phaeoisaria clematidis (Fuckel) Hughes (=P. bambusae Höhn.)

Teleomorphic genus: Peroneutypella Berl., one species is reported to have a Phaeoisaria anamorph (Deighton 1974).

Originally the genus was characterized as having synnemata with stems consisting of brown, parallel hyphae which sometimes branch towards the apex. The sympodially prolifering, subulate, cylindrical or clavate conidiogenous cells are arranged along the sides of the upper portion of the synnemata. The conidia which develop singly on distinct, cylindrical denticles are dry, 1-celled, hyaline to pale brown, and fusiform, ellipsoid or subglobose. De Hoog & Papendorf (1976) grew an isolate of P. clematidis in pure culture and argued that since the synnemata did not always develop under such conditions, the synnemata should not be used as the main diagnostic feature of the genus. Their generic diagnosis included the appearance of the colonies in culture, i.e. "Colonies restricted or effused, powdery to velvety, pale brown to blackish brown", but reduced the importance previously attributed to the synnemata. They also mentioned chlamydospores, and the rare presence of 1-septate conidia. Since they no longer considered the presence of

synnemata a diagnostic character of Phaeoisaria, de Hoog & Papendorf (1976) added two species which lacked synnemata, but possessed conidiogenous cells resembling those formed by other Phaeoisaria species in pure culture.

Members of this genus are found in litter, on branches, decaying wood and a variety of other plants (Ellis 1971; de Hoog & Papendorf 1976).

The distinct, 0.5 - 1.5 μm long, cylindrical denticles and the smooth-walled conidia which lack basal frills or distinct scars are characters which separate Phaeoisaria species from members of somewhat similar genera. Species of Rhinocladiella Nannf. produce shorter and more crowded denticles, and many also produce budding cells and have annellidic synanamorphs. Those of Nodulisporium Preuss and Tharoopama Subramanian produce conidia with basal frills. For further discussion of species of various genera which share some features in common with Phaeoisaria species, see de Hoog & Papendorf (1976).

De Hoog & Papendorf (1976) treated six Phaeoisaria species, and since then at least three more have been described. Deighton (1974) found synnemata of the Phaeoisaria-type mixed with perithecia of Peroneutypella echidna (Cooke) Deighton and considered these constituted a holomorph. However, this supposed anamorph-teleomorph connection was based on examination of herbarium material, and not proven culturally.

Phaeoisaria clematidis (Fuckel) S. J. Hughes, Can. J. Bot. 36:795. 1958

Fig. 29. a-i.

≡Stysanus clematidis Fuckel, Symb. mycol. (Jahrb. Nassau. Ver. Naturkd.) 23, 24:365. 1870

=Phaeoisaria bambusae Höhn., Sitzungber. Akad. Wiss. Wien, Abt. 1, 118:329. 1909

For further synonymy see Deighton (1974).

Colonies attaining a diameter of 10 - 18 mm in 21 days at 20°C in darkness on MEA.YE. Light grey or grey to light olive grey (5Y $^{6}/_{1}$ to $^{6}/_{2}$) where the dark grey (5Y $^{4}/_{1}$) surface of the medium is covered with short aerial hyphae bearing short lateral and terminal (nematogenous) conidiophores; the conidia are clustered on short rachises. Usually the colonies appear raised with irregular radial furrows, occasionally cerebriform, but sometimes with flat areas or sectors. In reverse, colonies are grey, dark grey to very dark grey (2.5Y $^{5}/_{0}$, $^{4}/_{0}$ to $^{3}/_{0}$) with a thin light grey (5Y $^{7}/_{1}$) margin. Occasionally synnemata formed on MEA.YE. Odour, exudate, and crystals lacking. Hyphae hyaline to brown, smooth-walled, and 1.5 - 3.0(3.5) µm wide. The colonies also produce abundant brown, submerged hyphae whose somewhat inflated cells are 5.5 - 10.5(12) µm in diameter (Fig. 29. a,b). Similar cells are produced in clusters or short, lateral chains on the aerial hyphae, and then resemble chlamydospores. Conidiophores are sympodial, primarily micronematous, but some which are macronematous and synnematous may also develop. Micronematous conidiophores comprise terminal, lateral, or intercalary

Fig. 29. Phaeoisaria clematidis (Fuckel) S. J. Hughes
(isolates: 89d, 100b''', 136d'')

a. Inflated cells produced by the hyphae growing in the medium.

b. Inflated cells produced by the aerial hyphae (centre), and inflated cells produced by the hyphae growing in the medium (left and right)

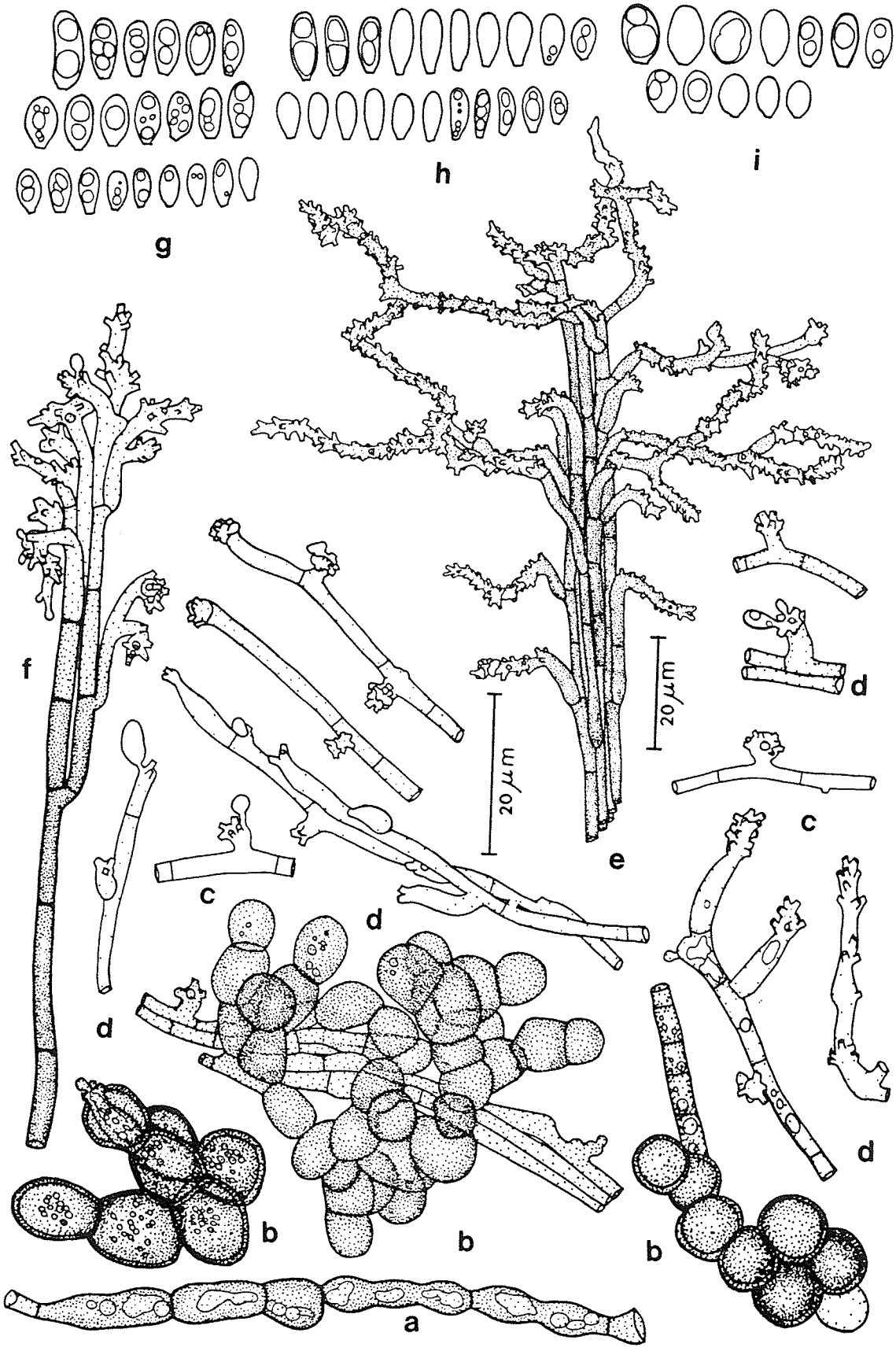
c-d. Micronematous conidiophores.

e. A synnema apex with sympodulae and long, undulate, branched rachises.

f. A simpler, macronematous conidiophore.

g-i. Sympodioconidia.

Isolates as illustrated: 89d: b, d, g.
100b''': i.
136d'': a, c, e, f, h.


a
b
b
b
c
c
d
d
d
d
e
f
g
h
i
20 µm
20 µm

conidiogenous cells produced on undifferentiated aerial hyphae, and they may be separated from the hyphae by a basal septum (Fig. 29. c,d). When present, synnemata have an upper portion bearing sympodulae, and a stem of parallel, dark brown hyphae which are 2.0 - 2.5 μm wide; the smaller synnemata are often produced by a single, repeatedly branching basal hyphal element and are up to 15 μm wide below the conidiogenous area and 300 - 600 μm long (Fig. 29. e); the larger synnemata are cylindrical, and 700 - 1000 μm long and 30 - 60 μm wide. Conidiogenous cells are sympodial and integrated or rarely discrete; subhyaline to brown; smooth-walled; cylindrical or inflated at the apices (clavate to spathulate) and 2.0 - 2.5 μm wide, but up to 5.5 μm wide in the inflated areas (Fig. 29. c,d); when intercalary, conidiogenous cells may resemble hyphal cells except for the presence of lateral denticles. The conidia are produced singly on nearly cylindrical denticles which are 0.8 - 1.6 μm long and 0.5 - 0.8 μm wide; these form both laterally and terminally on the sympodulae; rachises are 2.0 - 3.2(5.5) μm wide and may become curved or undulate and up to 55 μm long on the synnemata in aging cultures (Fig. 29. e). Sympodioconidia dry; 1-celled; subhyaline to light-brown and smooth-walled; clavate, oval, elliptical, or subglobose with rounded apices, but often tapering towards the base which may be indistinctly pedicellate and truncate or, if the conidia are broad, rounded; 4.0 - 8.5(10.0) x (1.7)2.0 - 4.0 μm, and usually containing large oil drops (Fig. 29. g,h,i).

HOSTS: Pinus radiata, Podocarpus sp.

CULTURES EXAMINED: **New Zealand:** 89d, 100b''', isolated from P. radiata, off Road 41, Whangapoua State Forest, Coromandel, collected 19 May 1982; 136d'', isolated from Podocarpus sp., near Minginui, Urewera National Park, Taupo, collected 11 June 1982.

Common on a wide variety of living and dead plant material, this species is also reported from other substrata e.g. soil, bat guano, soybean nematode cyst, an ascomycete etc. (Anon 1987a; Anon 1987b; Carris et al. 1989; Deighton 1974; de Hoog & Papendorf 1976; Ellis 1971; Holubová-Jechová 1979; Hughes 1978; Matsushima 1971, 1975, 1980; Shearer 1972). It does not appear to be geographically restricted, and has previously been reported from New Zealand (Hughes 1978).

Originally described as Stysanus clematidis Fuckel from a rotten stem of Clematis vitalba L. in Germany, it was also described under a variety of names by later authors (see Deighton 1974; de Hoog & Papendorf 1976). On natural substrata, the synnemata which were considered a diagnostic feature of the fungus always form, but not so in culture (de Hoog & Papendorf 1976; Matsushima 1975), and this is why de Hoog & Papendorf (1976) redescribed the species and stressed cultural characteristics while reducing the importance of the synnemata in delimiting the species. However, while they did not give a separate name to the micronematous synanamorph, Matsushima (1975) referred it as a Rhinocladiella-state.

Of the New Zealand isolates, 136d'' most readily produced synnemata

in culture. Its conidia were clavate to ellipsoid-fusiform and (1.7)2.0 - 3.0(3.5) μm wide (Fig. 29. h), while the conidia of the other two isolates were chiefly broader and more circular, then 2.4 - 4.0(5.0) μm wide (Fig. 29. g,i). Although isolates 89d and 100b''' produced fewer clavate to ellipsoid-fusiform conidia than isolate 136d'' these were usually present amongst the broader ones. Isolate 136d'' produced more aerial mycelium in culture than either of the other isolates.

Previously, Hutchison & Reid (1988a,b) determined these isolates could stain wood, but had identified them as isolates of Leptodontidium elatius var. elatius; these authors did note the isolates differed from de Hoog's (1977) description of L. elatius var. elatius.

In this study it was found that the conidia are always produced on distinct denticles, and this presence of distinctly denticulate rachises specifically excludes these isolates from Leptodontidium; Leptodontidium species have rachises with indistinct scars, but never denticles. This revised identification was confirmed by CBS, Baarn (W. Gams, pers. comm.). Hughes (1978) reported his New Zealand collections had somewhat narrower conidia (1.6 - 1.8 μm) than those of the three isolates studied here.

P. clematidis can be separated from most other Phaeoisaria species by the size of its conidia. They are longer (i.e. > 4 μm) than those of P. clavulata (Grove) Mason & S.J. Hughes, P. curvata de Hoog & Papendorf or P. glauca (Ellis & Everh.) de Hoog & Papendorf, but are shorter (i.e. < 10 μm) than P. sparsa Sutton. The only species with conidia in the same length range is P. magnifica Deighton, but this species produces

somewhat broader conidia and synnemata which develop readily in culture and have flaring hyphae in the upper portion.

None of the reports of P. clematidis listed above suggests any relationship with wood-inhabiting insects, although it is reported to be common on wood and various plant remains (Ellis 1971). However, as it grows quite slowly in culture, it may have been overlooked during previous isolations from bark beetle galleries, especially as it often occurs amongst faster growing species.

Phialographium Upadhyay & Kendrick, Mycologia 66:183. 1974

Type species: Phialographium sagmatosporae Upadhyay & Kendrick, the anamorph of Ceratocystis sagmatospora Wright & Cain

Teleomorphic genus: Ceratocystis Ellis & Halst. sensu lato.

Upadhyay & Kendrick (1974) described the genus as Graphium-like except the conidia were produced by phialides and referred to the description of the anamorph of Ceratocystis sagmatospora in Wright & Cain (1961). It is thus comprised of fungi which produce 1-celled, hyaline or lightly pigmented phialoconidia which aggregate in slimy masses at the apex of determinate synnemata which are slender, pigmented and comprised of a single kind of hyphae.

The genus consists of the synnematal anamorphs of four species of Ceratocystis sensu lato (Solheim 1986; Upadhyay 1981) which are associated with wood-inhabiting insects, and are thus potential wood staining organisms.

Two species with ornamented cells as components of the synnematal stems were assigned to Phialographium by Rao & Sutton (1975) but later considered synonyms of species of Stilbella Lindau (Seifert 1985).

Phialographium species are the synnematal counterparts of species of the genus Phialocephala Kendrick, which are macronematous, mononematous and produce 1-celled phialoconidia by means of penicillately arranged phialides. The phialide shape resembles that found in the genus Phialophora Medlar, whose species lack macronematous phialophores,

and in terms of general morphology, it is only the presence of the synnema which separates members of Phialographium from species of Phialophora. Phialographium species known to date are anamorphs of Ceratocystis species but Phialophora species, as discussed below, have other teleomorph affinities.

Phialophora Medlar, Mycologia 7:202. 1915

=Cadophora Lagerb. & Melin in Lagerberg et al., Sv. Skogsvårdsf. Tidskr. 25:263. 1927

=Margarinomyces Laxa, Zentbl. Bakt. ParasitKde, Abt. II, **81**:392. 1930.

Type species: Phialophora verrucosa Medlar

Teleomorphic genera: Ascocoryne Groves & Wilson, Coniochaeta (Sacc.) Massee, Gaeumannomyces von Arx & D. Olivier, Lasiosphaeria Ces. & de Not., Mollisia (Fr.) P. Karst., Pyrenopeziza Fuckel.

The genus Phialophora comprises a diverse assemblage of fungi possessing discrete phialides with distinct collarettes, and simple or basitonously branched phialophores, or sometimes the stem is lacking and the phialides arise directly from the vegetative mycelium. They produce 1-celled, hyaline or lightly pigmented conidia which either aggregate in slimy masses or form chains (the latter comprise the section Catenulatae W. Gams).

Individual species, or groups of species of this genus have been treated by Cole & Kendrick (1973), Domsch et al. (1980), Gams in Gams & Holubová-Jechová (1976), Schol-Schwarz (1970), Sivasithamparam (1975), etc. The taxonomy of this group of fungi is still developing, since certain of these entities are clearly aggregate species comprised of only slightly different, but clearly distinct individuals which lack markedly distinct morphological characters; this view is supported by the teleomorphic connections. Gams & McGinnis (1983) transferred

members of one of the aggregate species, the P. hoffmannii-group, to Lecythophora Nannf. and thus re-established a genus which had been erected for Phialophora-like species which were primarily adelophialidic but later synonymized with Phialophora. Other problematic areas remain unresolved in the taxonomy of the fungi traditionally assigned to Phialophora (Domsch et al. 1980; Gams & McGinnis 1983).

Phialophora species are well known as wood-staining organisms (Eslyn & Davidson 1976; Hutchison & Reid 1988b; Lagerberg et. al. 1927; Melin & Nannfeldt 1934; Robak 1932) but also as human and plant pathogens, and as saprophytes in soils (Domsch et al. 1980; Hawksworth et al. 1976; de Vries et al. 1984).

Domsch et al. (1980) list the number of Phialophora species as 44 but stress that it is not a definitive number.

Phialographium taxonomic sp. 1. Fig. 30. a-f.

Synanamorph: Phialophora taxonomic sp. 1.

Colonies attaining a diameter of 9 mm in 14 days and 15 mm in 21 days at 20°C in darkness on MEA.YE. When young, colonies are light grey (10YR 7/1) in the centre and at the margins, but greenish grey (5GY 6/1) in between; the centre is plectonematogenous to synnematogenous bearing crowded conidiophores, each with many tiny, whitish, moist conidial drops, on pale-brown, tapering strands. On aging, colonies become greenish grey to grey (5GY 6/1 to 5Y 6/1) and the surface of the medium becomes covered with a layer of greyish, slimy conidial masses, except for the light grey (5Y 7/1) margins; or the colonies are olive (5Y 5/3), and consist chiefly of short synnemata bearing greyish conidial masses. In reverse, colonies are greenish grey (5GY 5/1) with light grey margins, but on aging, the outer part becomes greyish green (5G 4/2). Colonies grown in alternating light and darkness grow more slowly, are zonate, and olive grey (5Y 4/2). Colonies grown on acidified MEA are snow-white in the centre, but are intensely green [7.5GY 5/10] especially at the sparsely covered margins of aging colonies. Odour indistinct; exudate is present in young colonies as medium-sized to large clear or blue-green drops. Blue-green to green pigment is present in the medium within colonies grown in darkness; the pigment is only present as a thin zone at the margin of colonies grown in alternating light and darkness. Hyphae subhyaline to dark-brown, or green, often with green oil droplets; walls distinct to thick (up to 1.5 μm), smooth to verrucose, with

Fig. 30. Phialographium taxonomic sp. 1. synanamorph: Phialophora taxonomic sp. 1.
(isolate: 75N (UM74-22))

a. Erect, macronematous phialophores; each synnemata has arisen by branching of a single hyphal element.

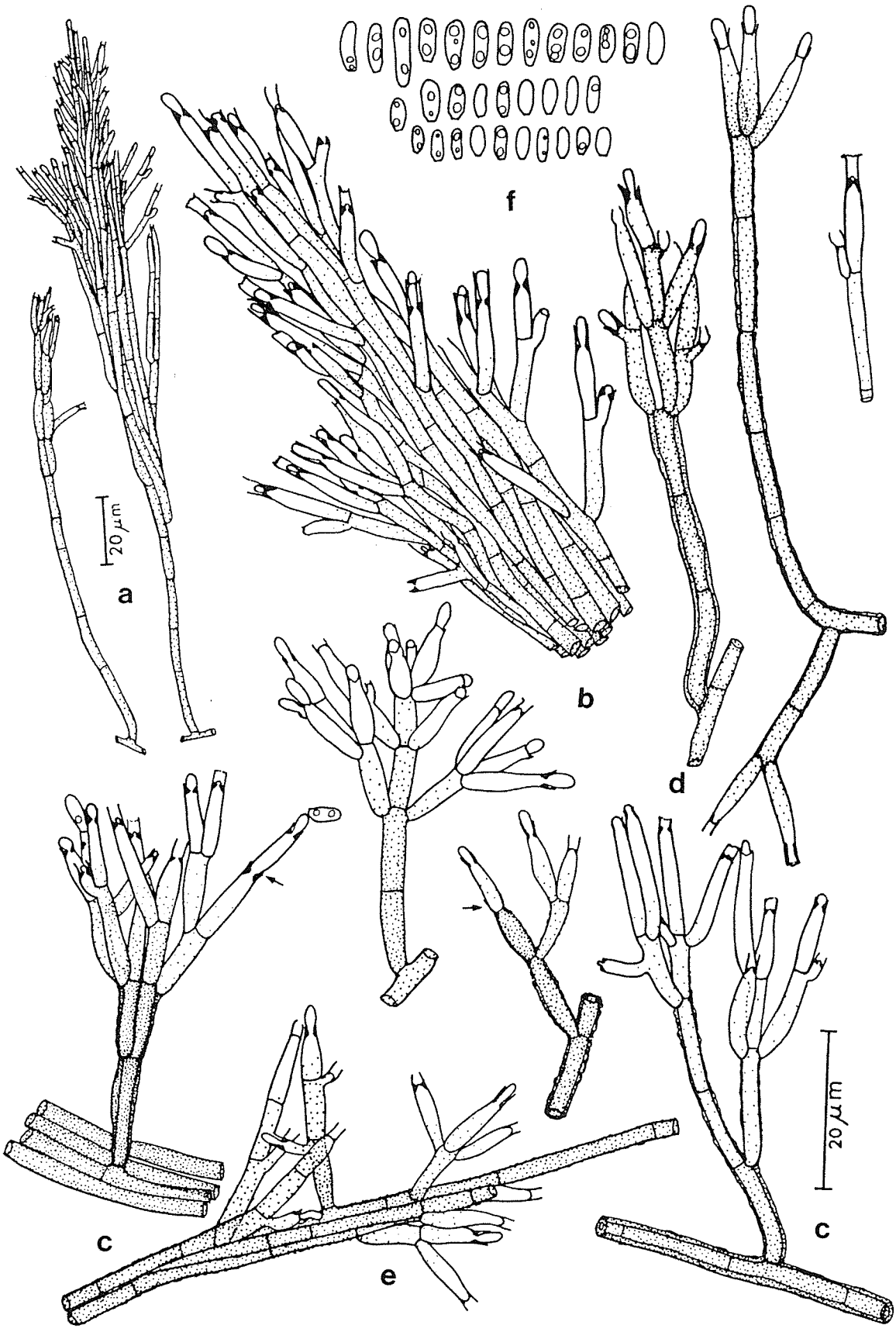
b. Details of the synnema apex of (a) (right side).

c-d. Mononematous phialophores; (c) note proliferating phialides («-); (d) with a convergent penicillus.

e. Simple phialophores with phialides arising from short branches.

f. Phialoconidia.

Isolate as illustrated: 75N (UM74-22): a-f.


20 µm
a
f
b
d
c
e
c
20 µm

the surface of the aerial hyphae sometimes appearing flaky, but the ornamentation on the submerged hyphae obscured by the medium. The hyphae measure 2.2 - 5.0 μm in diameter, but when funiculose, the strands are 5 - 20 μm wide, and consist of 2.0 - 4.0 μm wide hyphae. Chlamydospores were not seen. Phialophores are macronematous to semi-macronematous; brown, but more lightly pigmented at the apex; walls distinct to thick, and finely verruculose to verrucose. Macronematous phialophores are mononematous or synnematous; synnemata are not commonly produced, but when present, they are abundant and chiefly develop from a single hyphal element; they gradually become broader as the hyphae in the stem branch, and the synnemata are then clavate in outline (Fig. 30. a,b); 100 - 230 μm long and 10 - 30 μm wide just below the apex. Synnemata with a cylindrical stem are also very rarely produced. The mononematous phialophores are 30 - 240 μm long, and consist of a 1 - 7 celled, 10 - 200 x 2.4 - 3.5(4.0) μm stem bearing terminal penicillately branched systems of 0 - 3(4) series of short branches; these usually are somewhat divergent (Fig. 30. c), but sometimes are convergent and parallel to the stem (Fig. 30. d); each branch bears 1 - 4 phialides at the apex, and usually a phialidic peg is also present. Semi-macronematous conidiophores which consist of a short branch bearing 1 - 3 phialides and often a peg (Fig. 30. e) are also present. Conidiogenous cells are phialidic; discrete; subhyaline to brown; smooth-walled or sometimes verrucose in the basal portion; cylindrical, subcylindrical, or naviculate, and measure (6.5)8 - 15 x (2.0)2.3 - 2.8 μm (including the collarette) and taper to 1.5 - 1.8(2.0) μm at the apex. The collarette

is distinct, 0.5 - 2.5 μm long, and nearly cylindrical. Phialides rarely proliferate through the apex of older ones (Fig. 30. c, «-). Phialides are frequently subtended by cylindrical pegs which measure 2.5 - 6.5 x 1.5 - 2.8 μm including the collarette (Fig. 30. b-e). Phialoconidia aggregate in slimy masses; 1-celled, hyaline, and smooth-walled; cylindrical, short-cylindrical, or slightly asymmetric, measuring (3.5)4.2 - 6.5(8.0) x 1.2 - 2.4 μm, with rounded apex and tapering to the base, and often contain 2 - 3 oil drops, especially on aging (Fig. 30. f).

HOST: Pinus sylvestris

CULTURE EXAMINED: Norway: 75N (UM74-22) isolated from P. sylvestris, near Ås, Akershus, collected in October 1973.

This isolate produces green pigment into the medium and produces hyaline conidia which aggregate in whitish or light grey slimy masses which may cover the surface of the colonies so only the taller structures reach through. Colonies grow very slowly but eventually fill the plates. The aerial hyphae are often fasciculate bearing numerous but relatively short phialophores. The shorter phialophores are typical of those produced by Phialophora species, as the phialides have distinct collarettes, range from hyaline to brown, and on aging often become verrucose. The short to medium-sized phialophores are thus assigned as the Phialophora synanamorph but since the clavate synnema-like

conidiophores cannot satisfactorily be accommodated in Phialophora they are assigned to a separate genus, Phialographium. The species is described in Phialographium since priority is traditionally given to the most complex conidiogenous structure produced, in spite of its absence from young colonies and the fact that it may not develop at all. In view of the fact that the synnemata are often absent, the Phialophora synanamorph is specifically denoted. That should ensure that this organism is listed with other Phialophora species and included in keys, etc. so future collections could be identified independent of the Phialographium state.

W. Gams, CBS, Baarn (pers. comm.) did not think this species was a member of the genus Phialographium, but considered it a typical Phialophora species, characterized by the production of a green pigment and fasciculate phialophores, not synnemata. He was confident that this species has not been described before this.

De Vries et al. (1984) described P. cyanescens de Vries et al., a species which produces a blue pigment but that species is clearly different from this Norwegian fungus.

The slimy conidial masses and the synnematal structures produced by isolate 75N are features well adapted to spore dispersal by insects. The very rare development of true synnemata in culture does not exclude their presence on natural substrata. Indeed, in many species which produce complex conidiophores in nature, such structures are frequently reduced or disappear altogether after a short time in culture.

Pithomyces Berk. & Broome, J. Linn. Soc. 14:100. 1873

=Scheleobrachea S. J. Hughes, Can. J. Bot. 36:802. 1958

Type species: Pithomyces flavus Berk. & Broome

Teleomorphic genus: Leptosphaerulina McAlp.

The genus is characterized by species which form yellowish, olive, brown, or black colonies. The conidiophores are macronematous or semi-macronematous, and produce the holoblastic conidia singly on short to longer cylindrical pegs or denticles which arise from undifferentiated, integrated conidiogenous cells. The conidia are dry, with 0 - 13 transverse septa, and often 1 or more oblique or longitudinal septa; darkly pigmented; smooth-walled, echinulate or verrucose; ellipsoid, clavate, limoniform, obovoid or obpyriform. The pegs fracture to release the conidia which retain the apical portion of the pegs as a short, basal frill.

After examining P. flavus Berk. & Broome, the type of the then monotypic genus Pithomyces, Ellis (1960) redescribed the genus and concluded Scheleobrachea S. J. Hughes should be considered a synonym. He also assigned to it species with darkly pigmented, muriform conidia, some of which had earlier been described by Hughes (1953) as species of Sporidesmium Link.

The various Pithomyces species are to be found on various plant remains, and in litter or in soils (Carmichael et al. 1980; Ellis 1971). Ellis (1971) lists eleven species of Pithomyces although one of them,

P. maydicus (Sacc.) M. B. Ellis is not easily distinguished from P. chartarum (Berk. & Curtis) M. B. Ellis.

Pithomyces chartarum (Berk. & Curtis) M. B. Ellis, Mycol. Pap. 76:13. 1960 Fig. 31. a-b.

≡Sporidesmium chartarum Berk. & Curtis apud Berkeley, Grevillea 3:50. 1874

For full synonymy see Ellis (1960) and Dingley (1962).

Teleomorph: Leptosphaerulina chartarum Roux, Trans. Br. Mycol. Soc. 86:320. 1986

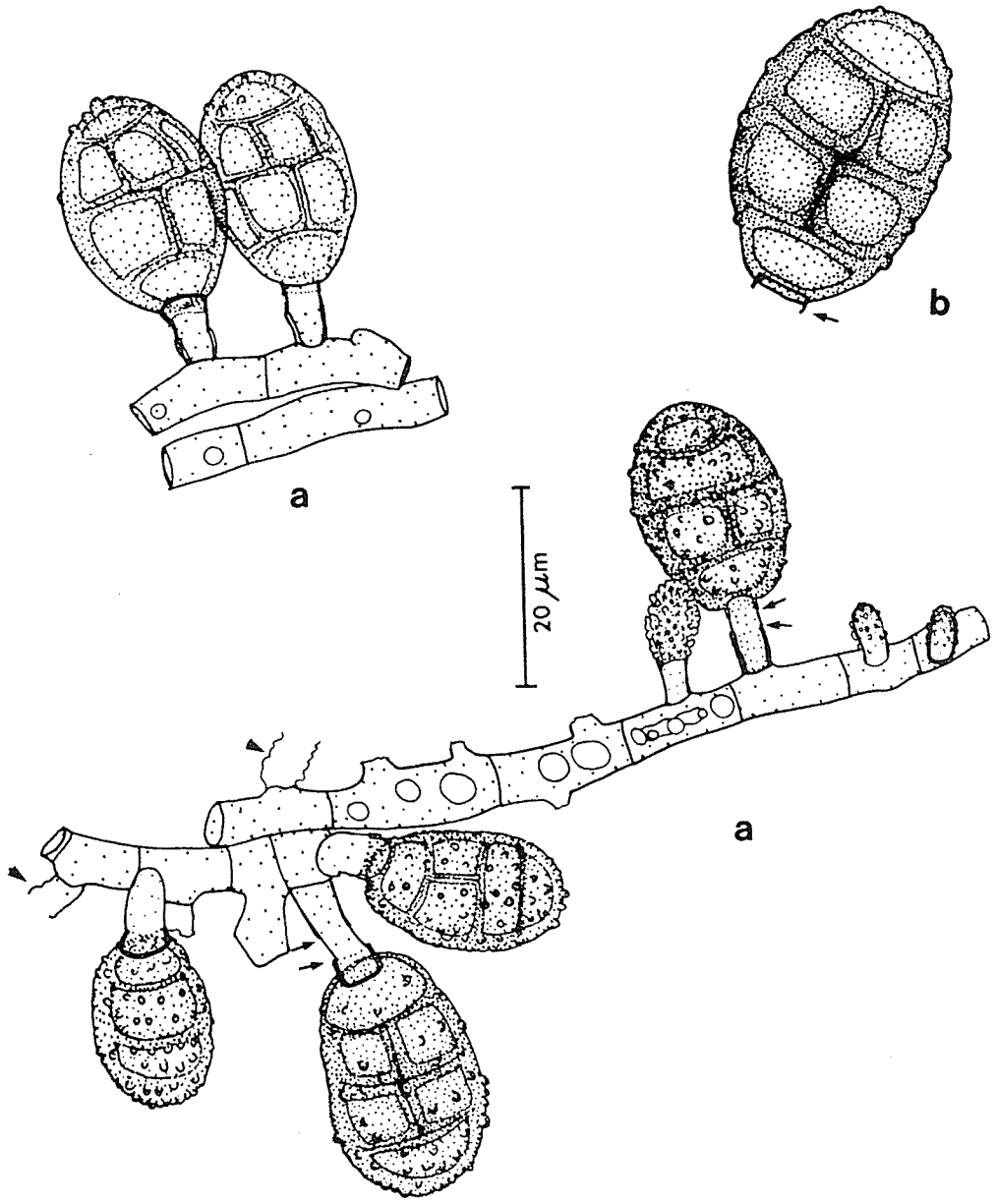
Colonies attaining a diameter of 65 mm in 10 days at 20°C in darkness on MEA.YE. Surface pale olive (5Y $^{6}/_{4}$) to pale yellow (2.5Y $^{8}/_{4}$); nematogenous; caespitose to lanose with greyish areas where the conidia are formed on the mycelium, and such areas gradually enlarge and sometimes merge; colony colour at first olive (5Y $^{5}/_{3}$ to $^{5}/_{4}$), gradually turning dark olive (5Y $^{3}/_{2}$) to olive grey (5Y $^{4}/_{2}$), then very dark grey (5Y $^{3}/_{1}$) on aging. The colonies often form discrete sectors and are clearly zonate when grown under conditions of alternating light and darkness. In reverse, young colonies are pale olive (5Y $^{6}/_{4}$ to $^{6}/_{3}$), then olive grey (5Y $^{4}/_{2}$), and finally dark grey (5Y $^{4}/_{1}$ to 10YR $^{4}/_{1}$). Brown pigment diffuses into the medium beneath the colony, and yellow crystals may be deposited both within and on the medium. Odour indistinct, and an exudate is present as small, clear droplets. Hyphae are hyaline to pale brown, but some submerged hyphae are brown; walls smooth, verruculose to distinctively verrucose; 2.5 - 9.0 μm in diameter and not aggregated in strands. Chlamydospores were not seen.

Fig. 31. Pithomyces chartarum (Berk. & Curtis) M. B. Ellis (isolate: 25bii)

a. Conidiophore, conidiogenous cells and conidia at various stages of development. Conidiiferous pegs bearing conidia; thin-walled dehiscence zones (-» «-); remnants of conidiiferous pegs («).

b. A conidium with the apical portion of the conidiiferous peg still attached as short frill («-).

Isolate as illustrated: 25bii: a-b.


a
b
20 µm
a

Conidiophores micronematous; undifferentiated, hyaline and smooth-walled; with cylindrical conidiiferous pegs (Fig. 31. a). Conidiogenous cells monoblastic, integrated, intercalary or terminal, bearing cylindrical conidiiferous pegs, measuring 5.0 - 12.0(18) x 3.0 - 3.5(3.9) μm, each of which forms a solitary blastoconidium which is released by dehiscence of a thin-walled zone just below the conidium (Fig. 31. a -» «-); the peg then collapses (Fig. 31. a «). Conidia holoblastic; solitary; light brown and densely verrucose when young, but as they mature the protuberances are not as densely aggregated on the conidial surface, and the conidium becomes brown to dark brown, thick-walled and ellipsoidal with 3(-4) transverse septa; central cells are usually further divided by 0-2 longitudinal septa; usually slightly constricted at the septa; 16 - 35(39) x 9.5 - 20(23) μm; the apex of the conidiiferous peg remains attached to the conidium as a short hyaline frill (Fig. 31. b «-).

HOST: Larix sp.

CULTURE EXAMINED: **New Zealand;** 25bii, isolated from Larix sp., Compartment 5, Waiotapu, Kaingaroa State Forest, Taupo, collected 8 May 1982.

Normally a saprophyte, P. chartarum has been isolated from air, soil, paper and from decaying material of over 50 plant species, particularly fodder grasses. However, it is also know as a pathogen of rice and sorghum in Africa and India, as well as a producer of mycotoxins

(sporidesmins) which cause facial eczema in sheep (Domsch et al. 1980; Ellis 1960, 1971; Sutton & Gibson 1977). It is considered cosmopolitan in its distribution (Ellis 1971), possibly more common in tropical and temperate climates (Sutton & Gibson 1977), but it has been found in cooler climates when conditions are favourable (Gregory & Lacey 1964).

In New Zealand, this species has been studied primarily to understand how its presence on various plant remains in pastures causes outbreaks of facial eczema in animals, and how this disease can be controlled (DiMenna & Parle 1970; Dingley 1962; McKenzie 1971).

Sutton & Gibson (1977) note that it has been isolated from sawn timber, and Matsushima (1975) isolated it from forest soils.

Dingley (1962) studied P. chartarum both in culture and on natural substrata, and found the species to be quite variable in its morphology. She also outlined the history of P. chartarum and its taxonomy which also was treated in detail by Ellis (1960).

The species was isolated only once in the New Zealand surveys, and while the spore measurements recorded here are slightly larger than those given by Ellis (1960, 1971), the differences are not considered significant, and this isolate is confidently assigned to P. chartarum. However, since it is commonly found on decaying plant material, bark beetles could occasionally encounter it and transport it to the galleries. It is possible it could survive in such sites because of its cellulolytic ability (Sharma 1974).

Rhinocladiella Nannf. in Melin & Nannfeldt, Sv. Skogsvårdsf. Tidskr. 32:461. 1934

For synonymy see de Hoog (1977).

Type species: Rhinocladiella atrovirens Nannf.

Teleomorphic genera: Unknown for most species but a species of Capronia Sacc. has a Rhinocladiella anamorph.

According to de Hoog (1977) the genus is characterized by fairly slow-growing, grey, greenish or oliveaceous brown colonies which are velvety, lanose, funiculose, or nearly smooth. Hyphae are hyaline to brown, with the aerial hyphae usually more darkly pigmented than the submerged ones, and chlamydospores are lacking. The conidiophores are micronematous to semi-macronematous, brown in colour and often branched. The conidiogenous cells are usually sympodial, integrated, cylindrical to acicular, and produce 1-celled, hyaline to subhyaline, smooth-walled conidia. The conidia are variable in shape, cylindrical to short-clavate or oval to subglobose, and develop on small denticles which might also be considered elevated scars. These are either borne laterally on elongating rachises, or are clustered at the conidiophore apices; the conidia may develop either singly or in chains. Budding cells and Exophiala synanamorphs may be present.

Rhinocladiella species are known from (rotten) wood, human tissues, soil, etc.

Presently, the genus consists of hygrophobic, mainly sympodial

states of darkly pigmented, pleomorphic, yeast-like fungi; a group commonly referred to as the black yeasts (de Hoog & McGinnis 1987). These fungi do not possess many stable morphological features suitable for delimiting taxa, and this has resulted in a rather confused taxonomy as well as nomenclature. Detailed examinations of a number of individual species (de Hoog 1977; Iwatsu et al. 1987; Schol-Schwarz 1968; Tsuneda et al. 1986; etc.) have made apparent the pleomorphic nature of such fungi, and shown that age of the isolates, cultural conditions, etc., may determine which synanamorph will be produced. De Hoog & McGinnis (1988) outlined the attempts made until then to establish order in the taxonomy of the black yeasts, a task not yet near completion!

As in many instances the Rhinocladiella state only represents one phase of the development of an organism, synanamorphs, often with different modes of conidiogenesis, must be included in species descriptions. However, the Rhinocladiella states seem to predominate in aging isolates, while Exophiala synanamorphs and budding cells are often present in recently isolated cultures (de Hoog 1977; Tsuneda et al. 1986).

The genus Exophiala consists of species which in many aspects resemble Rhinocladiella, but differ therefrom by producing annello-conidia on variable annellides, some of which are reduced to pegs. The genus Fonsecaea Negroni was considered synonymous with Rhinocladiella (de Hoog 1977), but it is used by many authors to accommodate R. pedrosoi (Brumpt) Schol-Schwarz, a species which lacks yeast-like synanamorphs. Members of Ramichloridium Stahel ex de Hoog differ from those of Rhinocladiella in producing distinct conidiophores (sympodial,

macronematous, mononematous) and lacking synanamorphs. The genus Phaeococcomyces de Hoog consists of species with ascomycetous affinities which produce yeast cells but no mycelium. One "species", P. exophialae (de Hoog) de Hoog buds multilaterally, has short, annellated pegs, and represents the yeast-like synanamorphs of Exophiala species (de Hoog & McGinnis 1988).

Rhinocladiella species generally have not been associated with teleomorphs, although Capronia parasitica (Ellis & Everh.) E. Müller et al. is reported to have a Rhinocladiella anamorph. Some other Capronia species (Dothideales: Pseudosphaeriineae: Herpotrichiellaceae) have Exophiala anamorphs (Müller et al. 1987).

Hawksworth et al. (1983) list Rhinocladiella as having 4 species, i.e. those treated by de Hoog (1977). An addition thereto is the anamorph of C. parasitica and, possibly, one other species, R. aquaspersa (Borelli) Schell et al. which de Hoog (1977) considered synonymous with Ramichloridium cerophilum (Tubaki) de Hoog, but which others believe is a Rhinocladiella.

Rhinocladiella atrovirens Nannf. in Melin & Nannfeldt, Sv. Skogsvårdsf. Tidskr. 32:462. 1934 Fig. 32. a-l.

For synonyms see de Hoog (1977).

Colonies attaining a diameter of 12 - 16 mm in 12 days (and 22 - 26 mm in 21 days) at 20°C in darkness on MEA.YE. Olive grey, grey, dark grey to very dark greyish brown (5Y 5/2, 5/1, 4/1 to 2.5Y 3/2); nematogenous, dry, raised, and quite dense except at the margins; the conidiophores arise from the aerial hyphae and bear the dry conidia at their apices. On aging, the colonies become powdery with increasing conidial production and, as the conidiophores branch and continue to grow apically, their conidiogenous loci are often separated by short stem segments (Fig. 32. b). In reverse, the colonies are black to dark olive grey (5Y 2/1 to 3/2), but sometimes olive grey (5Y 4/2) at the margins. Odour and exudate lacking. On aging, red, fan-shaped crystals (Fig. 32. a) consisting of needle-shaped units are deposited in the medium within colonies. Yellowish-red pigment diffuses slowly into the medium imparting a pale yellowish tint to the medium surrounding aging colonies. Hyphae light to dark brown; wall smooth and often rather thick; 1.5 - 4.5 µm wide, often gently undulate or having cells that are slightly inflated (Fig. 32. c). Chlamydospores were not seen but inflated cells in chains, many with pegs, were occasionally present (Fig. 32. d). Conidiophores are sympodial; micronematous to semi-macronematous; brown or darkest at the base, but usually becoming lighter brown towards the apex; walls are smooth and thin in young

Fig. 32. Rhinocladiella atrovirens Nannf.
(isolates: 2B, 14', 116c'', 165a)

a. Diagrammatic representation of the crystals produced in the medium as seen in the reverse of colonies.

b. Diagram of old conidiophores bearing rachises separated by short stem segments; the rachises would be bearing conidia.

c. Hypha constricted at the septa.

d. Inflated cells, some with pegs.

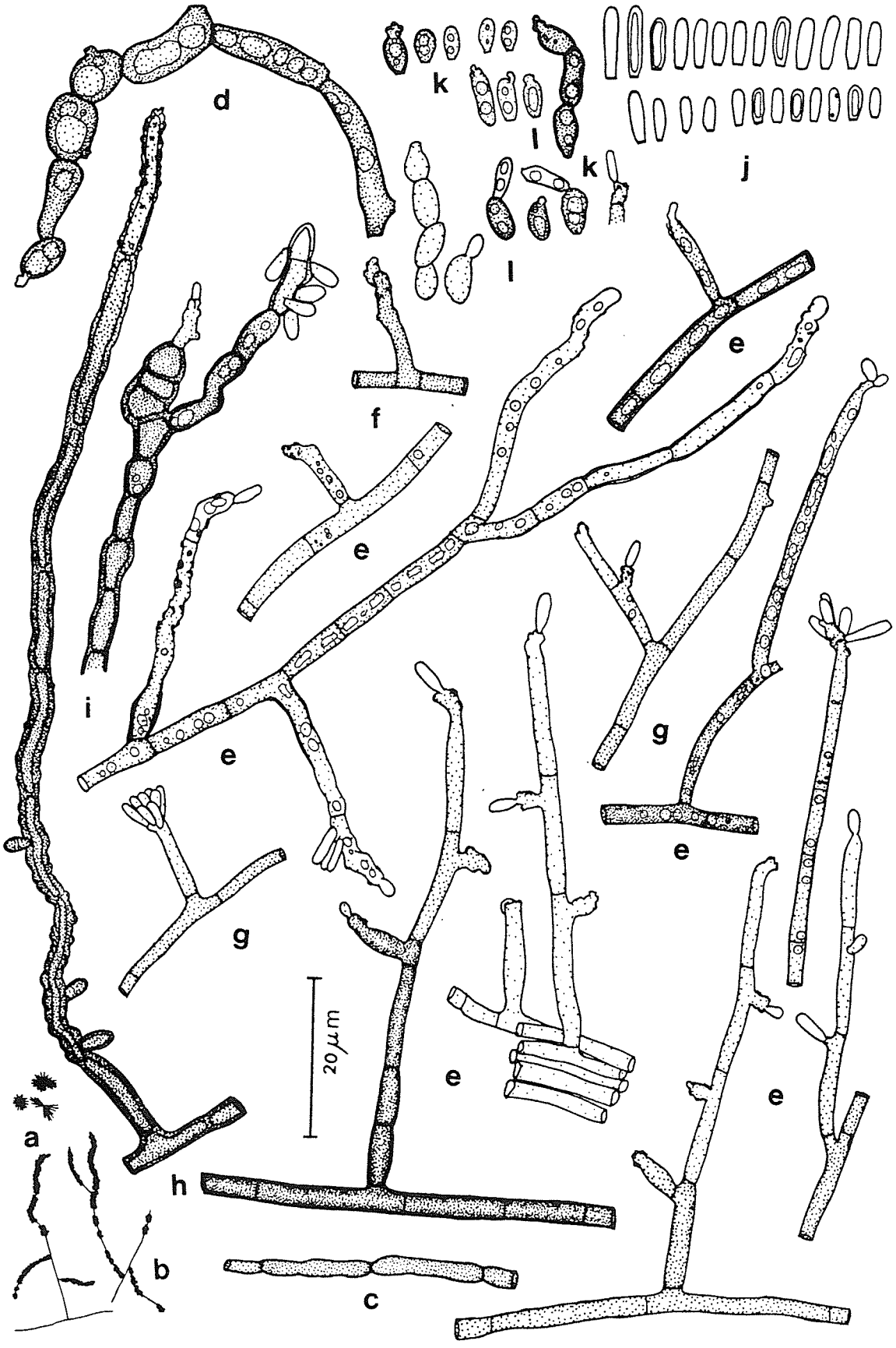
e-g. Young conidiophores.

h-i. Old conidiophores.

j. Sympodioconidia.

k-l. Conidia producing secondary conidia and the secondary conidia.

Isolates as illustrated: 2B: c, f.
14': i.
116c'': b, g, h, k.
165a: d, e, j, l.


a
b
c
d
e
f
g
h
i
j
k
l
20 µm

conidiophores, but may become thick on aging. Conidiophores are 5.0 - 70 x 1.7 - 3.2 μm, and arise primarily from the aerial hyphae as short lateral branches, and their stems consisting of 1 - 4 cells. Each stem bears 1 - 2 terminal sympodulae, but the subtending stem cell(s) may also produce conidia from lateral pegs (Fig. 32. e,g); or the stem is lacking and the sympodulae arise directly from the vegetative hyphae (Fig. 32. f,(e,g)). On aging, the sympodulae may proliferate apically, or sometimes branch, and this results in 70 - 230 μm long conidiophores with 4 - 15 septa whose conidiogenous areas are separated by stem segments (Fig. 32. b,h). Conidiogenous cells are sympodial, integrated, or discrete; brown but sometimes more lightly pigmented towards the apices; they are smooth-walled, cylindrical, measure 5 - 16 x 1.8 - 2.6 μm, and produce the conidia singly on tiny, crowded denticles (or raised scars) on rachises which are 2.0 - 2.6 μm wide (Fig. 32. e-h). Sympodioconidia dry; 1-celled; subhyaline to light-brown and smooth-walled; cylindrical or narrowly clavate, with a rounded apex tapering slightly at the truncate base; the latter has an indistinct scar (Fig. 32. j). Conidia usually 4.0 - 6.5(8.5) x 1.4 - 2.0 μm, but inflated conidia were observed which were 5.0 - 7.5 x 2.5 - 4.3 μm, and produced secondary conidia on tiny denticles (Fig. 32. k,l).

HOSTS: Pinus contorta Dougl. ex Loud., Pinus nigra, Pinus radiata, Pseudotsuga menziesii (Mirb.) Franco

CULTURES EXAMINED: **Canada:** 14', isolated from P. contorta, Taylor Lake

Hiking Trail, Banff National Park, Alberta, collected 23 September 1987; 2B, isolated from P. menziesii, Highway 14, 15 km west of Sooke, Vancouver Island, British Columbia, collected 17 September 1987. **New Zealand:** 165a, isolated from P. nigra, Compartment 1091, Kaingaroa State Forest, Taupo, collected 10 June 1982; 116c'', isolated from P. radiata, Compartment 24, Woodhill State Forest, Auckland, collected 25 May 1982; 49B'', isolated from P. radiata, Woodhill State Forest, Auckland, collected 6 February 1988.

Since it was first reported from pine wood and white water (Nannfeldt in Melin & Nannfeldt 1934), R. atrovirens has been reported most often from wood, especially from coniferous trees in association with rotten areas, but also from stored wood chips, poles buried in forest soils, and as an endophyte from the xylem of Fagus sylvatica L. (de Hoog 1977; Käärik 1968; Petrini & Fisher 1988; Shields 1969). It has also been isolated from humans, sewage, peat, stream beds, and pine leaf litter (de Hoog 1977; Kendrick 1963). Tsuneda et al. (1986) isolated R. atrovirens from galleries of the bark beetles Xyleborus seiryorensis Murayama in Quercus serrata Thunb., and Dendroctonus monticolae Hopk. in Pinus contorta Dougl. var. latifolia Engelm. This species does not appear to be geographically restricted, having been isolated numerous times in Canada (de Hoog 1977), but no earlier reports from New Zealand were located.

The original description of R. atrovirens was based solely on the sympodial synanamorph (Nannfeldt in Melin & Nannfeldt 1934), but later

it was recognized as a pleomorphic species which often produced chains of globose cells and annelloconidia on inflated to subulate conidiogenous cells (de Hoog 1977; Schol-Schwarz 1968).

The treatment of the various synanamorphs, however, is a source of much confusion.

Schol-Schwarz (1968) considered R. atrovirens and many other species of Rhinocladiella to be forms of R. mansonii (Castell.) Schol-Schwarz (teleomorph: Dictyotrichiella mansonii Schol-Schwarz). She clearly recognized many of the species or forms she was synonymyzing exhibited differing methods of conidiogenesis, but nonetheless she treated them as conspecific. De Hoog (1977) disagreed with her treatment of R. mansonii, for he found that in the culture derived from the type, conidiogenesis was annellidic and not sympodial. He therefore transferred R. mansonii to Exophiala as E. mansonii (Castell.) de Hoog. Now since his concept of E. mansonii excluded the presence of sympodial conidiogenesis, R. atrovirens with its sympodial development was separated from E. mansonii by him. This in spite of the fact that one of the synanamorphs of R. atrovirens, E. jeanselmei (Langer.) McGinnis & Padhye var. heteromorpha (Nannf.) de Hoog, was morphologically very close to E. mansonii.

A further confusion to non-specialists in this field is that de Hoog (1977) treated the annellidic synanamorphs of R. atrovirens under separate names. They are to be found under E. jeanselmei var. jeanselmei, E. jeanselmei var. heteromorpha (Nannf.) de Hoog, or E. jeanselmei var. lecanii-corni (Benedek & Specht) de Hoog, depending

on the actual nature of the basic annellidic conidiogenous mechanism.

Such taxonomic confusion faces anyone dealing with the black yeasts. Minter (1987) seems to support the concept of giving each holomorph one name instead of naming each of the different anamorphs occurring within a holomorph. Such a system would clarify nomenclature problems, since one would not be ascribing names to different states in the life cycle of a single organism. Rather variation in morphology would merely be recognized for what it is; the inherent plasticity of the organism which is under control of the genome of that species.

In the isolates studied, most of the conidia are produced sympodially from the apices of well differentiated conidiogenous cells on tiny denticles which also may be considered as raised scars, and thus the isolates have been placed in Rhinocladiella. Swollen conidia producing secondary conidia on small denticles do occur as do chains of swollen cells; some of the cells of such chains may produce conidia on small pegs. The latter forms have not been named separately.

R. atrovirens is distinguished from other Rhinocladiella species by its small scars, which are less than 1 μm in diameter on tiny denticles, and cylindrical conidia which are produced singly.

As R. atrovirens is a well known inhabitant of coniferous wood and has previously been associated with bark beetles, this report reinforces the association with the bark beetles and adds New Zealand to its known distribution.

Taxonomic genus 1.

Colonies exhibiting slow to medium growth rates; white or cream-coloured, and partly covered with slimy masses of conidia; phalacrogenous, with the conidiophores occurring singly or aggregated into loose, clavate, synnemata-like structures; the conidiophores are macronematous or semi-macronematous, simple or branched, with the branches forming at acute angles to the main hyphae or stem, and thus developing parallel to the latter. Each branch develops a terminal, cylindrical, conidiogenous cell from which relatively long, repeated percurrent proliferations develop. The annelloconidia are 1-celled; hyaline and smooth-walled; cylindrical to oblong or short-clavate.

Isolated from bark beetle galleries in Pinus contorta Dougl. ex Loud., Alberta, Canada.

This new genus will be erected to accommodate a single species currently represented by two isolates obtained from bark beetle galleries in P. contorta. It will be characterized by species possessing hyaline hyphae, 1-celled, oblong to short-clavate annelloconidia, and cylindrical percurrently proliferating conidiogenous cells, whose every proliferation produces a rather pronounced incremental elongation. As no evidence of any teleomorphic structures were encountered, the search for a referrable genus was restricted to the hyaline Hyphomycetes where no single genus with the particular characteristics exhibited by this organism was found. Based on their published descriptions, two species

which appear to have some similarities to this fungus, are Filosporella annelidica (Shearer & Crane) Crane & Shearer and the anamorph of a Pyxidiophora sp. described by Blackwell & Malloch (1989). The possible relationship of these to the new fungus is discussed following the species description.

Taxonomic genus 1, species 1. Figs. 33A. a-c, 33B. a-j.

Colonies attaining a diameter of 16 - 32 mm in 12 days or 26 - 80 mm in 21 days at 20°C in darkness, and 13 - 17 mm in 12 days in alternating light and darkness on MEA.YE. White to very pale brown (10YR $^{8}/_{2}$ to $^{8}/_{3}$) in the centre where the conidiophores and the surface are covered with thick, slimy conidial masses. The outer portions of the colonies are white (10YR $^{8}/_{2}$) to translucent depending upon the mycelium density; phalacrogenous, the medium being sparsely covered with both appressed hyphae producing short, lateral branches at near right angles, and groups of conidiophores bearing slimy masses of conidia at their apices. Initially conidiophores are erect, but they often collapse and are then partly covered with their conidial masses. Most of the mycelium forms within the medium where the immersed conidiogenous cells produce conidia in dense crescent-shaped spots in the agar. In dark--grown colonies, the margins are often irregular as fast-growing main hyphae rapidly extend into the agar. These hyphae develop short, lateral branches, and this creates a feathery or dendroid growth pattern where main hyphae surrounded by numerous branches alternate with areas almost devoid of hyphae. The distinctness of this pattern varies slightly between the two isolates examined, but in both isolates the pattern is less pronounced when colonies are grown in alternating light and darkness. In reverse the colonies are white (10YR $^{8}/_{2}$) under areas of relatively dense mycelium, but colourless where growth is sparse. Odour indistinct, exudate lacking, and colonies growing adjacent to one

Fig. 33A. Taxonomic genus 1, species 1.
(isolates: 4I, 14A)

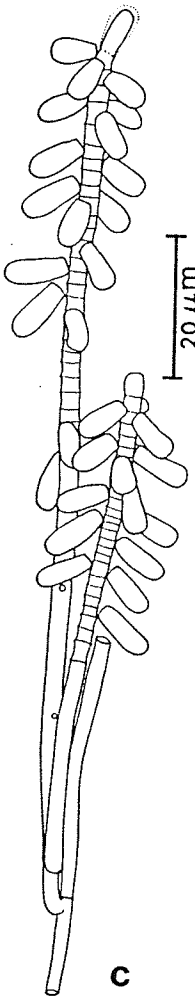
a. Habit sketch of a synnemata-like aggregation of individual conidiophores.

b. Complex conidiophore.

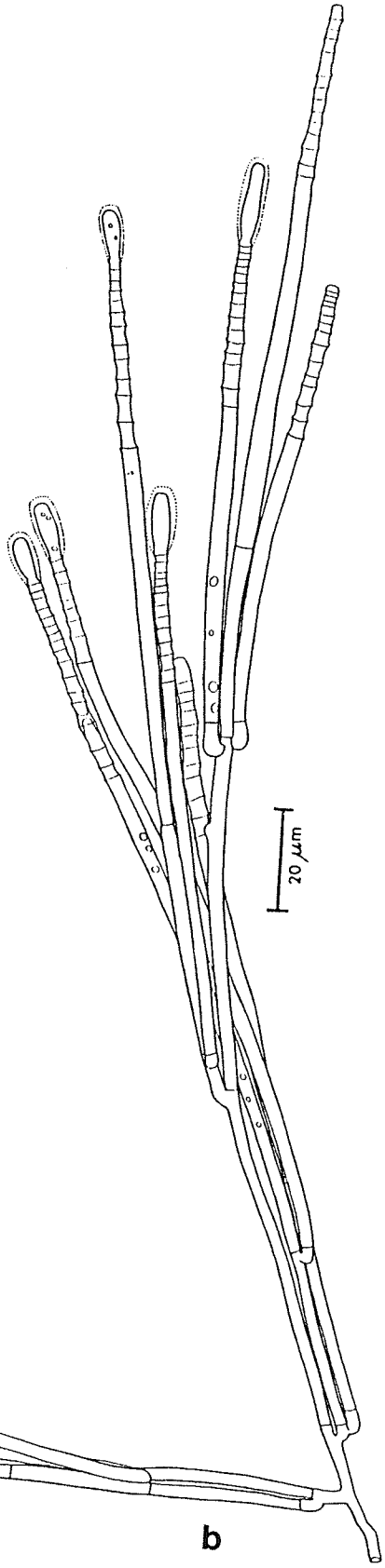
c. Conidiophore with conidia adhering to the annellation zone.

Isolates as illustrated: 4I: c.
14A: b.

a



c



b

Fig. 33B. Taxonomic genus 1, species 1.
(isolates: 4I, 14A)

a. A moderately complex conidiophore.

b. A simple conidiophore.

c. Annellides; the lateral branches begin producing conidia much in arrears of the main conidiophore branch. When initially delimited, a conidium initial is subtended by a slight constriction in the original annellide («-), and the first-formed annellations are usually longer than those formed later.

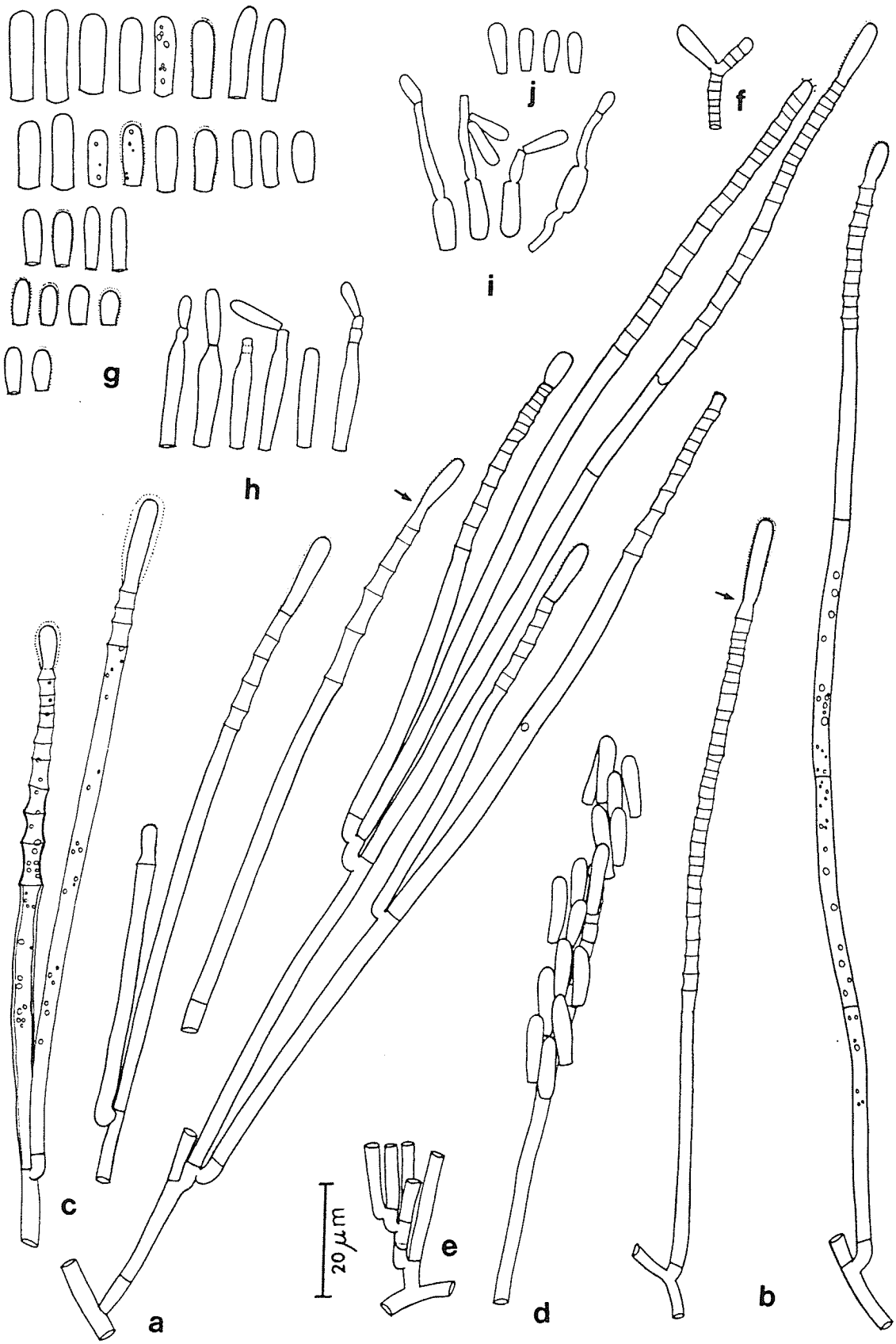
d. Simple conidiophore produced by the hyphae submerged in the medium, its annellation zone surrounded by the conidia it produced.

e. Details of the most complex basal branching seen at any branch point observed.

f. A portion of an annellation zone where a conidium did not secede, but was simply displaced laterally.

g-j. Conidia; (g) annelloconidia; (h,i) primary conidia producing secondary conidia; (j) secondary conidia.

Isolates as illustrated: 4I: b, i, j.
14A: a, c, d, e, f, g, h.


a
b
c
d
e
f
g
h
i
j
20 µm

another are mutually inhibitory. Hyphae hyaline, smooth-walled, and 1.5 - 3.2 μm in diameter. Chlamydospores were not seen. Conidiophores annellidic; macronematous or semi-macronematous; hyaline and smooth-walled. Macronematous conidiophores, which initially arise as a single hyphal element, are 220 - 400 μm long (Fig. 33A. b), and produce up to 5 series of branches, the first series usually arising basally. All branches curve sharply immediately after initiation and grow parallel to the stem; each branch arises immediately below a septum in the element from which it originates and has a septum just above its base (Fig. 33B. a,e). The main stem and branches are each terminated by a percurrently proliferating conidiogenous cell. These branched conidiophores occur either singly or are loosely aggregated into clavate, or occasionally broadly cylindrical, bundles without a clear distinction apparent between the stem and the conidiogenous area (Fig. 33A. a). Semi-macronematous conidiophores develop from hyphae both in the medium and on the surface; these consist of a short stem bearing 1 - 2 terminal conidiogenous cells (Fig. 33B. b); intermediate forms between these and the more complex macronematous conidiophores also exist. Conidiogenous cells are annellidic and integrated or, rarely, discrete; hyaline and smooth-walled; cylindrical or narrowest at the base, but gradually broadening and becoming cylindrical above; 25 - 90(100) x 2.5 - 3.4(4.0) μm. The conidia are delimited from the full width of the apex and each conidium initial adds 0.5 - 7.0 μm to the length of the annellation zone. In aging conidiogenous cells, the annellation zone, or its upper portion, is filled with cytoplasm but the cell appears vacuolate; the

longest annellations are formed first, but subsequent ones are shorter (Fig. 33B. a,c). Annellation zones up to 150 μm in length were present on aging cells; these reflect production of over 60 conidia (110 μm long: produced 60 conidia). Annelloconidia aggregated in slimy masses or adhered individually to the sides of the annellation zone of the conidiogenous cells (Fig. 33A. c). These conidia are 1-celled, hyaline, and smooth-walled; oblong or occasionally short-clavate, with an obtuse apex and truncate base which virtually lacks a frill; 6.5 - 16(18.5) x 2.5 - 4.2(4.4) μm, the base being 2.0 - 3.7 μm wide (Fig. 33B. g). The conidia often germinate and produce a short conidiogenous cell (Fig. 33B. h,i), presumably annellidic, from which smaller secondary conidia develop. Such conidia are clavate, with a rounded apex and narrow truncate base. The secondary conidia are 6.8 - 8.2 x 2.4 - 2.9 μm, the base being 1.7 - 1.9 μm wide (Fig. 33B. j).

HOST: Pinus contorta Dougl. ex Loud.

CULTURES EXAMINED: Canada: 4I, 14A, isolated from P. contorta, Taylor Lake Hiking Trail, Banff National Park, Alberta, collected 23 September 1987.

The two isolates differ slightly in growth rate and colony morphology. In darkness 14A is faster growing and produces less compact colonies with more pronounced feathery patterns, particularly in aging colonies. However, in alternating light and darkness growth was much

slower in 14A, and it then closely resembled colonies of isolate 4I; the latter did not show differential growth rates related to degree of illumination. The slimy conidial masses consisted mainly of annello-conidia, and no budding cells were present. However, a small proportion of the primary conidia in these masses produced secondary conidia from pegs or proliferating conidiogenous cells; these are presumed to be annellidic, but they are not very distinct (Fig. 33B. h,i). On aging, an increasing number of the conidia in these masses germinate.

The annellations are most easily observed in old, vacuolate conidiogenous cells; when cytoplasm is present in the annellation zone, the annellations are obscured. Occasionally, conidia remain attached to the conidiogenous locus, having failed to secede (Fig. 33B. f), and this causes a bending in the annellation zone. However this is different from the situation where seceded conidia sometimes remain adherent to the annellation zone after secession (Fig. 33A. c), presumably as the result of a mucilaginous material either on the conidia or the walls of the proliferated conidiogenous cells. When viewed with interference contrast optics, both conidium initials and some conidia have a thin halo surrounding them; this may be due to the presence of mucilaginous material.

No genus was found which would accommodate this organism. Filosporella annelidica (Shearer & Crane) Crane & Shearer (1977) (Shearer & Crane 1976) does have conidiophores somewhat similar to this species, but it differs in producing multiseptate, curved to sigmoid scolecospores and possessing pigmented hyphae.

Recently, Blackwell & Malloch (1989) described the anamorph of a Pyxidiophora sp. as being hyaline and synnematous, with 200 - 300 μm long conidiophores. The conidia, which aggregated in slimy masses, were produced on percurrently proliferating conidiogenous cells, with long annellations; the conidia were oblong or slightly broader at the apex and measured 6 - 10 x 2.5 - 4.0 μm. While the new species seems to resemble this anamorph in the mode of conidiogenesis and in the basic shape of the conidia, the two clearly represent different species. This became clear after examination of a prepared slide of the Pyxidiophora sp. kindly supplied by D. Malloch. The main differences were: (1) the conidia were shorter than those produced by isolates 14A and 4I; (2) the synnemata were cylindrical with the base as wide as the apex, and the hyphae of the stem rarely branch, but bear the long, cylindrical conidiogenous cells at the apex; and (3) on the rare occasions when the hyphae of the stem branch, the method of branching was quite different from that of the two isolates.

These isolates will probably best be be accommodated by recognizing them as representing a unique genus because of the differences between them and either of the two species which shared some of their morphological characteristics.

Verticillium Nees, Syst. Pilze Schw. 57. 1816

=Acrostalagmus Corda, Icon. Fung. 2:15. 1838

=Pochonia Batista & Fonseca, Publ. Inst. Micol. Recife, 462. 1965

Type species: Verticillium luteo-album (Link: Fr.) Subramanian (=V. tenerum (Nees: Fr.) Link, the anamorph of Nectria inventa Pethybr. Teleomorphic genera: Cordyceps (Fr.) Link, Nectria Fr., Nectriopsis Maire, Hypomyces (Fr.) Tul. & C. Tul., Torrubiella Boud.

This genus is characterized by its hyaline hyphae and moderate growth rates on culture media. The phialophores are verticillately branched, and bear aculeate to slender flask-shaped phialides in whorls along most of their length. The collarettes are inconspicuous, and the 1-celled and hyaline or brightly coloured phialoconidia aggregate in small slimy drops, or are occasionally catenate (Domsch et al. 1980).

The genus Verticillium has been divided into four sections plus a residual group whose relationships are not yet clear (Gams in Gams & van Zaayen 1982; Gams 1971): 1. Section Verticillium with a single species, V. luteo-album (Link: Fr.) Subramanian (=V. tenerum (Nees: Fr.) Link), the anamorph of Nectria inventa Pethybr. which has erect phialophores that are coloured an intense orange-brown, and bear conidial masses of the same colour. 2. Section Nigrescentia W. Gams (type species: V. nigrescens Pethybr.) which consists of species with erect and sometime darkly pigmented phialophores and resting structures, e. g. hyphae (usually inflated), chlamydospores, or microsclerotia. 3.

Section Prostrata W. Gams (type species: the Verticillium anamorph of Cordyceps militaris (L.) Link) which consists of species that develop white or yellowish floccose colonies, and have at least partly prostrate phialophores which, when erect, are thin-walled and resemble the aerial hyphae. The phialides are verticillate or solitary, and arise chiefly from prostrate hyphae. Some species have hyaline dictyochlamydospores. The teleomorphs belong to Cordyceps and Torrubiella (Clavicipitaceae). 4. Section Albo-erecta W. Gams (type species: V. fungicola (Preuss) Hassebr.) which consists of species with erect phialophores that differ from the aerial hyphae in wall thickness and are repeatedly verticillate. Colonies are white to yellowish, densely floccose, and most are colourless in reverse. Dark resting structures are absent and chlamydospores are usually absent. The teleomorphs are of the genus Nectriopsis (Hypocreaceae). 5. A residual group of species whose colonies are of pink to orange hues, which is further divisible into very fast or very slow growing subgroups. The relationship of the species in group five to other Verticillium species as well as the general taxonomy of the genus is currently under further investigation, but has apparently not yet been completed (Gams & van Zaayen 1982).

The arrangement of the lateral branches and the production of slender phialides in whorls is central to members of the genus Verticillium. The extent to which the species produce their phialides in whorls, and the degree of differentiation of the phialophores are, however, variable. Gams (1971) erected the section Prostrata for species which produced only slightly differentiated, prostrate

phialophores and phialides arising singly and in pairs as well as in whorls. Since such prostrate phialophores can be quite long, only the presence of a terminal whorl of phialides really distinguishes them from the vegetative hyphae. This study follows the example of Gams (1971), who treated the phialides as if they originated directly on the hyphae, or on short lateral branches, while the actual length of the phialophores was not given. At that time Gams retained all other Verticillium species within the section Verticillium sensu stricto. Later Gams, in Gams & van Zaayen (1982), defined the sections Nigrescentia and Albo-erecta, assigned the type species of the genus to the section Verticillium, and noted the presence of the residual group of species which could not then be accommodated in any of these four sections.

Some members of the section Nigrescentia are well known plant pathogens, but others are soil saprophytes. The members of the section Albo-erecta are primarily fungicolous, but V. luteo-album (section Verticillium) is commonly found on various organic remains, while species of the section Prostrata which are mostly saprophytes, are found in soils and on chitinous substrata, or are entomogenous and fungicolous.

Verticillium species differ from those of Gliocladium and Clonostachys Corda in lacking appressed penicillate phialophores and having straight symmetrical conidia, and from Sarocladium W. Gams & Hawksworth by having more regular whorls of phialides that are never appressed. Verticillium species of the section Prostrata resemble members of

Acremonium section Albo-lanosa, except that the latter produce only solitary phialides.

Hawksworth et al. (1983) reported the number of Verticillium species as 40, and since then at least four additional species have been described. In addition, several ascomycete species have Verticillium anamorphic states which, may or may not have anamorph names (Gams 1971; Gams & van Zaayen 1982).

Although many species of Verticillium are well defined and have been thoroughly studied, others are either less well known or are not clearly delimited.

Verticillium lamellicola (F.E.V. Smith) W. Gams, Cephalosporium-artige Schimmelpilze (Hyphomycetes), 183. 1971 Fig. 34. a-g.

≡Cephalosporium lamellaecola F.E.V. Smith, Trans. Br. Mycol. Soc. **10**:93. 1924

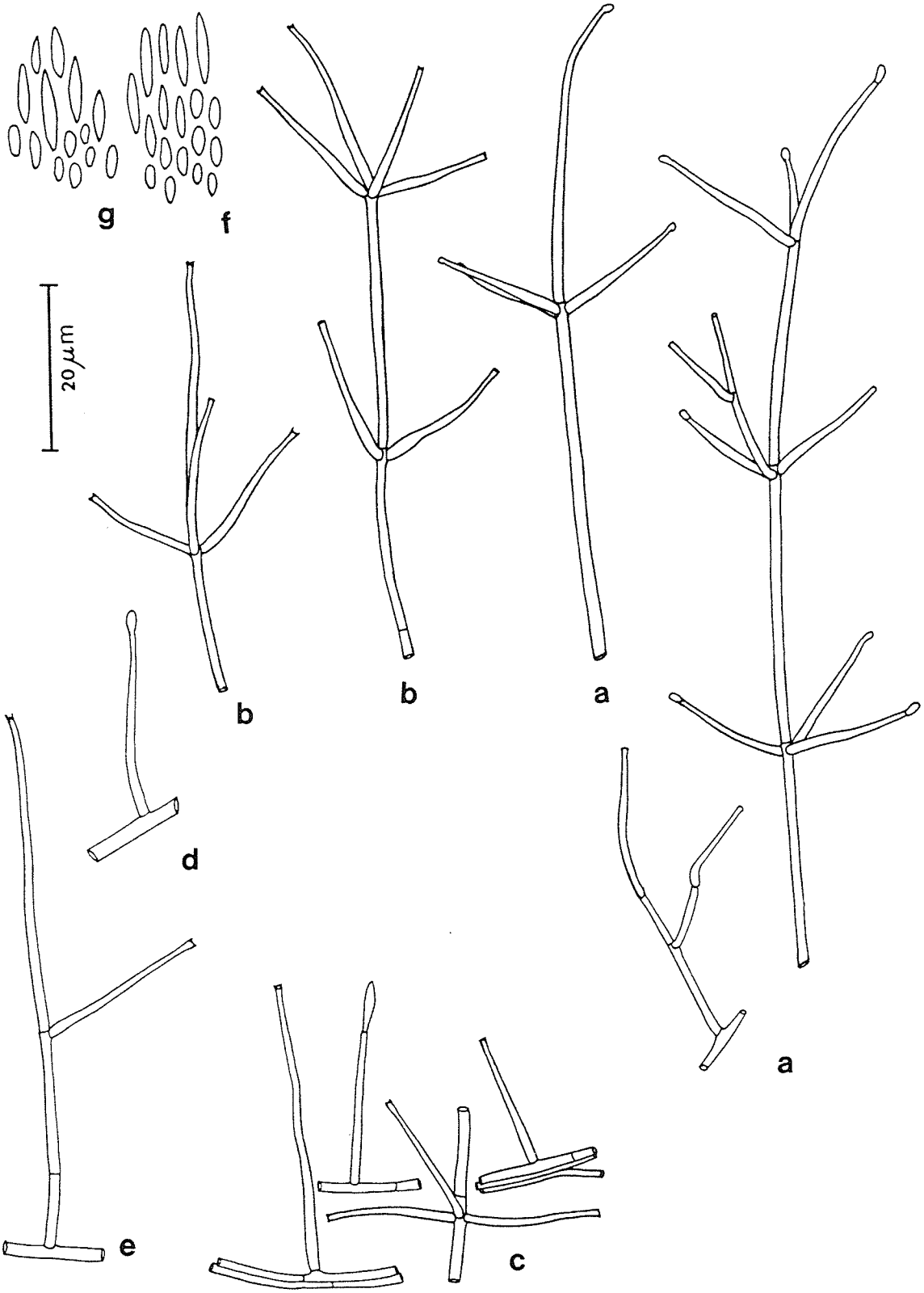
Colonies attaining a diameter of 30 - 36 mm in 12 days at 20°C in darkness on MEA.YE. White (2.5Y $^{8}/_{0}$), floccose and dense, but thinning towards the margin, and often becoming white (2.5Y $^{8}/_{2}$) on aging. Sporulation occurs throughout the colonies, with the conidia aggregating in small white droplets at the apices of individual phialides. In reverse, colonies are pale yellow (2.5Y $^{8}/_{4}$), but gradually become brown to dark brown (7.5YR $^{4}/_{2}$ to $^{4}/_{4}$) in the centre, and sometimes in sectors, but strong brown to very pale brown (7.5YR $^{5}/_{6}$ to $^{7}/_{4}$, $^{8}/_{4}$) towards the margin. Odour indistinct. An exudate is present as small clear drops. Small crystals may be present in the medium amongst the hyphae. Hyphae are smooth-walled; the aerial hyphae are hyaline and 1.0 - 2.0 µm in diameter; the submerged hyphae are hyaline or pale yellowish-brown, up to 2.5(3.0) µm in diameter, and sometimes filled with an oily substance; when funiculose (the number of strands produced differs between isolates), strands are up to 10 µm in diameter and comprised of 1.0 - 2.0 µm wide hyphae. Chlamydospores were not seen. Phialophores micronematous, hyaline, and smooth-walled, with the phialides arising in terminal whorls of (2)3 - 5 (Fig. 34. a,b), or rarely singly, occasionally subtended by a basal cell (short branch); the hyphae bearing the phialides are quite long and resemble the vegetative aerial hyphae in

Fig. 34. Verticillium lamellicola (F.E.V. Smith) W. Gams (isolates: 52', 64, 65b, 70bii, 110ai)

a-e. Phialophores.

f-g. Phialoconidia; dimorphic.

Isolates as illustrated: 52': d.
64: c.
65b: e.
70bii: b, g.
110ai: a, f.


g
f
20 µm
b
b
a
a
d
e
c

width and wall-thickness, usually with several whorls of 2 - 4 phialides or single phialides arising along their length (Fig. 34. a-e). Conidiogenous cells monophialidic; discrete or integrated; hyaline and smooth-walled; acicular; the central phialide in each terminal whorl is usually longer than the lateral ones; 15 - 45 x 0.9 - 1.5 μm, most being 1.0 - 1.3 μm wide and tapering to 0.6 - 0.8(0.9) μm at the apex; collarettes are indistinct or lacking; some phialides are narrowest approximately 1 μm below the apex. Phialoconidia aggregate in small slimy drops; 1-celled, hyaline, and smooth-walled; dimorphic, either (1) fusiform with sharply pointed ends, (4.0)4.5 - 8.5(10.5) x (1.0)1.2 - 1.6 μm (Fig. 34. f,g, above), or (2) short oblong-elliptical to short oval-elliptical; 2.4 - 4.0 x 1.2 - 1.6 μm (Fig. 34. f,g, below).

HOSTS: Cupressus macrocarpa, Pinus elliotii, Pinus radiata

CULTURES EXAMINED: **New Zealand:** 110ai, isolated from C. macrocarpa, Compartment 14, Woodhill State Forest, Auckland, collected 25 May 1982; 70bii, isolated from P. elliotii, Camp Gully Rd, Tairua State Forest, Coromandel, collected 21 May 1982; 52', isolated from P. radiata, south end of Tairua State Forest, Coromandel, collected 21 May 1982; 64 & 65b, isolated from P. radiata, Pokohino Rd, Tairua State Forest, Coromandel, collected 21 May 1982.

This species was originally described from England where it was

assumed to occur widely on the gills of the cultivated mushroom without causing extensive damage until late in its growth when its mycelium covered and blackened the host's gills (Smith 1924). It has also been isolated from many other different fungi, as well as other substrata, e.g. plant parts, hay, air, soils, collembola, and humans in Europe, North America, Nigeria, and Malaysia (Arnebrant et al. 1987; Gams 1971; Visser et al. 1987). Rudakov (1978) considered V. lamellicola to be necrotrophic, but the results of Kuter's (1984) investigation of its ability to parasitize isolates of Rhizoctonia solani Kühn in vitro were inconclusive.

No earlier records of this species from New Zealand were located.

Gams (1971) corrected the spelling of V. lamellicola, and assigned it to the section Prostrata. He augmented Smith's (1924) description by stressing the dimorphic nature of the conidia and the whorled arrangement of the phialides on the phialophores.

There was no significant difference between the five New Zealand isolates, and all agreed with Gam's description except they produce longer phialides (measuring up to 45 μm) in the central position of the terminal whorls. However, the majority do measure 15 - 35 μm as reported by Gams.

V. lamellicola is one of the Verticillium species with fusiform conidia; conidia which are thinner than those of V. fusisporum W. Gams, a species whose colonies are red in reverse. And it has straighter and thinner conidia with sharper ends than V. psalliotae Treschow. However as Gams (1971) points out, variation does exists amongst isolates of

V. lamellicola, and some may produce conidia with less sharply pointed ends, or conidia that are slightly curved, thus making the distinction between it and V. psalliotae difficult. However, it was not difficult to distinguish between the New Zealand isolates of V. lamellicola and V. psalliotae because isolates of the latter produced markedly larger conidia than those of the former.

V. lamellicola is a fungicolous species with agarics as its major substrata (Gams 1971; Hawksworth 1981). It does not appear to have previously been associated with bark beetles or stained coniferous wood. It may have been parasitizing one or more of the other fungi which were also obtained from these wood samples, but as it was one of the more frequently isolated species (excluding members of the Ophiostomataceae) during the New Zealand surveys, it may well be of common occurrence in such sites.

Verticillium lecanii (A. Zimmerm.) Viégas, Rev. Inst. Café Sao Paulo 14:754. 1939 Fig. 35. a-f.

≡Cephalosporium lecanii A. Zimmerm., Korte berichten uit's Lands Plantentuin, 1898.

For a full synonymy see Gams (1971).

Teleomorph: Torrubiella confragosa Mains (not proven in pure culture)

Colonies attaining a diameter of 30 - 50 mm in 12 days at 20°C in darkness on MEA.YE. White (2.5Y $^{8}/_{0}$); floccose and ranging from dense to fluffy; sporulation sparse to abundant, the conidia aggregating in white droplets at the apices of individual phialides. In reverse, colonies are white (2.5Y $^{8}/_{0}$), but may become strong brown (7.5YR $^{6}/_{6}$) in small areas, or yellow (isolate 136b) (at first 2.5Y $^{8}/_{2}$, $^{8}/_{8}$ becoming 10YR $^{7}/_{8}$). Odour indistinct or lacking. Exudate present as small to medium-sized clear drops. Crystals may be present in the medium surrounding the colony margin, but usually are only present amongst the submerged hyphae. Hyphae hyaline and smooth-walled; 0.9 - 2.5 µm in diameter; the submerged hyphae are usually filled with an oily substance, and are sometimes slightly inflated and up to 3.5 µm wide. Phialophores micronematous to semi-macronematous; hyaline and smooth-walled; phialides arising singly or in whorls of up to 5 (Fig. 35. a-d); both the individual phialides and the whorls are occasionally borne on short branches; such branches bearing phialides may also be a part of a whorl (Fig. 35. b). The hyphae bearing the phialides resemble the

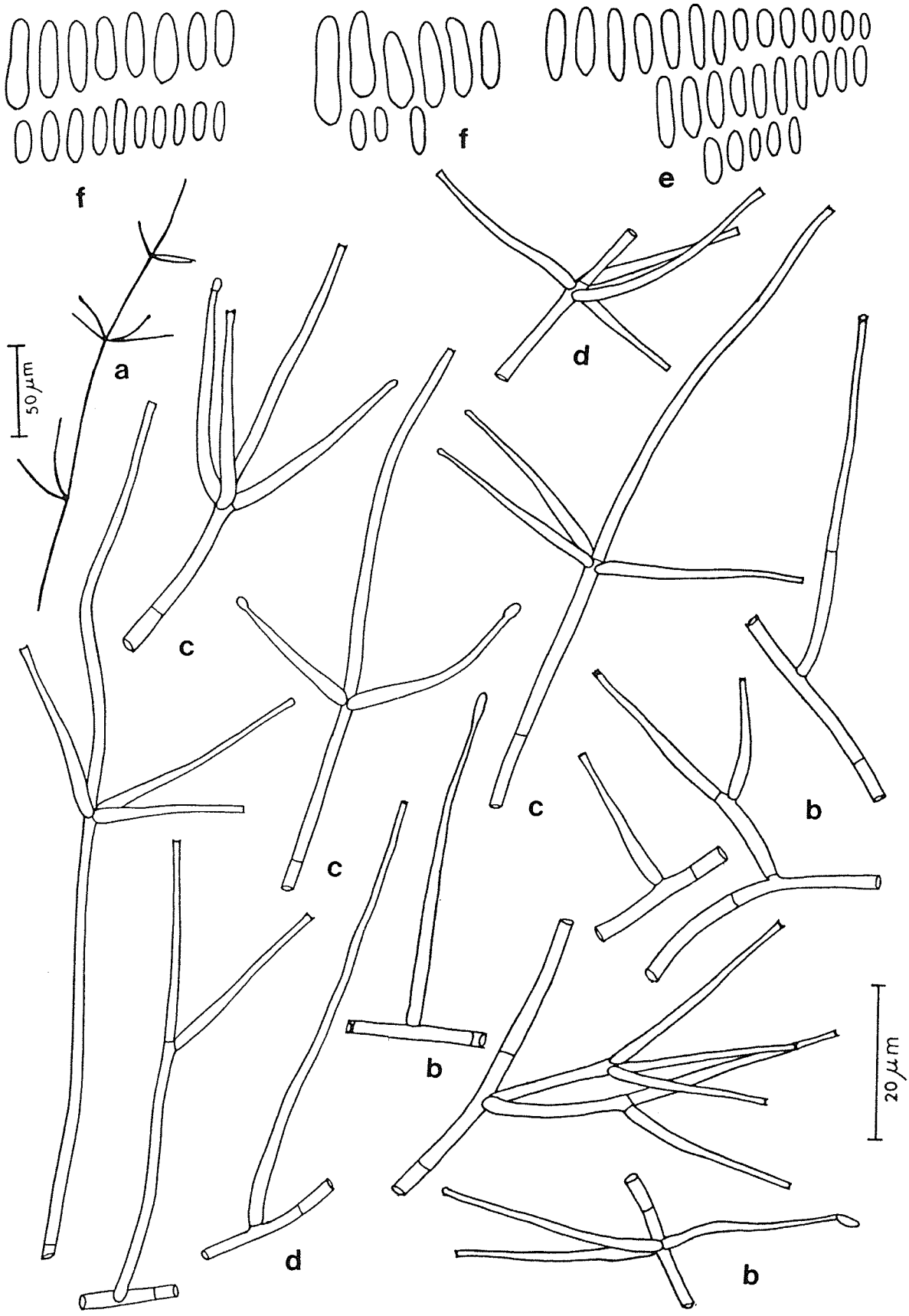
Fig. 35. Verticillium lecanii (A. Zimmerm.) Viégas (isolates: 136aiii, 136b, 141f)

a. Phialophore.

b-d. Phialophores or portions thereof.

e-f. Phialoconidia.

Isolates as illustrated: 136aiii: d.
136b: a, c, f.
141f: b, e.


f
f
e
a
d
50 µm
c
c
c
b
b
d
b
20 µm

vegetative aerial hyphae in width and wall-thickness, but usually have either several whorls of up to 4 phialides or single phialides arising along their length. Conidiogenous cells monophialidic; discrete or integrated; hyaline and smooth-walled; acicular; 15 - 50 x 1.2 - 1.8(2.3) μm tapering to 0.6 - 1.0(1.2) μm at the apex; collarette indistinct or lacking. The phialoconidia aggregate in small slimy drops; 1-celled, hyaline, and smooth-walled; cylindrical, oblong-elliptical, or some conidia are oval or irregularly clavate; (3.2)4.0 - 11.0(13.5) x (1.3)1.5 - 2.4 μm (Fig. 35. e,f), except for the clavate conidia that are up to 2.8(3.4) μm wide (Fig. 35. f); both ends are rounded.

HOST: Podocarpus sp.

CULTURES EXAMINED: **New Zealand:** 136aiii, 136b, and 141f, isolated from Podocarpus sp., near Minginui, Urewera National Park, Taupo, collected 11 June 1982.

As treated by Gams (1971), the name V. lecanii is probably being applied to a very heterogeneous assemblage of entities (Domsch et al. 1980), which may not represent a single species. Many of the entities Gams united under this name in the section Prostrata produced conidia and phialides of different sizes, but overlapping in range. And as the other morphological characters used to describe the synonymized species were often of questionable value, Gams elected to lump many former

species under V. lecanii. The validity of such a broadly defined species has been questioned (Hawksworth 1981), but final resolution of the problem of species delimitation in this aggregation will require the use of other than morphological criteria.

As defined, V. lecanii is one of the commonest entomogenous hyphomycetes and is pathogenic to the insects. It is of worldwide distribution (Domsch et al. 1980), and it parasitizes all of the developmental stages of insects of all major groups, as well as spiders (Brady 1979). Petch (1925) summarized the previous records of Cephalosporium (Acrostalagmus) lecanii A. Zimmerm., and estimated it had been observed as early as 1861 destroying Lecanium scales on coffee trees in Sri Lanka. For numerous records of V. lecanii in relation to insects see Petch (1925, 1931a, 1931b, including various synonyms), Gams (1971), Leatherdale (1965), Hall (1976), Kuter (1984), and Evans & Samson (1982).

The potential use of V. lecanii as an insect biological control agent has long been recognised, and it has been so employed successfully with a number of insects (Brady 1979; Hall 1980b). An unique outcome of such applications, however, was the report of Spencer & Atkey (1981) who, in attempting aphid control with this fungus, found it also successfully infected the carnation rust fungus, Uromyces dianthi (Pers.) Niessl, and Puccinia recondita Rog. ex Desm. the fungus causing leaf rust of wheat, thereby demonstrating the ability of a single isolate to attack both fungi and insects. Thus this species has been suggested as a possible biological control agent of both insect pests

and fungal diseases of the same host (Hall 1980a). However, because of the broad spectrum of organisms V. lecanii attacks, its application as a pesticide should be very carefully undertaken (Evans & Samson 1982).

Barson (1976) isolated V. lecanii from elm bark around dead adults of the large elm beetle (Scolytus scolytus (F.)), as well as from diseased larvae. And although under laboratory conditions he found this fungus was highly pathogenic to these larvae, under field conditions it caused relatively low larval mortality. Another report of V. lecanii from a bark inhabiting insect is that of Carroll (1987) who listed it as one of the prevalent fungi associated with unhatched gypsy moth eggs.

Primarily entomogenous (Hawksworth 1981), V. lecanii is also fungicolous, and has been isolated from members of the Urediniomycetes (Allen 1982; Gams 1975; Garcia Acha et al. 1965; Hall 1980b; McKenzie & Hudson 1976; Spencer 1980; Spencer & Atkey 1981; Uma & Taylor 1987), and Ascomycetes (Gams 1971; Hall 1980b; Raghavendra Rao & Pavgi 1978), as well as a variety of other substrata (Anon 1987b; Arnebrant et al. 1987; Bissett & Parkinson 1979; Clarke & Hill 1981; Domsch et al. 1980; Dunn & Baker 1983; Gams 1971; Kuter 1984; Visser et al. 1987). Petch (1925) lists one collection of V. lecanii on a scale insect on Citrus from New Zealand.

To date, only one possible teleomorph, Torrubiella confragosa Mains (Clavicipitales) has been suggested for this fungus (Evans & Samson 1982). However, this was based on association of the fungi on a common substratum, and not proven culturally.

Although the conidia of the three New Zealand isolates overlap the

size range(s) given by Gams (1971), many were certainly longer than he records. Similarly the New Zealand isolates produced terminal phialides which were far longer than noted by Gams. Isolate 136b regularly produced conidia which were broader at one end, and it also produced a yellow pigment. The rather broad range of growth rates reflects the difference between isolates, 141f being the slowest and 136aiii the fastest growing. Such variation clearly suggests that more than one discrete entity could be included under the name V. lecanii as it has been applied to these isolates.

V. lecanii differs from V. fungicola (Preuss) Hassebr. (section Albo-erecta) in having undifferentiated phialophores, and from the other species of the section Prostrata by producing straight, cylindrical to oblong-elliptical conidia on rather long but thin phialides.

The three isolates studied were from two wood samples of a Podocarpus sp. taken in the same locality. They were a part of a rather diverse fungal population isolated from these samples. Whether they are entomogenous, pathogenous to the insects, or fungicolous is not known from this study, but members of this species are able to decompose cellulose, chitin, pectin, starch, are strongly proteolytic, and can produce the insecticidal cyclo-depsipeptide bassianolide (Domsch et al. 1980). However, based on Barson's (1976) findings, this fungus could have been attacking the bark beetles, or their larvae, which were present in the samples.

Verticillium leptobactrum W. Gams, Cephalosporium-artige Schimmelpilze (Hyphomycetes), 194. 1971 Fig. 36. a-e.

Colonies attaining a diameter of 34 - 36 mm in 12 days at 20°C in darkness on MEA.YE. White (2.5Y $^{8}/_{0}$ to $^{8}/_{2}$), but sometimes with pale yellow (2.5Y $^{8}/_{4}$) areas; floccose and rather dense; often with a reddish yellow (5YR $^{7}/_{6}$ to 7.5YR $^{7}/_{6}$) margin where the reddish-yellow tinted surface of the medium is sparsely covered with mycelium. The conidia form delicate chains which can be difficult to observe. The colonies have a strong tendency to produce sectors that differ in coloration and amount of aerial hyphae. In reverse, colonies are reddish yellow, red, pale yellow or very pale brown to yellow (5YR $^{7}/_{8}$, 10R $^{5}/_{8}$, 2.5Y $^{8}/_{4}$ or 10YR $^{7}/_{4}$ to $^{7}/_{6}$), often forming sectors that are darker or paler than the rest of the colony. Odour indistinct. An exudate is present as small to medium sized clear drops. Hyphae hyaline and smooth-walled; 0.7 - 3.5 µm in diameter, except for some of the submerged hyphae that are irregularly inflated and filled with an oily substance, and up to 7.3 µm in diameter (Fig. 36. a). Chlamydospores were not seen. Phialophores micronematous to semi-macronematous; hyaline and smooth-walled; phialides arising either singly (Fig. 36. b) or in whorls directly from the aerial hyphae, or 1 - 2 phialides arising terminally from 1- or 2-celled lateral branches that are usually of the same width as the phialide bases (Fig. 36. c). Conidiogenous cells monophialidic, hyaline, and smooth-walled; integrated or discrete; acicular; (8.0)12.0 - 23.0 x (1.0)1.3 - 1.8(2.4) µm tapering to 0.6 - 0.9 µm at

Fig. 36. Verticillium leptobactrum W. Gams
(isolate: 105b'')

a. Inflated hyphal cells.

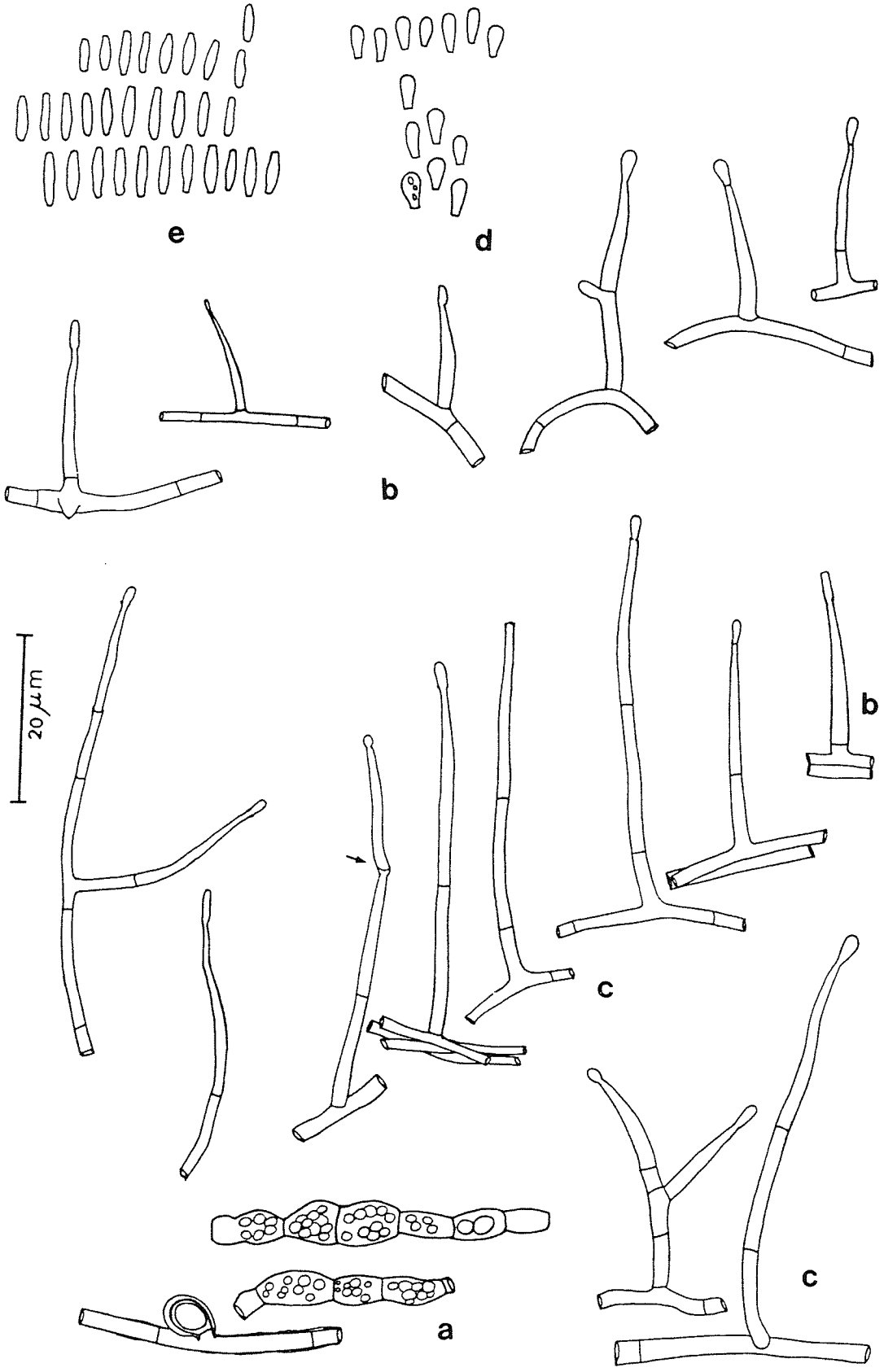
b. Single phialides.

c. Phialophores with phialides borne on a short branch; secondary proliferated phialide («-).

d. Short-clavate to obpyriform, first-formed conidia.

e. Cylindrical to fusiform conidia.

Isolate as illustrated: 105b'': a-e.


e
d
b
20 µm
b
c
c
a

the apex; collarettes lacking. Secondary phialides occasionally proliferated terminally through the apex of the primary ones (Fig. 36. c «-). Phialoconidia catenate, 1-celled, hyaline, and smooth-walled; dimorphic: The first conidium produced by each phialide is short-clavate to obpyriform; 3.2 - 4.7 x 1.4 - 2.0(2.4) μm with broadly rounded apices and thin, truncate bases (Fig. 36. d). All the other conidia are cylindrical-fusiform, and sometimes slightly broader towards one end; 3.5 - 6.0(6.5) x 0.9 - 1.4(1.6) μm, both ends narrowly truncate (Fig. 36. e).

HOST: Pinus radiata

CULTURE EXAMINED: **New Zealand:** 105b'', isolated from P. radiata, off Highway 25, Whangapoua State Forest, Coromandel, collected 19 May 1982.

The description of V. leptobactrum was based on an isolate from decaying wood in Poland by Gams (1971) who also reported its isolation from members of the Hymenomycetes, and the humus layer of forest soils. This species has also been recovered from collembola, nematode cysts, sphagnum, and from sori of the coffee leaf rust fungus Hemileia vastatrix Berk. & Broome (Anon 1987a; Anon 1987b; Visser et al. 1987); it is known from Europe, North America, and Brazil.

This appears to be the first record of V. leptobactrum from New Zealand.

V. leptobactrum belongs to the section Prostrata because the

phialides arise from hyphae that do not differ from the vegetative aerial hyphae. An appreciable number of the conidia produced by this isolate are broader, and some are longer, than the measurements given in the original description (i.e. 4.3 - 5.0 x 0.7 - 1.0 μm). However, based on the orange reverse of the colonies, and the clavate nature of the first formed conidium from a phialide, which differs markedly from the shape of subsequently formed conidia, this isolate clearly belongs in V. leptobactrum.

Of those species which belong to the section Prostrata and produce their conidia in chains, V. leptobactrum appears most similar to V. insectorum (Petch) W. Gams. The latter is the only other species with truncate, cylindrical-fusiform conidia, but it does not produce dimorphic conidia nor an orange-coloured pigment.

V. leptobactrum appears to be fungicolous as well as saprophytic in litter and on decaying wood. As it was isolated only once in the New Zealand surveys, it is unlikely to be a common inhabitant of the bark beetle galleries. However, since it is very delicate, it could easily be overlooked during isolation and purification of the isolates from the wood samples.

Verticillium psalliotae Treschow, Dansk bot. Ark. 11:7. 1941

Fig. 37. a-f.

=Cephalosporium curtipes Sacc. var. uredinicola Sukap. & Thirumalachar, Bull. Torrey Bot. Club 93:307. 1966

Colonies attaining a diameter of 25 - 40 mm in 12 days at 20°C in darkness on MEA.YE. White (2.5Y $^{8}/_{0}$ to $^{8}/_{2}$); floccose, and sometimes fluffy; sporulation occurs throughout the aerial mycelium with the conidia aggregating in white droplets at the apices of individual phialides. In reverse, colonies are pale yellow (2.5Y $^{8}/_{4}$) or become light yellowish brown, and light brown to reddish yellow (10YR $^{6}/_{4}$, and 7.5YR $^{6}/_{4}$ to $^{6}/_{6}$) in the central areas on aging. Odour lacking. Exudate is present as small to medium-sized clear drops which are sometimes pink in aging colonies. Small rectangular crystals are present outside of the colony margin, and small crystals occur in the medium amongst the hyphae. Hyphae hyaline and smooth-walled; (0.9)1.4 - 3.5 µm in diameter; the submerged hyphae, which may become filled with an oily substance, are sometimes slightly inflated and up to 5.5(6.5) µm wide. Chlamydospores were not seen. Phialophores micronematous to semi-macronematous; hyaline and smooth-walled; phialides arising in terminal whorls of 2 - 4, but rarely single; occasionally subtended by a basal cell (Fig. 37. a,b). The hyphae bearing the phialides resemble the vegetative aerial hyphae in width and in wall-thickness, but bear a few whorls of up to 3 phialides or single phialides along their length. Conidiogenous cells monophialidic; discrete or integrated; hyaline and

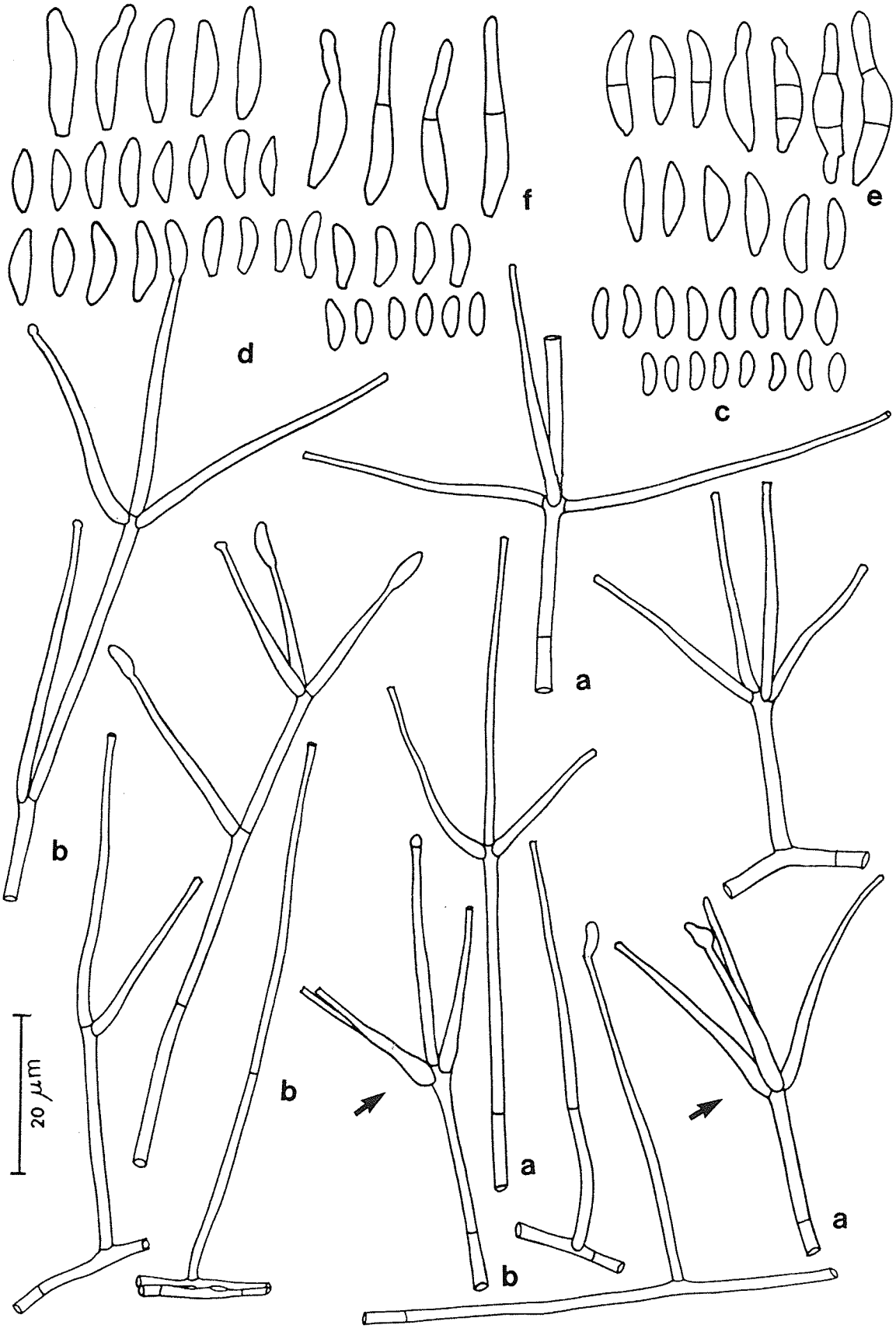
Fig. 37. Verticillium psalliotae Treschow
(isolates: 89di, 100c)

a-b. Phialophores; note phialides which are inflated at the base («-).

c-d. Phialoconidia.

e-f. Germinating conidia.

Isolates as illustrated: 89di: a, c, e.
100c: b, d, f.


f
e
d
c
a
b
b
a
a
b
20 µm

smooth-walled; acicular or sometimes slightly inflated at the base (Fig. 37. a,b «-), but tapering to a long thin neck; 16 - 50 x (1.0)1.5 - 1.8 μm wide at the base, but when inflated they are up to 2.4 μm wide; both types of conidiogenous cells tapering to 0.7 - 1.1 μm at the apex and the thinner phialides are usually narrowest approximately 1 μm below their apices; collarettes indistinct or lacking. Phialoconidia aggregate in small slimy drops; 1-celled, hyaline, and smooth-walled; dimorphic. The larger conidia are short-fusiform and slightly curved to crescent shaped with thin, blunt ends, while the smaller conidia are cylindrical and sometimes slightly curved to cylindrical-fusiform with a truncate base. The conidia are (4.0)5.0 - 12.5(13.5) μm long and 1.6 - 3.2 μm wide (Fig. 37. c,d); 1-septate conidia measuring 10.5 - 13.5 x 2.5 - 3.3 μm are present, and similar germinating 1 - 2 septate conidia (Fig. 37. e,f) are usually also present.

HOST: Pinus radiata

CULTURES EXAMINED: **New Zealand:** 89di & 100c, isolated from P. radiata, off Road 41, Whangapoua State Forest, Coromandel, collected 19 May 1982.

Described by Treschow in 1941, V. psalliotae is an important pathogen of the cultivated mushroom Agaricus brunnescens (Brady & Waller 1976). It is clearly a broadly-based fungicolous species (Gams 1971; Dayal & Barron 1970) although Hawksworth (1981) considers species of Agaricus to be its primary hosts and, based on Rudakov's (1978) report,

it is a facultative biotroph. However, it is not restricted to fungi, having also been isolated from scale insects, ticks, soil mites, collembola and their exuviae, forest soils, leaf litter, and from stored wood chips (Anon 1975; Arambarri et al. 1981; Gams 1971; Gochenaur 1978; Hoover-Litty & Hanlin 1985; Kuter 1986; Mankau 1968; Samsináková et al. 1974; Visser et al. 1987). Indeed it appears to be cosmopolitan in distribution.

Although V. psalliotae has been isolated from soil in Australia (Domsch et al. 1980), this may be the first record of it from New Zealand.

V. psalliotae belongs to the section Prostrata, but based on the range of variation reported in the literature, it may represent an aggregate species. However, the morphological criteria employed in delimiting this species are such that it is impossible to group various isolates into more narrowly defined taxa at this time. Thus it is still maintained as a distinct species although the species concept is considered unsatisfactory (W. Gams pers. comm.).

This problem of variation between isolates was clearly seen in the two New Zealand isolates. Isolate 100c produced yellowish-red pigment, phialides with a broader base ((1.6)2.0 - 3.2 μm wide) and, in the smaller portion of the size range, cylindrical-fusiform conidia. However, isolate 89di produced thinner phialides (1.6 - 2.9(3.2) μm wide) that were closer to the 1.0 - 1.7 μm width reported by Gams (1971) and, in the smaller portion of the size range, cylindrical, slightly curved conidia of the smaller category. Nonetheless, because this

species is so broadly defined, both isolates can be accommodated therein.

The differences between V. psalliotae and V. lamellicola have been discussed earlier, and the phialophores of V. psalliotae are less differentiated than those of V. fungicola (section Albo-erecta), a species which also produces some fusiform conidia.

V. psalliotae does not appear to have been found in association with bark beetles or their galleries before. This species was isolated from two wood samples in the same locality, which both yielded rather diverse fungal flora. Isolated only twice, V. psalliotae is unlikely to be a common inhabitant of the bark beetle galleries, but whether it is a parasite of one or more of the other fungi found in the galleries remains unknown.

Volutella Fr., Syst. mycol. 3:466. 1832

=Thysanopyxis Ces., in Rabenhorst in Klotzsch, Herb. Mycol. no. 1432. 1850

=Chaetodochium Höhn., Mitt. bot. Inst. techn. Hochsch. Wien 9:44. 1932

=Psilonia Fr., Syst. mycol. 3:451. 1832

=Medusula Corda, Icon. fung. 1:18. 1837

Type species: Volutella ciliata (Albertini & Schwein.) Fr. (lectotype)

Teleomorphic genera: Nectria (Fr.) Fr., Pseudonectria Seaver

The genus Volutella is characterized by sessile or short-stalked sporodochia with straight, sterile setae; the phialoconidia are 1-celled and aggregate in white or pale coloured slimy masses.

The name Volutella Fr. was proposed for conservation against the older name Volutella Forsk., a plant genus, by Hawksworth & Tulloch (1972); the proposal was adopted in 1975. The name Volutella was first used by Tode in 1790, but his illustrations suggest the two species he studied were discomycetes (Hawksworth & Tulloch 1972), and none of his material now exists. V. ciliata (Albertini & Schwein.) Fr. was selected as the genus lectotype because it represented the concept of the genus which had evolved (Saccardo 1886; Lindau 1910; Gilman 1957), and was one of the four species treated by Fries (1832). There is, however, no modern taxonomic treatment of the genus, and this makes it difficult to determine how many species have been described. Domsch et al. (1980) suggested that the species with darkly-pigmented conidial masses had

more affinity to Myrothecium Tode than to Volutella, but they did not make the appropriate transfers. The few teleomorphs of Volutella species that are known belong to the genera Nectria and Pseudonectria Seaver.

Members of the genus Volutella are primarily known from soils, plants, and decaying plant material.

Hawksworth et al. (1983) estimated the number of species as 20, but Hawksworth & Tulloch (1972) reported that 110 species have been described within the genus. No reports of representatives of the genus Volutella being associated with bark beetles or stained wood were found, although some may be saprophytes of the leaf litter.

Volutella ciliata (Albertini & Schwein.) Fr., Syst. mycol. 3:467. 1832

Fig. 38. a-g.

≡Tubercularia ciliata Albertini & Schwein., Consp. Fung. 68. 1805

≡Atractium ciliatum (Albertini & Schwein.) Link, Mag. Ges. Nat. Fr. Berlin 7:32. 1816

≡Fusarium ciliatum (Albertini & Schwein.) Link, Spec. Plant. 2:105. 1825

=Psilonia rosa Berk., Engl. Flora 5:355. 1837

Colonies attaining a diameter of 20 - 23 mm in 12 days at 20°C in the dark and in alternating light/dark on MEA.YE. Colonies are white (2.5Y $^{8}/_{2}$) and nematogenous in the centre, especially in darkness, and produce their conidia in small, white, slimy drops at the apices of individual phialides. However, they are phalacrogenous towards the margin, especially in light, and produce the conidia in white to pale yellow slimy masses which usually cover the individual phialophores. Aging colonies produce discrete, sessile sporodochia with marginal, or occasionally also central, yellow setae. In reverse colonies are pale yellow to white (2.5Y $^{8}/_{4}$ to $^{8}/_{2}$). On cellulose medium, colonies are mostly phalacrogenous and may produce their conidia from non-sporodochial phialophores in white, pale yellow to yellow (2.5Y $^{8}/_{2}$, $^{8}/_{4}$ to 10YR $^{8}/_{6}$), slimy masses of various sizes, sometimes with associated individual setae, but discrete sporodochia are more numerous than on MEA.YE. On OA production of aerial mycelium is very limited, and sporulation is less than on cellulose medium, but the larger sporodochia sometimes

Fig 38. Volutella ciliata (Albertini & Schwein.) Fr.
(isolate: 105ai'')

a. Habit sketch of a sporodochium.

b. A seta, basal and apical portions, and a half of one cell showing the surface ornamentation.

c. Phialides from sporodochia.

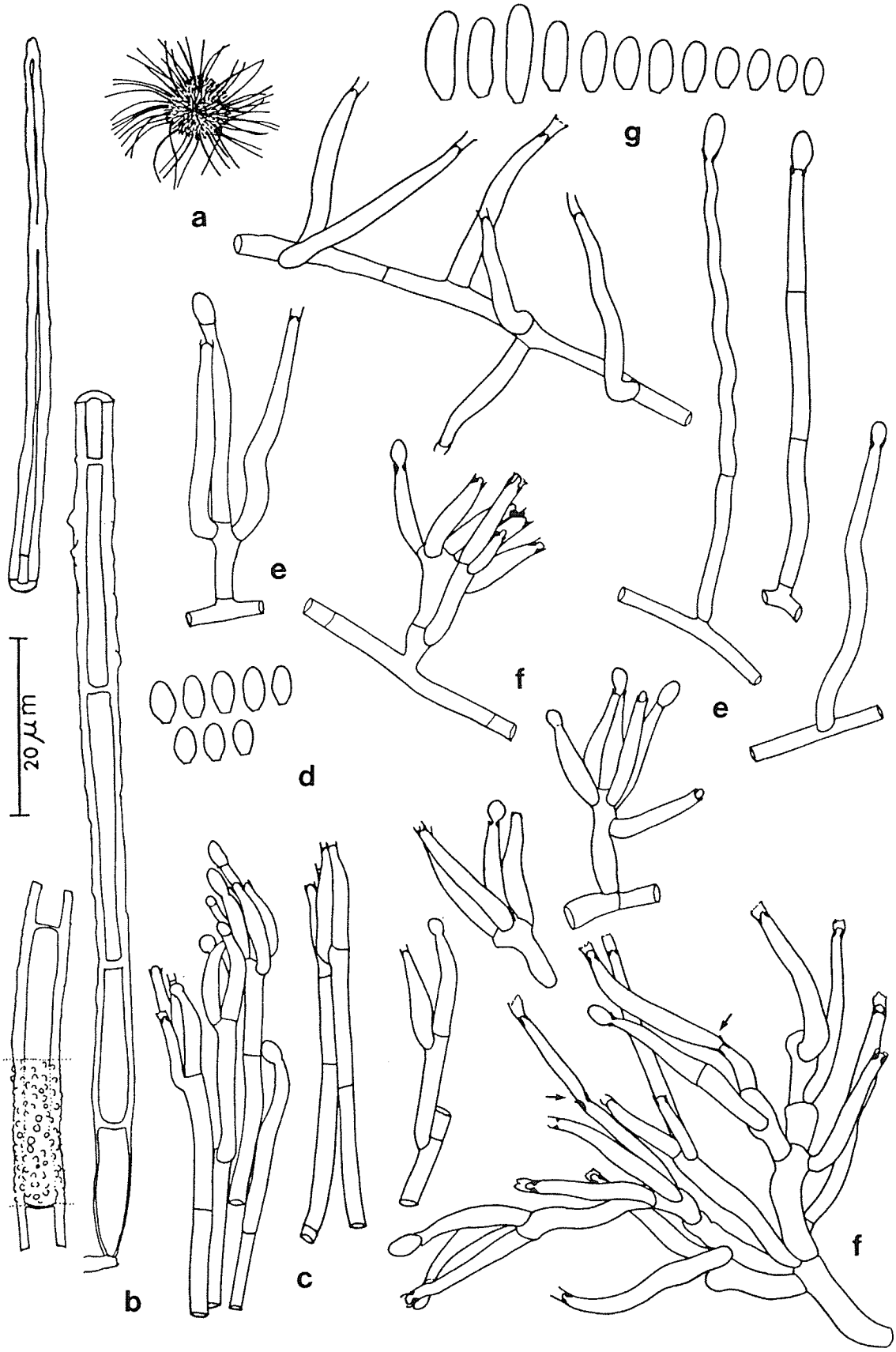
d. Phialoconidia from sporodochia.

e. Micronematous and semi-macronematous phialophores bearing long phialides.

f. Portions of macronematous phialophores arising from surface hyphae.

g. Phialoconidia produced by non-sporodochial phialophores.

Isolate as illustrated: 105ai'': a-g.


a
b
c
d
e
f
g
e
f
20 µm

become pink (5YR $^{7}/_{4}$) on aging. In reverse, colonies on both cellulose medium and OA become pale yellow (2.5Y $^{8}/_{4}$) below the sporodochia, but in other areas the colour of the medium remains unchanged. Colonies are zonate in alternating light and darkness. Odour indistinct. An exudate is present as small clear drops. Hyphae hyaline and smooth-walled; 1.3 - 5.0 µm in diameter. Chlamydospores were not seen. Phialophores of varying complexity: (1) Micronematous to semi-macronematous, with long phialides arising singly from the aerial hyphae or comprised of 1 - 3 phialides subtended by a short stem (Fig. 38. e); (2) macronematous, arising from the surface hyphae, irregularly basitonously branched several times with phialides arising at the lower levels amongst the branches and at their apices, loose to compact ranging from verticillate to penicillate arrangement of the convergent phialides, which are usually relatively short in the latter arrangement (Fig. 38. f); (3) macronematous (sporodochial), the sporodochia sessile, setose (Fig. 38. a), and the layer of short phialides subtended by a few series of short branches, each bearing 3 - 6 phialides at the apex (Fig. 38. c). The sporodochial base is pseudoparenchymatous, and gives rise to the setae and phialophores. Setae yellow, usually verrucose, thick-walled, and 7 - 15(30) septate; 230 - 450(700) µm long and 4.0 - 6.5 µm wide at the base; tapering to a round or sharply pointed, often hyaline apex (Fig. 38. b). Conidiogenous cells monophialidic, hyaline, and smooth-walled; integrated or discrete; subulate to cylindrical; most are slightly curved and some are strongly undulate (Fig. 38. e); (8.0)11.0 - 35 x 1.6 - 2.8(3.5) µm tapering to 0.9 - 1.7 µm at the apex and sometimes

proliferating terminally (Fig. 38. f «-); collarette distinct, 1.0 - 2.0 μm long. Phialoconidia aggregating in slimy masses or drops; 1-celled, hyaline, and smooth-walled; oval-elliptical or oblong-elliptical; straight; 4.3 - 8.5 x 2.4 - 3.2 μm; apex rounded, base indistinctly pedicellate, truncate (Fig. 38. d,g).

HOST: Pinus radiata

CULTURE EXAMINED: **New Zealand:** 105ai'', isolated from P. radiata, off Highway 25, Whangapoua State Forest, Coromandel, collected 19 May 1982.

Widely distributed, V. ciliata and has been recovered from a broad range of substrata and ecological sites, e.g. soils, decaying plants (including pine needles), collembola and soybean nematode cysts, and from rotten wood (Bhatt 1970; Bissett & Parkinson 1979a; Carris et al. 1989; Chilton 1954; Domsch et al. 1980; Eicker 1976; Frankland 1966; Huang & Schmitt 1975; Lindau 1910; Matsushima 1975; Pugh et al. 1963; Shearer 1972; Stenton 1953; Visser et al. 1987; Visser & Parkinson 1975; Yadav & Madelin 1968). And while there are two earlier reports of Volutella species from New Zealand (Bell 1975; Ruscoe 1973), neither refer specifically to V. ciliata.

V. ciliata has not been connected to any teleomorphic state(s). Samuels (1977) reported V. ciliata was the anamorph of Nectria concors (Ellis & Everh.) Seaver (=N. ignea Höhn.), based on collections from the U.S.A. and New Zealand, but Domsch et al. (1980) state his isolates

represent two geographically distinct groups of entities, neither of which were V. ciliata, and in Samuels & Dumont (1982), V. minima is given as the anamorph of N. concors.

The New Zealand isolate corresponds well with the current concept of V. ciliata (Domsch et al. 1980; Matsushima 1975), which is easily distinguished from other Volutella species with straight, yellowish setae and light coloured conidial masses, on conidial size. It has broader conidia than V. minima whose conidia are strictly cylindrical, and shorter than those of either V. gilva (Pers.:Fr.) Sacc. or V. lini Mukerji et al.

V. ciliata was one of the cellulose decomposers isolated by Pugh et al. (1963) from sand dunes. The New Zealand isolate produced more abundant sporodochia when grown on cellulose medium than it did on MEA.YE. From the studies on its ecology, V. ciliata appears to prefer moist habitats and substrata which have already undergone some decay. Although reported from rotten wood and pine needles, this species does not appear to have been associated with insects or stained wood before this.

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