A STUDY OF THE MORPHOLOGY AND TAXONOMY OF CERTAIN SOUTH AFRICAN SPECIES OF *COLLETOTRICHUM* CORDA

by

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"TAXONOMY IS IN THE HEAD OF MAN:

THE FUNGUS IS THE TRUTH"

(Hennebert, 1981: pers. comm.)

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1. SUMMARY

The extensive literature concerning the taxonomic and nomenclatorial history of *Colletotrichum* Corda, its morphology, development and variability, was reviewed.

South African collections of *Colletotrichum* were examined on host material and in pure culture. A key to the eleven species identified was constructed and their culture characteristics and morphology were described and illustrated. Morphological and cultural data were statistically analysed using cluster and ordination techniques. Relatively distinct groups were formed, corresponding to most of the species, and the contribution of various criteria to group delimitation was indicated. The taxonomic value of various cultural and morphological criteria was discussed.

2. OPSOMMING

Die uitgebreide literatuur oor die taksonomiese en nomenklatoriese geskiedenis, morfologie, ontwikkeling en veranderlikheid van *Colletotrichum* Corda is nagegaan.

Suid-Afrikaanse *Colletotrichum*-versamelings is op gashere en in suiwerkultuur ondersoek. 'n Sleutel vir die identifikasie van die elf geïdentifiseerde spesies is opgestel en hul kultuur-eienskappe en morfologie is beskryf en geïllustreer. Morfologiese- en kultuurgegewens is met behulp van trosanalises en ordinasie statisties ontleed. Betreklik duidelike groepe is gevorm wat met meeste van die spesies ooreenkom en die bydrae van verskeie maatstawwe tot groepsafbakening is aangedui. Die taksonomiese waarde van verskeie kulturele- en morfologiese maatstawwe is bespreek.

3. INTRODUCTION

Species of the coelomycete genus *Colletotrichum* Corda are ubiquitous facultative pathogens, causing major diseases of many crops (Firman & Waller, 1977). In South Africa certain representatives have been recorded as pathogens on forty seven cultivated plants (Gorter, 1977).

From the earliest history of *Colletotrichum* Corda confusion surrounded its relation to the older genus *Vermicularia* Tode, and later, to *Gloeosporium* Desmazières & Montagnè. The separate status of these genera was questioned by Duke (1928). In addition, unjustified description of numerous species within this complex resulted from the lack of objective definition of species (Ainsworth, 1971), the frequently erroneous assumption of host specificity (Arx, 1957a) and from misconceptions concerning the extent of morphological variation of individual species.

Several attempts were made to clarify the resulting systematic confusion, notably by Stoneman (1898), Shear & Wood (1907 , 1913), Wilson (1914), Dickson (1925), Duke (1928), Grove (1937) and Wollenweber & Hochapfel (1949), culminating in the comprehensive revision undertaken by Arx (1957a & b).

Arx (1957a & b) included many fungi previously described as *Gloeosporium* species in *Colletotrichum* Corda, which Duke (1928) had found to be identical to *Vermicularia* Tode *ex* Fries, and drastically reduced the number of species in the genus. These included *C. gloeosporioides* Penz. with 600 synonyms, *C. dematium* (Pers. *ex* Fries) Grove with 90 synonyms and *C. graminicola* (Ces.) Wils. with 35 synonyms (Arx, 1957a).

Sutton (1962), however, expressed the opinion that Arx's (1957a & b) conclusions were based on inadequate examination of original material and insufficient study of the biology of the species concerned. Inevitably, as the synonomies proposed by Arx (1957a & b) were investigated, some taxa were recognised as being distinct (Gorter, 1962; Sutton, 1962, 1968, 1980; Hindorf, 1973a, b & c).

Accurate delimitation of *Colletotrichum* species within the broad limits set by Arx (1957a) and Sutton (1980) remains uncertain and supplementary information is necessary to facilitate their determination.

The use of culture characters to distinguish between species has already been applied successfully to *Colletotrichum* (Sutton, 1973), but little attention has been paid to the value of conidiophore structure and details of conidium ontogeny (Morgan-Jones, 1971) or to characteristics of the appressoria as suggested by Sutton (1968). These criteria may be of significance at the specific level.

Gorter (1956, 1962) published the only taxonomic research into the *Colletotrichum* complex in South Africa other than the two new species described by Verwoerd & Du Plessis (1931, 1933). His (Gorter, 1956, 1962) work dealt with problems associated with the identification of a fungus causing anthracnose of olives.

The purpose of the present study is to report on the culture characteristics of a variety of South African collections of *Colletotrichum*, the development and morphology of conidiogenous cells, conidia, setae and appressoria and their use in the taxonomy of the genus.

4. LITERATURE REVIEW

4.1 TAXONOMIC AND NOMENCLATORIAL HISTORY OF *COLLETOTRICHUM* CORDA

Corda (1831) established the genus *Colletotrichum,* based on one species, *C. lineola,* which was found on dead stems. It was characterized by setose acervular fructifications from which hyaline, curved fusiform conidia were produced. As pointed out by Sutton (1966, 1977), the name was originally spelt *"Colletothricium"* (Corda, 1831) and later changed to its present spelling (Corda, 1837).

Tode (1790) had previously created *Vermicularia* with three species forming fructifications interpreted as astomate ascocarps. Fries (1925), the validating author for the name *Vermicularia,* placed it in the ascomycete genus *Sphaeria,* but regarded Tode's (1790) descriptions with suspicion. Later, Fries (1849) adopted the genus "*Vermicularia* Fr. *nec* Tod." for twelve species of his own description. Saccardo (1884), however, doubted that these species formed enclosed ascocarps, as described by Fries (1849). Saccardo (1884) regarded the fructifications as stroma-like structures or tubercles and *Colletotrichum* as possibly an unripe stage in the development of *Vermicularia.*

Desmazières & Montagnè (1849) erected *Gloeosporium* with *G. castagnei* as type species. Arx (1957b) maintained that the type specimen had had two-celled conidia, not unicellular conidia as described by Desmazières & Montagnè (1849). Saccardo (1884), however, applied the name *Gloeosporium* to leaf-inhabiting fungi with unicellular, hyaline conidia and glabrous acervuli, while designating *G. castagnei* Desm. & Mont. as *Marssonia castagnei* (Desm. & Mont.) Sacc.

Stoneman (1898) investigated the overlapping characteristics of *Gloeosporium* and *Colletotrichum* and their associated teleomorphs (Hennebert & Weresub, 1977) in an attempt to elucidate their taxonomic position. She (Stoneman, 1898) concluded that they had evolved from a common pyrenomycetous form.

Allescher (1901) was of the opinion that many *Vermicularia* species would possibly fit into the genus *Colletotrichum,* as they had "incomplete or *Peziza*-like" fructifications. Allescher (1903) also drew attention to the occurrence of transitional forms between *Colletotrichum* and *Gloeosporium.* Shear & Wood (1907) suggested that the teleomorphs of several *Gloeosporium* and *Colletotrichum* species were variants of the same fungus, *Glomerella rufomaculans* (Berk.) Spauld. & Schrenk.

In 1914, Wilson transferred species of grass anthracnose fungi classified in *Vermicularia* to *Colletotrichum graminicolum* (Ces.) Wils. Dickson (1925) supported this opinion and transferred several other *Vermicularia* species to *Colletotrichum*, observing that further study would probably reveal the necessity to transfer more.

Taubenhaus (1911, 1912) examined the problem presented by the description of large numbers of *Colletotrichum* and *Gloeosporium* species on the grounds of assumed host-specificity. He concluded that these numbers would be reduced if the fungi were subjected to cross-inoculation tests. Diedicke (1913), too, remarked on the close relationship of *Colletotrichum* to *Gloeosporium* and on the fact that *Colletotrichum* and *Vermicularia* were separated only by the difference in development of their fructifications.

Schaffnit & Böhning (1925) considered the maintenance of *Colletotrichum* and *Gloeosporium* as separate genera to be unjustified. They had found that the formation of setae – the absence of which separated *Gloeosporium* from *Colletotrichum* – was inconstant and was influenced by the nature of the substrate.

Small (1926), too, deprecated the naming of conidial fungi morphologically similar to *Colletotrichum coffeanum* Noack according to their hosts. He was of the opinion that these forms should be united under the priority name, *C. gloeosporioides.*

Duke (1928) undertook a study of the history and comparative morphology of *Colletotrichum* and *Vermicularia* to clarify their taxonomic position. She concluded that the two genera were indistinguishable and that the type species of *Vermicularia, V. dematium* Fr., and of *Colletotrichum, C. lineola* Corda, were possibly based on the same fungus, Corda (1831) alone having recognised the acervular nature of their fructifications. Duke (1928) suggested the conservation of the name *Colletotrichum* for the genus, being the better known and more widely used, with *C. dematium* (Fr.) Grove as the valid designation of the type species.

According to Sutton (1966, 1977), Duke (1928) overlooked the fact that *Vermicularia* Tode *ex* Fries is a later homonym of *Vermicularia* Moench of the Verbenaceae and should have been rejected in any case on the grounds of its illegitimacy.

Grove (1937) maintained *Vermicularia* and *Colletotrichum* as separate genera despite the conclusions reached by Duke (1928). Grove (1937) regarded *Colletotrichum* Corda as a *Vermicularia sensu* Fries and *Colletotrichum* Briosi & Cavara (*non* Corda) as a *Gloeosporium* with setae. Further evidence of the link between *Colletotrichum* and *Gloeosporium* was provided by Baker, Crowdy & McKee (1940). They discovered that the many strains of these two anamorphic (Hennebert & Weresub, 1977) genera causing anthracnose of tropical fruits all belonged to the teleomorph *Glomerella cingulata* (Stonem.) Sp. & Schr., although they had been described under diverse names.

Carvajal & Edgerton (1944) identified the teleomorph of *Colletotrichum falcatum* Went. as *Physalospora tucumanensis* Spegazzini. Arx & Müller (1954), however, considered the teleomorph of *Colletotrichum* Corda to belong to the pyrenomycete genus, *Glomerella* Spauld. & Schr. They (Arx & Müller, 1954) associated the following species with *Colletotrichum: G. cingulata* (Stonem.) Spauld. & Schr., as the teleomorph of *C. gloeosporioides* Penz., and *G. tucumanensis* (Speg.) Arx & Müller, the teleomorph of *C. graminicola* (Ces.) Wils.

Wollenweber & Hochapfel (1949) also noted the difficulty in delineating the genera *Vermicularia, Colletotrichum* and *Gloeosporium.* They remarked on the heterogeneity of *Gloeosporium* Desm. & Mont. and were of the opinion that *Vermicularia* and *Colletotrichum* could be maintained separately if properly defined.

Tiffany & Gilman (1954) drew attention to the problems associated with delineating *Colletotrichum* species. This difficulty arose largely from the use of host plants as criteria for recognition of pathogens in pathology, as opposed to the use of morphological identity as in mycology (Tiffany & Gilman, 1954).

Arx (1957a) attempted to terminate the taxonomic uncertainty surrounding *Colletotrichum* Corda. This necessitated an investigation of fungi described as *Gloeosporium* species (Arx, 1957b) as this genus was separated from *Colletotrichum* only on the basis of its lack of setae, a characteristic found to be inconstant in both genera. Arx (1957a) concluded, after considerable pure culture studies and pathogenicity tests, that many anamorphic fungi formerly placed in the genera *Colletotrichum, Vermicularia* and *Gloeosporium* actually belonged in the same genus. He regarded the hundreds of species described in these genera as representing substrate forms of only a few species.

Arx (1957a) accepted Duke's (1928) decision that *Colletotrichum* Corda be conserved against *Vermicularia* Tode *ex* Fries with *C. lineola* Cda. = *C. dematium* (Pers. *ex.* Fr.) Grove as type species. In addition, Arx (1957a & b) rejected the name *Gloeosporium* Desm. & Mont. on the grounds of its unacceptable heterogeneity, placing the species of Melanconiales described as *Gloeosporium* in various other genera according to their natural affinities (Arx, 1957b).

The generic concept of *Colletotrichum* was consequently broadened and Arx (1957a) listed eight synonyms for the genus: *Colletostroma* Petr., *Colletotrichopsis* Bub., *Ellisiella* Sacc., *Fellneria* Fuck., *Gloeosporopsis* Speg., *Steirochaete* A. Braun & Casp., *Vermicularia* Fr. and *Gloeosporium pro parte* (*non* Desmazières & Montagnè). The number of distinct species in *Colletotrichum* was drastically reduced to eleven (Arx, 1957a), of which two had several relatively host specific forms. These species were *C. dematium* (Pers. *ex* Fr.) Grove, the type, with three forms and *C. gloeosporioides* Penz. with eight forms. The name *C. gloeosporioides* Penz. was chosen to designate the extremely variable anamorph of *Glomerella cingulata* (Stonem.) Spauld. & Schr., not on the grounds of priority, but because it was the most widely used in the literature and did not suggest a specific substrate. Arx (1957a) listed nearly 600 synonyms for this species. The eight host specific forms were left under their existing names on the grounds that they were distinct in culture and that they had not yet been connected with the *Glomerella cingulata* teleomorph with certainty.

Four other more or less polyphagous species were distinguished, namely *C. crassipes* (Speg.) Arx; *C. destructivum* O'Gara; *C. atramentarium* (Berk. & Br.) Taubenh. and *C. graminicola* (Ces.) Wils.,regarded as the anamorph of *Glomerella tucumanensis* (Speg.) Arx & Müller. Arx regarded the remaining five species which he distinguished as being relatively host specific. These were *C. lini* (Westerd.) Tochinai (on *Linum usitatissimum*); *C. fuscum* Laub. (on *Digitalis* spp.); *C. fusarioides* (Ellis & Kell.) O'Gara (on *Asclepias* spp. in N. America); *C. phyllachorioides* (Ellis & Everh.) Arx (on *Artemisia* spp. in N. America) and *C. paludosum* (Ellis & Galw.) Arx (on *Peltandra virginica* in N. America).

Arx (1957a & b) drew attention to the variability of *Colletotrichum* species and to their frequently wide host ranges, emphasizing the necessity to heed these factors and to avoid the unfounded description of new species. His work, however, did not dispel the uncertainty complicating the identification of *Colletotrichum* species.

Negru (1960), in contrast to Arx (1957a & b), accepted Grove's (1937) conclusions and came to the decision that *Vermicularia* Fr., *Colletotrichum* Cda. and *Gloeosporium* Desm. & Mont. were separate genera. He (Negru, 1960) observed that the confusion surrounding the three genera arose from the fact that descriptions were based on morphology alone – the physiology and biology of the fungi being ignored – and that they did not include sufficient individuals to take their variability into account.

Gorter (1956, 1962) made a detailed investigation into the taxonomy and nomenclature of a chromogenic anthracnose fungus isolated from *Olea europaea* fruit in South Africa. Its comparison with olive anthracnose fungi from other parts of the world was necessitated, as well as with fungi causing similar diseases of other fruits. Gorter (1962) found that these fungi – all of which Arx (1957a) regarded as being *C. gloeosporioides* Penz. – fell into two groups. He (Gorter, 1962) named these the *"Glomerella – Colletotrichum"* and the *"Gloeosporium"* groups respectively. Gorter (1962) consequently did not uphold Arx's (1957a) concept of *C. gloeosporioides* Penz. with its extensive list of synonyms and identified the olive anthracnose organism, which fell into his (Gorter, 1962) *"Gloeosporium"* group, as *C. fructigenum* f. *chromogenum* in accordance with Arx's (1957a & b) decisions regarding *Gloeosporium.*

Sutton (1962) expressed the opinion that Arx's (1957a & b) synonomies had been based on insufficient experimental justification and inadequate examination or citation of original material. He (Sutton, 1966) investigated Arx's (1957a) placing of *C. trichellum* (Fr.) Duke in synonomy with *C. dematium* (Pers. *ex* Fr.) Grove and found qualitative and quantitative differences in morphology and development, thus upholding the species as distinct.

Simmonds (1965) described a new species of *Colletotrichum,* namely *C. acutatum,* which differed from the species listed by Arx (1957a). This description (Simmonds, 1965), however, bore a marked resemblance to that of Gorter's (1962) description of *C. fructigenum* f. *chromogenum.*

Sutton (1966) disagreed with Arx's (1957a) placing of *Ellisiella* Sacc. in synonomy with *Colletotrichum* Corda and preferred to keep the two genera apart because of differences in conidium morphology. He (Sutton, 1966) conceded that their separation was tentative and that in any system of classification they must be placed close together. Sutton (1968) was also of the opinion that the placing of *C. falcatum* Went. in synonomy with *C. graminicola* (Ces.) Wils. (Arx, 1957a) had been unjustified and that the two species were distinct.

Arx (1970), in the English translation of his (1957b) revision of the genus *Gloeosporium*, accepted Sutton's (1966) decision regarding the separate status of *C. trichellum* and included *C. acutatum*, described by Simmonds (1965), in his list of *Colletotrichum* species.

Hindorf (1973a, b, c; 1974) redistinguished *C. coffeanum* Noack from the synonomy of *C. gloeosporioides* Penz. given by Arx (1957a). This supported the results of previous work regarding the heterogeneity of the *Colletotrichum* population on *Coffea arabica* (Gibbs, 1969; Hindorf, 1970).

On the basis of Sutton's (1968) decision regarding the maintenance of *C. falcatum* and *C. graminicola* as separate species, Politis (1975) described the teleomorph of *C. graminicola*, naming it *Glomerella graminicola* Politis. He (Politis, 1975) distinguished it from the teleomorph of *C. falcatum*, *Glomerella tucumanensis* (Speg.) Arx & Müller, on the basis of morphological and pathogenic differences.

The continued uncertainty surrounding *Colletotrichum*, despite the numerous attempts to clarify the situation, was reflected in the work of Quimio (1977) on *Colletotrichum* species from the Philippines. Arx (1957a & b, 1970) had distinguished several host specific forms of *C. gloeosporioides*, retaining them under their original names as they had not yet been associated with the teleomorph of *C. gloeosporioides* with certainty. Their assumed relationship with *C. gloeosporioides* was therefore not reflected in their names. The same procedure was followed by Quimio (1977) with *C. melongenae* Libik, *C. merilli* (Syd.) Quimio and *C. arecae* Syd., perpetuating the phenomenon Arx (1957a) had attempted to eliminate, namely the naming of numerous morphologically similar fungi according to their host plants.

Quimio (1977), further, did not consider *C. truncatum* (Schw.) Andrus & Moore and *C. capsici* (Syd.) Butl. & Bisb. to be synonyms of *C. dematium* (Pers. *ex*. Fr.) Grove, as did Arx (1957a), but regarded them as separate, distinct species. She (Quimio, 1977) was also of the opinion that the valid name for the Cucurbitaceae anthracnose fungus was *C. lagenarium* (Pass.) Ellis & Halst., not *C. orbiculare* (Berk. & Mont.) Arx (Arx, 1957a) and that the tomato anthracnose fungus was *C. phomoides* (Sacc.) Chester, not *C. atramentarium* (Berk. & Br.) Taubenh. (Arx, 1957a).

Quimio's (1977) views on the status of *C. graminicola* (Ces.) Wils. and *C. falcatum* Went. were confusing. She listed them separately but cited *C. falcatum* Went. as a synonym of *C. graminicolum* (Ces.) Wils. and *C. graminicola* (Ces.) Wils. as a synonym of *C. falcatum* Went., remarking that the latter is specific to sugar cane.

The consequence of the difficulty in delineating and identifying existing described *Colletotrichum* species has been the continued description of new species. Examples are *C. typhae* Greene (Sutton & Sellar, 1963); numerous additional species from India, distinguished largely on the basis of new host records for *Colletotrichum* (Pavgi & Singh, 1964, 1965; Pavgi & Upadhyay, 1964) and *C. nymphaea* (Pass.) Van der Aa (Van der Aa, 1978). The latter was described as a distinct species even though Van der Aa (1978) admitted its similarity to the plurivorous *C. gloeosporioides* Penz.

Sutton (1980) published a collation of contemporary opinions concerning coelomycete taxonomy to serve as a basis for further revisionary work. The names "Coelomycetes" and "Hyphomycetes" were rejected as formal taxonomic ranks in favour of an experimental classificatory scheme in which the taxonomic ranks describe the manner of conidium formation and the nature of conidiomata. *Colletotrichum* is consequently placed in the suborder Phialostromatineae, order Phialidales of the subclass Enteroblastomycetidae, class Blastodeuteromycetes in the subdivision Deuteromycotina.

Sutton (1980) gave nineteen synonyms for *Colletotrichum* Corda but did not list *Gloeosporium* Desm. & Mont., included *pro parte* in Arx's (1957a, 1970) synonomy for the genus. Sutton (1980) included fifteen of the twenty three taxa recognised by Arx (1970) in his key to *Colletotrichum* species, excluding eight and adding seven not listed by Arx (1970) as separate species. The latter are *C. capsici* (Syd.) Butl. & Bisby, *C. higginsianum* Sacc. *apud* Higgins, *C. coffeanum* Noack, *C. falcatum* Went., *C. sublineolum* P. Henn. *apud* Kabát & Bub., *C. caudatum* (Sacc.) Pk. and *C. corchori* Ikata & Tanaka.

C. gloeosporioides, C. dematium, C. capsici and *C. sublineolum* were termed "group" species (Sutton, 1980) as subspecific elements cannot be separated satisfactorily in them at present.

Sutton (1980) drew attention to the need for further investigation of many *Colletotrichum* taxa in vitro and for the determination of their host ranges by cross inoculation.

4.2 MORPHOLOGY, ONTOGENY AND BIOLOGY OF *COLLETOTRICHUM*

The present generic concept of *Colletotrichum* Corda is given by Sutton (1980).

Conidiomata are acervular, subcuticular, epidermal, subepidermal or peridermal, separate or confluent, comprising hyaline to dark brown, thin- or thick-walled textura angularis. Two types of acervular development were indicated in Arx's (1957a) broad characterization of *Colletotrichum.* These were designated pulvinate (Ainsworth, 1971) and hypostromatic by Sutton (1966), who described them in detail.

Pulvinate development is the most common in *Colletotrichum*, involving the rupture of host tissue by mechanical force. Hyphae aggregate within the epidermal cells and adjacent parenchyma, rupturing the lateral walls and subsequently the outer walls and cuticle. The latter are pushed aside as the setae, conidiophores and pseudoparenchymatous stroma develop.

Hypostromatic development occurs in species on graminicolous hosts and is chiefly exhibited by *C. graminicola* and *C. dematium.* As in pulvinate development, hyphae develop in the epidermal cells, but they produce penetration hyphae which grow through the outer epidermal cell walls and form conidiophore and setal initials between these and the cuticle. As the initial increase in size, the cuticle ruptures. Epidermal cell walls, however, remain intact.

Sutton (1966) concluded that no taxonomic significance could be attached to these developmental types as they are dependant not only on the strain of fungus involved, but also on the nature of the substrate.

Conidiogenous cells are enteroblastic, phialidic, hyaline to brown, smooth, cylindrical to subcylindrical, integrated or discrete, colarette and periclinal thickening occasionally prominent.

Sutton (1962) and Sutton & Sellar (1963), in studies of *C. dematium* and *C. trichellum*, and *C. typhae*, respectively, gave brief descriptions of conidium ontogeny in these species. Their observations were corroberated by Morgan-Jones (1971), who investigated the conidium ontogeny of *C. pyrolae*, describing the process as follows:

During the formation of the first conidium from a conidiogenous cell, the apex of the conidiogenous cell becomes swollen and the conidium is released by a circumcissile break in the periclinal wall. This leaves an open end through which a basipetal succession of conidia is produced. Morgan-Jones (1971) noted that the base of the conidium in *C. dematium* is narrower than this aperture, while in other species examined it occupies the whole width.

Griffiths & Campbell (1972), however, found that the conidiogenous cells of *C. atramentarium* (B. & Br.) Taub. consisted of two layers, of which the innermost protruded into the "lumen" of the conidiogenous cell at the apex. This formed a "collar" which was forced outwards by the protrusion of cytoplasm during conidium formation, rupturing the conidiogenous cell wall. A cross wall was layed down prior to dehiscence. These authors concluded that this development could not be termed phialidic, according to the definition of Ellis (1971), unless a third wall could be envisaged, as the inner wall of the conidiogenous cell appeared to be involved in conidium formation.

Sutton (1973) described the conidiogenous cells of *Colletotrichum* as being monophialidic, not proliferating percurrently.

Cole & Samson (1979) revised the concept of phialidic development. They were of the opinion that the formation of phialoconidia occurs by extension growth of the inner phialide wall, after the holoblastic formation of the primary conidium and the rupture of the outer phialide wall. As each conidium seceeds, this inner wall ruptures, leaving a ring of torn wall material which results in the apical thickening characteristic of phialidic development. Morgan-Jones, Nag Raj & Kendrick (1972) had illustrated this accumulation of wall material, postulating that the blockage caused by this phenomenon might be one of the factors causing the percurrent proliferation of phialides.

Conidiogenous cells are usually aggregated in conidiomata, but may also be formed as side branches of the mycelium in a hyphomycetous manner (Clausen, 1912; Schaffnit & Böhning, 1925; Arx, 1957a; Schmiedeknecht, 1957; Blakeman & Hornby, 1966; Stephan, 1967b; Hindorf & Muthappa, 1974; Van der Aa, 1978).

Conidia are hyaline, aseptate becoming uniseptate just prior to germination, smooth, sometimes guttulate, straight or falcate, cylindrical to fusiform, one species with the apex elongated to form a simple cellular appendage. Stephan (1967b) noted that the conidia of *C. gloeosporioides* often formed an anastomosing network, their germ tubes forming fusion bridges ("Fusionsbrücken") between them.

The conidia collect in a slimy matrix. This mucilaginous material is fibrillar (Griffiths & Campbell, 1972; Kozar & Netolitzky, 1978), composed of polysaccharides and protein and is water soluble (Nicholson & Moraes, 1980). Nicholson & Moraes (1980) suggest that the matrix has two roles, namely in the protection of conidia against desiccation and in increasing the efficiency of germination and host penetration through the activity of the invertase and hydrolase which it contains.

Conidia do not function as survival structures as their viability declines rapidly (Blakeman & Hornby, 1966; Farly, 1976; Mishra & Siradhana, 1979). However, the fungus mycelium may remain viable for long periods in infected seeds or plant débris (Erb, Gallegly & Leach, 1973; Lukezic, 1974; Carroll, Jones & Swain, 1977; Naylor & Leonard, 1977; Warren, 1977), or as latent infections in plants not showing any disease symptoms (Böhni, 1949; Tiffany, 1951).

Dispersal is brought about by water or occasionally by insects (Arx, 1957a). Water flowing from infected bark plays an important role in the spread of coffee berry disease (Waller, 1972) and *Colletotrichum* conidia have been found on insects (Hanson, Milliron & Christensen, 1950). Conidia may also survive and be dispersed by wind in dry particulate matter (Nicholson & Moraes, 1980).

Stephan (1967b) found more than 90% of the conidia of *C. gloeosporioides* to be uninucleate, the remainder being bi- or trinucleate and on average twice as long as the uninucleate conidia, their width remaining the same. Germination takes place only in free water or at a relative humidity approaching 100% (Riley, 1955; Nutman & Roberts, 1960; Frost, 1964). On germination conidia swell, their nucleii divide, septa form between the daughter nucleii, and one cell, or both, produces a germ tube which may in turn produce an appressorium with an electron-dense outer wall (Politis & Wheeler, 1973).

Appressoria are brown, margins entire or crenate to irregular, simple or repeatedly germinating to produce chains of closely connected appressoria. They are produced from conidium germ tubes and from hyphal tips in the mycelium (Sutton, 1968).

According to Emmett & Parbery (1975), Frank introduced the term "appressorium" in 1883 for "spore-like organs" formed on the germ tubes of *Colletotrichum lindemuthianum, Polystigma rubrum* and *Fusicladium tremulae.* Southworth (1891a) and Atkinson (1891) had noted the production of "secondary, dark-coloured spores" and "peculiar enlarged cells, olive-brown in colour" respectively in their studies of *Colletotrichum gossypi.* Atkinson (1891) was of the opinion that they were resting bodies, while Hasselbring (1906) regarded appressoria primarily as adhesion organs. Emmett & Parbery (1975) used the term to designate structures having the capacity to adhere to a host surface and the ability to germinate and to penetrate the host.

The appressoria produced by simple, hyaline spores commonly have well-developed survival characteristics and represent an adaptation to overcome the vulnerable "germination-to-infection" phase of the life cycle (Parbery & Emmett, 1977).

Walker (1980), however, did not consider the use of the term "appressorium", in the wide sense of Emmett & Parbery (1975) and Parbery & Emmett (1977), to be appropriate in all cases. He (Walker, 1980) consequently restricted the definition of an appressorium to "a swelling, usually terminal, produced on germ tubes for attachment and penetration or terminally on a hypha within host tissue for cell wall penetration". Cells or swellings produced from vegetative epiphytic hyphae for attachment and penetration are termed "hyphopodia" (Walker, 1980).

Colletotrichum, therefore, may be considered to form both hyphopodia and appressoria. As the latter term is most commonly applicable, it will be used in the remainder of this dissertation.

Appressoria are produced from hyphal tips in a blastic manner (Sutton, 1968). The initial swelling or "proto-appressorium" (Parbery & Emmett, 1977) is delimited from the hypha by a septum and developes a thickened, pigmented cell wall. This reportedly consists of two layers in *C. lagenarium* (=*C. orbiculare*) (Akai & Ishida, 1968), *C. lindemuthianum* (Mercer, Wood & Greenwood, 1971) and *C. gloeosporioides* (Brown, 1977), namely an electron-dense outer layer and an inner, electron-transparent layer, but it is reportedly triple-layered in *C. graminicola* (Kozar & Netolitzky, 1978), where the inner layer is double. They are usually unicellar, but compound appressoria are also produced (Hasselbring, 1906; Sutton, 1962) and adhere to the host surface by means of hemicellulose mucilage (Lapp & Skoropad, 1978a).

Each appressorium has a pore through which a germ tube or infection hypha emerges, either by rupture (Akai & Ishida, 1968) or by dissolution of the outer wall (Politis, 1976; Kozar & Netolitzky, 1978). In *C. gloeosporioides* the pore has been found to be surrounded by a funnel-shaped collar of wall material, protruding inwards in the appressorium, from which the infection hypha is later formed (Brown, 1977).

Appressorium formation is primarily controlled by the fungal genotype (Emmett & Parbery, 1975) whose expression appears to be controlled by thigmotropic stimuli (Yang & Ellingboe, 1972; Staples, Laccetti & Yaniv, 1976; Lapp & Skoropad, 1978b). Their formation is stimulated by host material leachates (Swinburne, 1976) and by the presence of bacteria which cause nutrient stress (Lenne & Parbery, 1976; Blakeman & Brodie, 1977; Blakeman & Parbery, 1977), and inhibited by high temperatures (Miehle & Lukezic, 1972; Tani, Ishida & Furasawa, 1977).

Two main roles have been assigned to appressoria: They effect direct penetration of host tissue and, secondly, are more resistant than the conidia to unfavourable conditions (Hasselbring, 1906; Parbery & Emmett, 1977), having the capacity to endure conditions of high light intensity, desiccation and antagonism potentially lethal to unprotected germ tubes or hypha during host penetration (Emmett & Parbery, 1975). They may persist on the plant surface until the tissue can be invaded (Zwillenberg, 1959; Brown, 1975; Brown & Barmore, 1977), often situated between the wax layer and the cuticle (Binyamini & Schiffman-Nadel, 1972).

Sutton (1962, 1968) is of the opinion that they are of interspecific taxonomic value. Simmonds (1965), however, considers the differences in appressoria of *C. dematium, C. gloeosporioides, C. orbiculare, C. acutatum, C. musae* and *C. coccodes* insufficient to warrant a more detailed examination. Stephan (1967a) found that, although the appressoria of *C. gloeosporioides* and *C. crassipes* were of similar dimensions, their shape differed and could be used as a differentiating character as Arx (1957a) had suggested.

Sclerotia, formed sparsely by a few species, characterize *C. coccodes* both in culture and on host material. They are dark brown to black, often setose. According to the studies made by Schmiedeknecht (1957) and Griffiths & Campbell (1972), their development is of the "strand" type (Townsend & Willets, 1954), through which the intertwining of adjacent hyphae produces a rindless mass of pseudoparenchymatous cells with large lipid-filled vacuoles, which become darkly pigmented due to the extrusion of melanizing particles.

McIntyre & Rusanowski (1975) found that their observations of development on host tissue closely parallelled those made by Griffiths & Campbell (1972) in artificial culture. Campbell & Griffiths (1974) describe the fine structure of sclerotial germination in *C. coccodes:* Dormant sclerotia give rise to acervuli through the formation of "secondary hyphae" which arise at certain points, possibly utilizing the sclerotial food reserve.

According to Tu (1980), the sclerotia of *C. coccodes* originate from a stroma which initially forms an acervulus, and are three-layered. A mature sclerotium comprises an outer sclerotized spongy layer, a middle plectenchymatous layer and an innermost prosenchymatous layer consisting of loosely packed, living hyphal cells. Sclerotia expand laterally by repeating the process of acervulus development.

Sclerotia together with sclerotia-like aggregations of mycelium formed in *C. musae* (Elarosi, 1960, as *Gloeosporium musae*) as well as *C. dematium* and *C. fuscum* (Arx, 1957a) play an important role in the survival of *Colletotrichum* (Walker, 1921; Smith & Crossan, 1958; Blakeman & Hornby, 1966; Naylor & Leonard, 1977).

Setae are brown, subulate, multicellular, arising from the basal layer of the acervulus (Arx, 1957a). They are also produced from sclerotia, arising as filaments of hyphal cells which become sheathed with melanising material (Griffiths & Campbell, 1972). Negru (1960) implied that setae and conidiogenous cells are homologous. He noted that setae developed to the detriment of conidiogenous cells in *C. lindemuthianum* (Sacc. & Magn.) Br. & Cav. grown at temperatures above 20°C.

The variability in seta production and its control by environmental factors was observed and illustrated by Schaffnit & Böhning (1925), Frost (1964), Stephan (1967a) and Chahal (1978). Stephan (1967a) found that certain *C. gloeosporioides* isolates only produced setae on their natural substrate, while others only produced setae on certain culture media. Some isolates produced no setae under the conditions tested.

Structure and development of the teleomorph of *C. gloeosporioides,* namely *Glomerella cingulata,* were investigated by McGahen & Wheeler (1951). Perithecia were described as being initiated by two lateral initials which developed from adjacent cells of a hyphal strand. An outer and an inner coil of cells resulted from the proliferation of these initials, the perithecial wall being built up by proliferation of cells of the outer coil. The inner coil differentiated into an ascogonial coil, whose tip fused with a third hyphal branch. The resulting plasmogamy marked the beginning of the dikaryotic state, maintained by crozier proliferation until nuclear fusion occurred in the ascus.

Arx & Müller (1954) described the perithecia of *Glomerella cingulata* as being spherical or somewhat flattened, sometimes forming irregular crusts. The asci were clavate, cylindrical or ellipsoidal, containing 4, 6 or mostly 8 hyaline ascospores. The ascospores were ellipsoidal or narrowly clavate, both ends broadly rounded or somewhat narrowed, straight or inequilaterally falcate. The number of paraphyses varied. They disintegrated with age. *G. tucumanensis* (Speg.) Arx & Müller was described as being very similar to *G. cingulata* (Arx & Müller, 1954).

4.3 VARIABILITY IN *COLLETOTRICHUM* AND ITS GENETIC BASIS

4.3.1 Variability

The variability of *Colletotrichum* species, especially of *Glomerella cingulata* (Stonem.) Sp. & Schr. and its anamorph, *C. gloeosporioides* Penz., has been studied extensively.

Southworth (1891b) wrote that "the structure of the fungus is so variable that it is almost impossible to form a description that will be true under all circumstances". Shear & Wood (1913) commented that "No character, either morphological or physiological, seems to be well fixed". Burger (1921) concluded that it is a "polymorphic" species made up of strains differing in growth characters and conidium shape, and Andes & Keitt (1950) termed it a "composite of many variants", with only the chromogenic strains clearly differentiated.

Stephan (1967a) confirmed that *C. gloeosporioides* Penz. was greatly variable, even isolates originating from the same host plant. He found that the formation of acervuli and setae was strongly influenced by the culture medium and was of the opinion that the occurence of sectors in these isolates could be explained by heterokaryosis.

The variability of *C. musae* in culture (Ashby, 1931), *C. falcatum* Went. (Chona & Hingorani, 1950; Chona & Srivastava, 1960) and *C. graminicola* (Ces.) Wils. (Mishra & Prasad, 1975) has also been described.

In addition to morphological differences, races differing in pathogenicity have been reported to occur in *Colletotrichum* species. The description of races has been most prevalent in *C. lindemuthianum* (Sacc. & Magn.) Bri. & Cav., the cause of anthracnose in beans. Barrus (1918) initially described two strains, "alpha" and "beta", based on differential pathogenicity. Burkholder (1923) subsequently described a "gamma" strain. Frandsen (1953) reported nine physiological races; Yerkes & Ortiz (1956) demonstrated 10 new races in Mexico, and Yerkes (1958) reported additional races.

A more practical attitude was adopted by Leakey & Simbwa-Bunnya (1972), whose results supported the division of *C. lindemuthianum* races into two major groups corresponding to two major groups of *Phaseolus vulgaris* cultivars. Oliari, Vieira & Wilkinson (1973) noted the lack of a uniform international set of differential bean varieties and common criteria for comparison, which had resulted in the indiscriminate description of new races.

Pathogenic races have also been reported to occur in *C. linicolum* Pethyb. & Laff. *(C. lini* (Westerd.) Tochinai (Arx, 1957a)) (Schwinghamer, 1956); *C. orbiculare* (Berk. & Mont.) Arx (Goode, 1958; Barnes, 1972) and in *C. graminicola* (Ces.) Wils. (Mishra & Prasad, 1975).

Welty & Mueller (1979) indicate the possibility that pathogenic races or strains also exist in *C. trifolii* Bain & Essary.

4.3.2 The genetic basis of variability in *Colletotrichum*

The teleomorph of *Colletotrichum gloeosporioides, Glomerella cingulata,* is the only member of this group of fungi which has been the subject of extensive genetic investigations.

Edgerton (1908) was the first to discover the occurrence of differing sex strains in *Glomerella.* Lucas, Chilton & Edgerton (1944) found that the two strains reported, namely the "plus" and the "minus" strains, could be produced from ascospores of the plus as well as from the ascospores produced in perithecia formed on the line of contact between strains; in addition, the ascospores of the plus strain occasionally developed into strains differing from either the plus or the minus.

Edgerton, Chilton & Lucas (1945) concluded that fertilization took place between strains and indicated that the plus strain was the one ordinarily isolated from nature. Chilton, Lucas & Edgerton (1945) noted that the ability to produce conidia in culture was an inherited characteristic, separate from those responsible for the formation of perithecia.

Wheeler, Olive, Ernest & Edgerton (1948) attempted to find the basis of variability in *Glomerella* and a solution to problems concerning inheritance by investigating the nuclear cycle. They confirmed Lucas' (1946) report that the chromosome number was four and found that ascospores of the "plus A" strain contained a single haploid nucleus, which supported their hypothesis that minus variants produced by this strain resulted from mutations.

Chilton & Wheeler (1949a) found the inheritance of mating reactions and macroscopic culture characters of isolates from six strains of *Glomerella* to be controlled by genetic factors at two different loci on the same chromosome. They (Chilton & Wheeler, 1949b) concluded that the minus and other variants arose as the result of single gene mutations.

Wheeler (1950) found that "plus A" strains, capable of producing minus strains, and "plus B" strains, not producing minus strains, differed genetically by a factor which he designated the "mutator" gene, present in "plus A" strains but absent or represented by an inactive allele in the "plus B" strains.

Struble & Keitt (1950), attempting to explain variant behaviour previously described in *Glomerella cingulata,* found seven variant types. They (Struble & Keitt, 1950) were of the opinion that the negative strain was primarily a culture mutant.

McGahen & Wheeler (1951) gave a detailed account of perithecium development in *Glomerella.* They believed that their studies (Wheeler & McGahen, 1952) indicated the existance of three alleles at each of two loci, 'A' and 'B', affecting mating reactions, and mutant genes at two other loci, 'F' and 'st', causing complete self-sterility when introduced.

Wheeler & Driver (1953) reported a dwarf-spored mutant of *Glomerella,* with ascospores one third of the usual length. The dwarf-spored character was thought to be controlled by an apparently recessive single mutant gene, designated "dw", and Wheeler & Driver (1953) noted the taxonomic implications of not recognising the mutant's origin.

Wheeler (1954) viewed *Glomerella cingulata* (Stonem.) Sp. & Schr. as a "notoriously variable species" which could be divided into different types, the number of which was limited only by the industriousness of the investigator. In addition. Wheeler (1954) expressed the opinion that the mating types or compatibility groups within this fungus could not be classified into two or four, as with many other fungi, but that the sexual process occupied an intermediate position between typical homothallism and true heterothallism.

Together with genetically induced variation, Driver & Wheeler (1955) and Wheeler, Driver & Campa (1959) found chemical stimulation of self-fertilization in nearly sterile cultures of *Glomerella.*

Jenkins, Winstead & McCombs (1964) suggested that *Glomerella cingulata* var. *orbiculare* had a relatively broad base of genes for pathogenicity, and that the number of races that could be described was limited only by the number of hosts that elicit distinguishable disease reactions.

The question of variability in *C. gloeosporioides* was also investigated by Stephan (1966, 1967a, b, c; 1968). He (Stephan, 1967a) confirmed the variability and plasticity of *C. gloeosporioides* isolates and postulated that the non-uniformity of individual isolates, indicated by sectoring, could possibly be explained by heterokaryosis. Stephan (1967b) found that cytological conditions were indeed favourable for heterokaryosis and, by crossing morphologically well-defined wild types (Stephan, 1967c) as well as auxotrophic mutants (Stephan, 1968), he obtained heterokaryonts.

Chesters & Hornby (1965a) found that the frequency of sectoring in older isolates of *C. coccodes,* which had initially been stable, and the relative stability of the variants, suggest the dissociation of a heterokaryotic complex.

Stephan (1968) regarded parasexuality as a significant factor in the variability of *C. gloeosporioides.*

4.4 MULTIVARIATE PHENETIC ANALYSIS OF TAXONOMIC DATA

Sneath & Sokal (1973) define numerical taxonomy as the grouping of phenetically similar taxonomic units into taxa by numerical methods on the basis of their character states. These methods attempt to increase the objectivity of comparative processes (Kendrick & Proctor, 1964) but, as any other classification, have an inherent error resulting from poor sampling of the phenetic space and error in recording character states, in addition to the shortcomings of the cluster producing method (Sneath & Sokal, 1973). Sokal & Sneath (1963), Kendrick & Proctor (1964), Jardine & Sibson (1971) and Sneath & Sokal (1973) discuss these factors. However, a classification begins with and is determined by the choice of entities and of variables considered to be relevant (Everitt, 1974).

Statistical methods have been applied successfully in the taxonomy of fungi by, for example, Kendrick & Proctor (1964) in a cluster analysis of species in the hyphomycete genera *Phialocephala* Kendrick and *Verticladiella* Hughes; by Hindorf (1973a & b), who used discriminant analysis to distinguish between *Colletotrichum* species occurring on coffee and by Dabinett & Wellman (1978), who employed various cluster analyses and non-metric multidimensional scaling ordination in the numerical taxonomy of 88 Fungi Imperfecti and ascomycete taxonomic entities.

Discriminant analysis operates from the standpoint that the number of groups within the data matrix is thought to be well known, while cluster analysis is required to reveal category structure within the data set (Anderberg, 1973). A disadvantage of cluster analyses is that they tend to impose the taxonomic structure implied by the logic of the technique, whether it is there or not (Moss, Peterson & Atyeo, 1977).

Single linkage (SL) clustering groups the operational taxonomic units (OTU's = smallest taxonomic entity included in a study) which are most related, admitting more OTU's into a cluster by lowering the criteria of admission (Sokal & Sneath, 1963). OTU's or clusters are consequently joined by the single shortest or strongest link and every member of a cluster is more similar to another member of that cluster than to any other entity (Hartigan, 1975).

In complete linkage (CL) clustering the similarity between two joining clusters is the similarity existing between the farthest pair of members, one in each group (Sneath & Sokal, 1973). Entities in a cluster are, therefore, linked at a point of minimum similarity (Hartigan, 1975).

Both SL and CL analyses introduce extremes, the former producing elongate clusters or chains of OTU's and the latter producing compact clusters which exclude many of the less easily affiliated OTU's (Sneath & Sokal, 1973). Any cluster obtained using both methods is likely to be a well-defined group (Proctor, 1966).

Average linkage (AL) methods were developed to avoid these extremes introduced by SL and CL methods (Sneath & Sokal, 1973).Here, clusters are characterized by the average of all the links within them (Hartigan, 1975). Several AL methods have been developed.

The unweighted pair-group method using arithmetic averages (UPGMA) employs the arithmetic averages of the similarity or dissimilarity coefficients between an OTU candidate for admission and members of an existing cluster, or between members of two clusters about to fuse; only one OTU or cluster at a time may be admitted for membership and each OTU in a cluster is weighted equally, regardless of the structural subdivision of the cluster (Sneath & Sokal, 1973).

The UPGMA has been employed successfully by Moss, Peterson & Atyeo (1977) in the taxonomy of feathermites (family Eustathiidae) and by Dippenaar (1980) in the taxonomy of shrews (*Crocidura,* family Soricidae).

The weighted pair-group method using arithmetic averages (WPGMA) differs from the UPGMA by weighting the member most recently admitted to a cluster equal to all previous members (Sneath & Sokal, 1973). This equal weighting prevents undue influence by taxa represented by many OTU's at the expense of those with only a few representatives (Proctor, 1966). The WPGMA distorts overall taxonomic relationships in favour of the most recent arrival within a cluster (Sneath & Sokal, 1973), and Proctor (1966) dismisses it as being "too crude a method".

The unweighted pair-group centroid method (UPGMC) of AL computes the centroid of OTU's which join to form a cluster, represented by a point whose co-ordinates are the mean values of each character over the given cluster of OTU's; it then measures the dissimilarity of a candidate OTU or cluster from this point, computing the distance between centroids (Sneath & Sokal, 1973). Proctor (1966) preferred the centroid method of clustering to the UPGMA, as the latter appeared to overestimate the dissimilarity between clusters as they became more diffuse.

Ordination methods are used in addition to clustering methods in numerical taxonomy or multivariate analysis. Ordination is the placing of OTU's in a multidimensional attribute-space: Principal component analysis computes the principal axes (or factors) in the A-space which summarize the major dimensions of variation; the co-ordinate points of the OTU's are then computed in the space created by the principal axes (Sneath & Sokal, 1973).

Moss *et al.* (1977) relied primarily on ordinations for their taxonomic conclusions as Sneath & Sokal (1973) had pointed out that phenograms are notoriously prone to distortions, especially at lower levels. However, Sneath & Sokal (1973) also pointed out that principal component ordinations, although faithfully representing distances between the major clusters, falsify distances between close neighbours, as indicated by Rohlf (1968).

Sneath & Sokal (1973) conclude that formal taxonomic groupings should possibly be based on phenograms from the full A-space and ordinations used for investigating the general pattern of variation.

5. MATERIAL AND METHODS

5.1 MATERIALS

5.1.1 Specimens studied

This study is based on the examination of South African isolates of *Colletotrichum* Corda obtained from plant material collected by members of the Mycology Section, Plant Protection Research Institute, Pretoria, or from plant material or cultures received there for examination. Dried cultures of the collections examined were deposited in the Pretoria Mycological Herbarium (PREM).

5.1.2 Culture media

The following culture media were used (Appendix 1):

Czapek-Dox (CMI, 1968) + 2% dextrose (CD)
Czapek-Dox (CMI, 1968) + 2% dextrose + 0,1% yeast extract (CDY)
Malt extract agar (MEA)
Malt salts agar (MSA) (Van der Westhuizen & Holtzhausen, 1980)
Potato carrot agar (PCA) (CMI, 1968) + Albamycin T (PCA+ N)

5.2 METHODS

5.2.1 Incubation, isolation and storage of material

Incubation took place at room temperature (± 25°C) for host plant material, or 20°C for pure cultures, under intermittent mixed irradiation, 12 hours/day. Near ultra-violet (NUV) and "daylight" type fluorescent tubes (Phillips TL 40W/08RS, F40 BLB and TL40W/33RS, respectively) were suspended 50 cm above the plates. Pyrex petri dishes were used (90 mm diameter).

Infected host plant material was surface sterilized for approximately thirty seconds in a 5% sodium hypochlorite solution, rinsed in sterile distilled water and incubated on PCA + N plates under the conditions described above. Isolations were made on PCA + N.

Pure cultures were stored at 20°C in McCartney bottles on MSA slants.

5.2.2 Culture descriptions

For comparative culture descriptions of isolates and for the examination of micromorphology, five replicates of each isolate on each medium were made in 90 mm diameter Pyrex petri-dishes, employing a mass inoculation technique. Cultures were incubated as described above (5.2.1).

Culture characteristics were described and photographed on the tenth day of incubation.

Linear increase in colony diameter was measured from day three to seven of incubation. The mean of measurements along two perpendicular axes was recorded. Growth rate was calculated in millimetres per 24 hours (Edgerton, 1915).

Texture of aerial mycelium, nature of colony edges and zonation, if present, were described, using the terminology of Long & Harsch (1918), Campbell (1938) and Ainsworth (1971), given in Appendix 2.

Colour of colony surface and reverse was described with reference to Ridgway's (1912) standards and nomenclature. This was correlated with Rayner's (1970) determination of the ISCC-NBS (Kelly & Judd, 1963) colour groupings. These colour equivalents are listed in Appendix 3.

5.2.3 Light microscopy

Slide preparations were made in lactophenol from ten day old colonies. They were not stained, in order to facilitate observation under phase contrast illumination (Nag Raj & Kendrick, 1975).

Appressoria were studied in slide culture, prepared according to the method of Sutton (1962) but using MSA instead of PCA. Cultures were incubated at 20°C under the conditions described above (5.2.1). Lactophenol was used as mounting medium.

Conidia, appressoria and setae were measured with an ocular micrometer at a magnification of 1000x. Measurements were taken to the nearest 0,5 µm, in accordance with the recommendations of Hawksworth (1974), to accommodate personal error and avoid the misleading appearance of excessive precision.

The minimum number of measurements of each dimension necessary to obtain an acceptably low standard error of the mean was calculated using a computer program based on the work of Taylor (1961). For each isolate included in the statistical analysis, thirty conidia, thirty setae and twenty appressoria were measured. The maximum, minimum and mean of each set of measurements were calculated.

An objective random sampling method was devised. The appropriate structure, eg. conidium, nearest the middle calibration of the ocular micrometer was measured, skipping alternate microscope fields and also alternate traverses across the preparation. This procedure was followed until the required number of measurements had been made.

Descriptions of shapes of conidia and appressoria were based on the terminology of Ainsworth (1971), given in Appendix 2. Line drawings were made with the aid of a drawing tube attached to a microscope.

5.2.4 Scanning electron microscopy

Material for scanning electron microscopy was prepared as described by Hayat (1972) and Glauert (1975).

Agar blocks 2 - 3 mm in length and ± 2 mm deep were cut from colonies grown on PCA (1,5% agar) and incubated at 20°C under the conditions described above (5.2.1). The slimy conidial matrix was removed by washing on a slow rotating disc for 5 - 20 minutes with 1% periodic acid, 20 – 30 minutes in 1% KOH solution, 5 minutes in 1% acetic acid and, finally, for 5 - 10 minutes in phosphate buffer.

Double fixation took place with 2,5% glutaraldehyde in 0,1M phosphate buffer, pH 7,2 , containing 3% sucrose plus a wetting agent. The material was then washed four to five times in phosphate buffer and fixed in 1% osmium tetroxide in phosphate buffer for two hours. This was followed by another four to five washes in phosphate buffer.

Dehydration was carried out in an acetone series, ending with absolute acetone. Critical point drying (with CO_2) was employed, according to the method of Anderson (1951).

Dried material was mounted on stubs with electrically conductive paint and coated with an approximately 250 Angstrom thick layer of gold-palladium. It was viewed with the JEOL JSM 35 scanning electron microscope of the Plant Protection Research Institute, Pretoria.

5.2.5 Multivariate phenetic analysis of taxonomic data

The exemplar approach (Sneath & Sokal, 1973) to selecting OTU's was employed, whereby single or only a few representatives of each taxon were chosen as reference points to indicate subgeneric groupings. This method is based on the assumption that OTU's within a taxon, even if the latter is variable, are more similar to each other than to OTU's of another taxon.

Twenty eight isolates were selected as reference points to represent the range of variation found within the thirteen subgeneric taxa described in this study. These OTU's are listed in Appendix 4 with details of their hosts.

Twenty seven criteria were selected for analysis, including both culture and morphological characters and dimensions. Data were obtained from ten - day old cultures grown on MSA under the conditions described above. The characters and character states used are listed in Appendix 5.

Multivariate analyses were performed with the Numerical Taxonomy System of Multivariate Statistical Programs (NT-SYS) developed by Rohlf, Kishpaugh & Kirk (1974) which was employed by Dippenaar (1980).

A rectangular data matrix, n X t, with n rows (= characters) and t columns (= OTU's), was standardised by rows (STAND program, Rohlf *et al.*, 1974) so that each measurement was expressed in terms of standard deviation units from the mean. Average Taxonomic

Distance (ATD) and Pearson product-moment correlation coefficients were computed between the OTU's (SIMINT program, Rohlf *et al.*, 1974).

The following cluster analyses were performed on the symmetric distance and correlation matrices using the TAXON (Rohlf *et al.*, 1974) program: Single linkage (SL); complete linkage (CL); unweighted pair-group method using arithmetic averages (UPGMA); weighted pair-group method using arithmetic averages (WPGMA) and unweighted pair-group method using centroid averaging (UPGMC).

The Principal Component Analysis method of ordination was used with a matrix of product-moment correlation coefficients between characters, computed by the SIMINT program. The co-ordinates of OTU's with respect to the principal axes were computed (PROJECTION program), together with a minimally connected graph (Minimum Spanning Tree = MST) computed by the MST program. This type of graph is referred to as "directly connected" by Dippenaar (1980).

Two ordinations were performed. In the first, 8 OTU's with missing characters were discarded and, in the second 8 characters not present in all OTU's or shown to be highly correlated, were discarded.

Analyses were undertaken at the Centre for Computing Services (CCS) C.S.I.R., Pretoria, where the NT-SYS was available on an IBM S/370 model 158 computer.

6. RESULTS

6.1 MATERIALS AND METHODS

Eighty one collections belonging to 12 subgeneric taxa were studied and identified. Isolates were obtained with ease from material surface sterilized and incubated as described. They grew readily and sporulated well on most media tested under the conditions described above. Of five media originally used, namely CD, CDY, MEA, MSA and PCA, it was found that CDY and MSA promoted both good mycelium growth and abundant sporulation. These two media were consequently selected for the comparison of isolates in pure culture. MEA promoted excessive mycelium development, while CD supported only restricted growth. Colonies on PCA were effuse and essentially characterless.

The slimy substance which sheaths the conidia and mycelium of *Colletotrichum* species creates a problem in SEM as it masks the form of underlying structures. The washing procedure followed, however, was effective in removing sufficient slime to facilitate observation.

Critical point drying was necessary to preserve the structure of the thin-walled conidia and the conidiogenous cells. Observations are included in the description of individual species below.

6.2 TAXONOMIC POSITION (SUTTON, 1980) AND GENERIC DIAGNOSIS OF *COLLETOTRICHUM*

Division:	Mycota
Subdivision:	Deuteromycotina
Class:	Blastodeuteromycetes
Subclass:	Enteroblastomycetidae
Order:	Phialidales
Suborder:	Phialostromatineae
Genus:	*Colletotrichum* Cda in Sturm, *Deutschlands Krypt. Flora* 3: 41 (1831 - 1832)

Full synonomy, which includes 19 names, is given by Sutton (1980).

Type species:	*C. dematium* (Pers. *ex* Fr.) Grove (= *C. lineola* Cda).
Teleomorph:	*Glomerella* (Stonem.) Sp. & Schr.

Conidiomata acervular, basal layer thin to stromatically thickened, hyaline to dark brown or black, glabrous or setose, erumpent. *Conidiophores* smooth, branched,hyaline to brown. *Conidiogenous cells* phialidic, cylindrical to subcylindrical, smooth, hyaline frequently becoming brown, collarette mostly absent or inconspicuous, periclinal thickening of phialidic apex mostly prominent. *Conidia* straight or falcate, cylindrical with rounded ends to fusoid or spindle-shaped, smooth, hyaline singly but cream-coloured to pale pink or orange in mass, aseptate becoming septate prior to germination. *Appressoria* with entire or crenate to irregular margins, pale to dark brown, simple or in chains. *Setae* subulate, brown to black, septate, infrequently fertile. *Sclerotia* sometimes present, spherical to subspherical or somewhat elongate, dark brown to black, glabrous or setose, often forming conidiomata.

6.3 KEY TO THE SPECIES OF *COLLETOTRICHUM* EXAMINED IN THIS STUDY

1. Conidia falcate or at least curved at the ends 2
1' Conidia mostly straight 3
2. Conidia fusoid, curved mainly at the ends, average width 3 µm .... 1 *C. dematium*
2' Conidia falcate, average width 4 µm .... 2 *C. graminicola*
3. Conidia mostly with obtuse ends 4
3' Conidia with tapered ends 5
4. Conidium width greater than 6 µm, appressoria lobed .... 3 *C. crassipes*
4' Conidium width less than 5,5 µm, appressoria mostly not lobed 7
5. Sclerotia absent or only scattered, conidia average 13 – 18 x 3 µm 6
5' Sclerotia present in abundance, conidia average 18 – 19 x 3,5 – 4 µm .... 4 *C. coccodes*
6. Conidia 13 – 15 x 3 – 3,5 µm, fusoid, setae rarely present, shorter than 80 µm, 0 – 2 septate 10
6' Conidia 16 – 18 µm, cylindrical, mostly with unilaterally tapering ends, setae longer than 80 µm, 1 – 7 septate .... 5 *C. destructivum*
7. Growth rate in culture relatively fast, colony diameter mostly exceeding 70 mm in 7 days; no setae; hosts *Musa* spp .... 6 *C. musae*
7' Growth rate slower than the above, diameter mostly not exceeding 50 mm in 7 days; setae often present 8

8. Growth rate 35 – 45 mm colony diameter in seven days, conidia average 17 – 20 μm in length, hosts Cucurbitaceae .... 7 *C. orbiculare*

8' Growth rate 20 – 30 mm diameter in 7 days, conidia average 10 – 15 μm in length 9

8" Growth rate variable, conidia 10 – 25 μm long averaging 15 – 16 μm, polyphagous .... 8 *C. gloeosporioides*

9. Colonies in culture near black with a whitish marginal zone; hosts mostly *Phaseolus* spp .... 9 *C. lindemuthianum*

9' Colonies in culture mostly in olive-green shades, hosts Leguminosae, especially *Medicago* spp .... 10 *C. trifolii*

10. Colony colour in culture in shades of gray .... 11 *C. fructigenum*

10' Colony colour in culture in shades of pink to reddish .... 12 *C. fructigenum* f. sp. *chromogenum*

6.4 NOTES ON THE MORPHOGENESIS OF *COLLETOTRICHUM* IN CULTURE

6.4.1 Conidiomata

Conidiomata comprise aggregations of branching conidiophores which form more or less compact structures. These conidiophores may arise from single hyphae or hyphal branches (Fig. 1B) or several adjacent branches may contribute to conidiomata formation.

In *C. graminicola* isolates from maize and in *C. fructigenum,* little or no branching of the conidiogenous cells takes place and they frequently remain simple (Fig. 3D; 4C). In *C. dematium,* however, large compact, darkly pigmented conidiomata are formed (Fig. 1C), often becoming stipitate with increasing age and continued elongation. Conidiomata may also be produced from germinating sclerotia, especially in *C. coccodes* (Fig. 9G).

6.4.2 Conidiogenous Cells and Conidiophores

Primary conidiogenous cells arise as projections from hyphal cells within the aerial or submerged mycelium. They elongate, enlarge and are separated from the mother cell by a septum. Conidiogenous cells may remain solitary, or the remaining basal projection may elongate further, becoming septate (Fig. 2A). These conidiophore cells may produce conidiogenous cells and the branching process be repeated, giving rise to a compact fertile structure.

Conidiophore and conidiogenous cells are initially hyaline, becoming pale to dark brown with age, sometimes becoming thick-walled. Percurrent proliferation of the phialidic conidiogenous cells takes place occasionally, a secondary conidiogenous opening being produced through the primary opening in place of an additional conidium (Figs. 2A2, 3C; 8E; 13C; 15C).

6.4.3 Conidium Ontogeny

Conidium ontogeny is phialidic. The first formed conidium from a conidiogenous cell is produced blastically, leaving an opening through which a basipetal succession of conidia is formed (Fig. 3D). Conidia are extruded from the phialide opening, initially appearing obovoid to clavate (Fig. 3C, F, G) . They enlarge, obscuring the opening, elongate and take on the form characteristic of the species concerned (Figs. 3H; 8D). A truncate attachment point is visible at the base of each conidium after it has seceeded (Fig. 2B).

The conidiogenous cells have no or only inconspicuous colarettes as the meristematic locus is situated near the tip of the cell (Figs. 2A; 3G). They do, however, mostly have typically thickened phialidic apices (Figs. 6C; 18B).

6.4.4 Conidium Germination and Appressorium Formation

Prior to germination the amerosporous *Colletotrichum* conidia become one or sometimes two septate. A germ tube arises from one or two of the daughter cells, elongating to various degrees or producing an appressorium directly (Fig. 4F, G).

Appressoria are formed by the blastic apical swelling of a germ tube or hypha, delimited later by a septum. They become multinucleate, thick-walled, pale to dark brown, and vary in shape from globose to irregularly lobed, sometimes septate or occurring in chains (Figs. 2C; 6F; 23C1 & C2). They have a germination pore through which infection hyphae are produced.

In *C. fructigenum,* appressoria are formed only infrequently by germinating conidia. The conidia become septate, but instead of producing germ tubes, one or both daughter cells become conidiogenous. A lateral phialidic opening is formed through which a secondary conidium is produced (Figs. 22G; 23B1 & B2). These secondary conidia may seceed or may remain attached and also produce conidia. This phenomenon gives rise to a network of connected conidia (Fig. 22H).

6.4.5 Seta Ontogeny

Setae may originate with conidiogenous cells as branches from a common mother cell (Fig. 2A), from adjacent cells (Fig. 3D), or the one may be produced as a side branch from the basal cell of the other (Fig. 7A). They elongate, becoming thick-walled, pale brown to black and septate.

Infrequently setae are found producing conidia (Fig. 18E). This indicates the homologous origin of setae and conidiogenous cells.

6.4.6 Sclerotium Ontogeny

Microsclerotia are formed by the intertwining of adjacent hyphal branches which in turn branch and form a compact mass of swollen cells (Fig. 9E, F). These cells become thick-walled and darkly pigmented. They may give rise to setae and conidiogenous cells, the sclerotium consequently becoming a conidioma (Fig. 9G).

6.5 DESCRIPTIONS OF *COLLETOTRICHUM* SPECIES EXAMINED

6.5.1 *Colletotrichum dematium* (Pers. *ex* Fr.) Grove, *J. Bot. Lond.* 56: 341 (1918)

Sphaeria dematium Pers., *Syn. Meth. Fung.* 88 (1801)
Vermicularia dematium Pers. *ex* Fr., *Summa Veg. Scand.* 420 (1849)
Colletotrichum lineola Cda. Sturm, *Deutschl. Krypt. Flora* 3: 41 (1831 –32)

A comprehensive synonomy which includes 83 additional names is given by Arx (1957a).

Culture description

Colonies on MSA are restricted to spreading, attaining a diameter of 30 to 55 mm in seven days. The margin is entire to somewhat irregular, submerged. Mycelium in the marginal zone is thinly, closely appressed to downy, colourless to Vinaceous-Buff or Pale Olive-Buff, becoming Hair Brown to Deep Mouse Gray and floccose to woolly or felty towards the centre, alternating with coarsely farinaceous concentric zones of Chaetura Drab to Olivaceous Black conidiomata (Fig. 1A). The reverse is Pinkish Buff to Pale Olive-Buff in the marginal zone, becoming Wood Brown to Deep Mouse Gray in the central zone with concentric zones of Chaetura-Drab to Olivaceous Black.

Colonies on CDY attain diameters of 35 to 60 mm in seven days. The margin is irregular, submerged. The marginal zone is thinly, closely appressed to cobwebby or downy, Buff-Pink to Pale Olive-Buff, becoming cottony or floccose to felty towards the centre, Grayish Olive or Quaker Drab to Deep Mouse Gray alternating with coarsely farinaceous concentric zones of Deep Mouse Gray to Deep Olive conidiomata (Fig. 1A). Reverse, marginal zone Warm Buff to Pale Olive-Buff, becoming Dark Mouse Gray or Vinaceous-Cinnamon in the central zone, with concentric bands of Blackish Mouse Gray or Iron Gray.

Conidiomata on both MSA and CDY are usually strongly developed, pulvinate, darkly pigmented, with abundant robust, black setae projecting above the white to pale orange conidial masses (Fig. 1B, C). They are formed in distinct, compact concentric zones, alternating with the grayish aerial mycelium (Fig. 1A). Scattered sclerotia are sometimes formed, later giving rise to conidiomata.

Morphology in culture

Conidiomata densely setose, stromatically thickened, pulvinate to somewhat conical, darkly pigmented, 220 – (330) – 500 µm in diameter on MSA and 285 – (600) – 800 µm on CDY (Fig. 1B, C).

Conidiogenous cells phialidic, cylindrical to narrowly clavate, hyaline to pale brown becoming dark brown or black with age, forming a compact mass on branching conidiophores (Figs. 1E; 2A; 3A), sometimes forming percurrent proliferations (Figs. 2A2; 3C). They are 8 - (16,7) - 33 x 2,5 - (3,1) - 4,5 µm on MSA and 12 - (17,2) - 24 x 2 - (3,0) - 4,5 µm on CDY.

Conidia hyaline, curved fusiform with truncate base (Figs. 1D; 2B; 3B), 18 - (23,4) - 32 x 2,5 - (2,9) - 4 µm, mostly 22 x 3 µm, on MSA and 16 - (23,1) - 34 x 2 - (2,9) - 4 µm, mostly 21 x 3 µm, on CDY.

Appressoria medium brown, oval to irregularly lobed, 7,5 - (11,7) - 18 x 4 - (7,1) - 12,5 µm (Figs. 1F, G; 3C), formed abundantly from both germinating conidia and vegetative mycelium. Mostly unicellular but frequently septate (Fig. 2C).

Setae abundant, robust, arising from conidiophore branches, distributed throughout conidiomata (Figs. 1B; 2A). Elongate fusiform, dark brown to black with increasing age, 1 - (4) - 18 septate on MSA and 72 - (165) - 640 x 3 - (5,3) - 8 µm, more robust on CDY, 1 - (4) - 9 septate, 63 - (172) - 400 x 2,5 - (5,8) - 10,5 µm.

Morphology on host material

On the host, acervuli are generally large, black, stromatic, densely setose, protruding from the ruptured tissue. Setae robust, erect, black, 45 - (109) - 280 x 3 - (5,8) - 13 µm, 2 - (3) - 5 septate, emerging above the white to orange conidial masses. Conidia curved fusoid, hyaline, 16 - (25,4) - 35 x 2 - (2,9) - 4 µm.

No teleomorph has been found in association with the anamorph in the present or previous studies.

In the present study *C. dematium* has been found as a saprobe or in association with irregular pale to dark brown lesions on a variety of hosts in different families.

Specimens examined

PREM 45809 on *Arachis hypogaea* stem, Vaalharts, 28th October, 1976;
PREM 45381 on *Arachis hypogaea* stem, Vaalharts, 28th February, 1977;
PREM 45738 on *Beta vulgaris* leaf, Pretoria, 18th February, 1977;
PREM 45811 on *Fragaria* sp. leaf, Pretoria, 28th February, 1977;
PREM 45374 on *Arachis hypogaea* stem, Vaalharts, 10th March, 1977;
PREM 45814 on *Capsicum frutescens* fruit, Pretoria, 28th March, 1977;
PREM 45373 on *Beta vulgaris* petiole, Nylstroom, 15th April, 1977;
PREM 45751 on *Allium cepa* "Texas Grano" leaf bases, Weenen, 14th December, 1977;
PREM 45820 on *Medicago sativa* roots, Brits, 21st November, 1977;
PREM 45821 on *Tribulus terrestris* leaflets, Middelburg C. Prov., 7th March, 1978.
PREM 45832 on *Lycopersicum esculentum* fruit, Pretoria, February, 1979.

Comment

The description and dimensions given above correspond generally with those given by Grove (1918, 1937), Wollenweber & Hochapfel (1949), Arx (1957a), Sutton (1962, 1980), Simmonds (1965) and Kulshrestha, Mathur & Neergaard (1976). Conidium widths, however, tend to be narrower than those quoted by these workers.

C. dematium is very variable. Wollenweber & Hochapfel (1949) and Kulshrestha *et al.* (1976) listed ranges in conidium dimensions of a large number of isolates from different hosts. They illustrated the wide spectrum of conidium shapes to be found in this species. Sutton (1962) reported considerable variation in culture characteristics as regards the distribution of aerial mycelium, sclerotia and acervuli.

Arx (1957a, 1970) grouped all the non-graminicolous *Colletotrichum* species with curved conidia in *C. dematium,* which he regarded as a variable, usually saprobic polyphage. He recognised three morphologically indistinguishable parasitic forms. Sutton (1980), however, divided *C. dematium sensu* Arx (1957a) into five species: *C. trichellum,* pathogenic on *Hedera* spp.; *C. circinans* on *Allium* spp.; *C. truncatum* on Leguminosae, together with *C. capsici* and *C. dematium,* both termed "group" species.

Arx (1957a, 1970) regarded the morphologically indistinguishable *C. circinans* and *C. truncatum* as host specific forms of *C. dematium* and designated them *C. dematium* f. sp. *circinans* and *C. dematium* f. sp *truncatum* respectively. According to the International Code of Botanical Nomenclature, this is the correct approach in distinguishing physiological differences within a morphological species (Ainsworth, 1971).

C. dematium and *C. capsici* are separated by Sutton (1980) on the grounds that the former is saprobic with slightly broader conidia than the latter, pathogenic fungus. However, Sutton (1980) concedes that the distinction between the two is not satisfactory because of their wide variability. He is of the opinion that more examination of the non-graminicolous falcate-spored *Colletotrichum* representatives is necessary before adequate separation of taxa can take place within this complex.

The retention of Arx's (1957a, 1970) concept of *C. dematium* is consequently upheld in this study.

C. dematium is characterized both in culture and on host material by strongly developed black or near black conidiomata and setae, together with relatively long, narrow curved fusiform conidia, curved mainly at the apex and base. It is primarily a polyphagous saprobe with an extensive host range (Arx 1957a, Sutton 1980).

6.5.2 *Colletotrichum graminicola* (Ces.) Wilson, *Phytopàthology* 4: 110 (1914)
Dicladium graminicolum Ces., *Flora* 35: 398 (1852)
Steirochaete graminicola (Ces.) Sacc., *Syll. fung.* 4: 316 (1886)

Teleomorphosis: *Glomerella graminicola* Politis, *Mycologia* 67: 61 (1975)

Arx (1957a) lists 35 synonyms, including; those given above, while Sutton (1980) lists only five.

Culture description

Colonies on MSA are mostly spreading, attaining a diameter of 42 to 60 mm in seven days. Colony margin is entire, sometimes submerged, marginal zone closely, thinly appressed or cobwebby, Vinaceous-Buff to Light Grayish Olive. Aerial mycelium becomes subfelty to cottony towards the centre of the colony, Dark Olive to Dark Vinaceous-Gray or Quaker Drab, alternating with coalescing concentric zones of coarsely farinaceous condiomata, Vinaceous-Fawn to Russet, or Blackish Mouse Gray (Fig. 4A). The reverse is colourless to Vinaceous-Buff in the marginal zone, becoming Deep Grayish Olive to Brownish Drab with concentric zones of Vinaceous-Fawn to Olivaceous Black in the centre.

On CDY colonies attain a diameter of 25 to 46 mm in seven days. The margins are entire to irregular, marginal zone closely, thinly appressed to cobwebby, Light Mouse Gray to Pale Ochraceous-Salmon or Pale Olive -Buff, becoming cottony to woolly towards the centre, Dark Grayish Olive to Chaetura Drab or Deep Mouse Gray (Fig. 4A). Reverse is Pale Ochraceous-Salmon to Olive-Buff in the marginal zone, becoming Dark Grayish Olive or Chaetura Drab to Fuscous or Chaetura Black in the centre.

Conidiomata are mostly irregular, radially elongated, forming a reticulate network both on and below the agar surface. They are astromatic to stromatic, in some isolates, darkening in colour with the development of setae. Dark setae are formed abundantly, projecting above the orange-coloured conidial masses.

Morphology in culture

Conidiomata setose, astromatic or somewhat stromatically thickened, irregular to pulvinate, 35 - (270) - 550 µm in diameter on MSA and 35 - (250) - 450 µm on CDY.

Conidiogenous cells phialidic, rather robust, cylindrical to slightly clavate, hyaline to pale brown becoming darker with age, especially on CDY; formed side by side on hyphae running parallel to the agar surface (Figs. 4C; 3D) in astromatic conidiomata, or on branched conidiophores (Fig. 3E) in stromatic conidiomata. They measure 7,5 - (13,4) - 32 x 3 - (5,2) - 6,5 µm on MSA and 7,5 - (13,7) - 27 x 3,5 - (5,5) - 7 µ m on CDY.

Conidia falcate, hyaline, tapering gradually to an acute apex and truncate base, apex frequently somewhat attenuated and more sharply curved than the rest of the conidium, especially in isolates from maize and sorghum (Figs. 4D, E; 5B). They are 16 - (27,3) - 36 x 3 - (3,9) - 5 µm on MSA, mostly 27 - 29 x 4 µm, and 17 - (24,6) - 31,5 x 3 - (4,1) - 5 µm on CDY, mostly 24 - 27 x 4 µm.

Appressoria medium brown, clavate but mostly irregularly lobed, unicellular or septate (Figs. 4F, G; 5C) 7 - (10,3) - 25 x 6 - (7,5) - 14,5 µm, formed from germinating conidia and vegetative mycelium.

Setae abundant, arising from hyphae running parallel to the agar surface (Fig. 3D) or scattered on branched conidiophores alongside the conidiogenous cells (Fig. 5A); subulate, dark brown, 50 - (116) - 305 x 3 - (5,6) - 7,5 µm on MSA and 2 - (4) - 6 septate; 55 - (115) - 280 x 4 - (5,8) - 8,5 µm and 1 - (3) - 6 septate on CDY, projecting above the conidial masses.

Morphology on host material

Acervuli on host material are mostly astromatic or slightly stromatically thickened, developing hypostromatically. Conidiogenous cells and setae are produced on penetration hyphae outside the outer epidermis wall. The basal layer of the acervulus frequently enlarges with age, causing the epidermis to rupture. Conidiogenous cells are robust, cylindrical, hyaline to pale brown. Conidia are falcate with an acute apex and truncate base,15 - (27,3) - 43 x 3 - (3,9) - 5,5 µm.

Setae are abundant, subulate with a slightly swollen base, brown, 45 - (130) - 305 x 3,5 - (6,5) - 11 µm, 1 - (4) - 7 septate.

No teleomorph has been found in association with the anamorph in the present study. However a teleomorph has been reported (Politis & Wheeler, 1972) and described (Politis, 1975) as *Glomerella graminicola* Politis.

Lesions caused by *C. graminicola* vary greatly in size and appearance but are mostly elongate, pale orange-brown to reddish brown or blackish, centres becoming grey with age, found on stems, roots, leaves or fruit. The fungus may penetrate the stem, causing a greyish discolouration of the pith. According to Arx (1957a), this species has a wide range of hosts in the Gramineae, but Sutton (1980) considers *C. graminicola, sensu stricto*, to be limited to *Zea.*

Specimens examined

PREM 45810 on *Zea mays* leaf, Ermelo, March 1977;
PREM 45832 on *Zea mays* leaf, Delmas, February 1977;
PREM 45815 on *Festuca erudinaceum* leaf, Cedara, 4th April 1977;
PREM 45822 on *Zea mays* fruit, Nylstroom, 20th June 1977;
PREM 45823 on *Lolium multiflorum* leaf, Stellenbosch, April 1977;
PREM 45744 on *Zea mays* leaf, Lions River Natal, 18th July 1978;
PREM 45747 on *Sorghum caffrorum stems,* Skandinawieëdrif W. Tvl., April 1978;
PREM 45779 on *Lolium multiflorum* seed, Howick, 30th May 1979;
PREM 45749 on *Zea mays* fruit, Delmas, July 1979.

Comment

The above description and dimensions correspond with those given by Wilson (1914), Böhning & Wallner (1936), Wollenweber & Hochapfel (1949), Arx (1957a), Tarr (1962), Mordue (1967b) and Sutton (1968, 1980).

There is a certain degree of taxonomic confusion surrounding the graminicolous *Colletotrichum* taxa. Wilson (1914), in a study of the species of grass anthracnose fungi similar to *Colletotrichum cereale* Manns., found that certain species in the genera *Dicladium, Psilonia, Vermicularia* and *Colletotrichum* could be considered identical and that the oldest valid binomial applicable to this fungus was *Dicladium graminicolum* Cesati. Wilson (1914) transferred this species to the genus *Colletotrichum* as *C. graminicolum* (Ces.) Wilson.

Saccardo (1886) had placed *Dicladium graminicolum* Ces. in the genus *Steirochaete* A. Br. & Casp. – which he regarded as being related to *Colletotrichum* and to *Ellisiella* – as *Steirochaete graminicola* (Ces.) Sacc. However, Saccardo (1886) added the question: "An *Colletotrichi* species?" (pg. 316). Both Cesati (1852) and Saccardo (1886) had described the conidia of this fungus as frequently occuring in chains before seceeding. This prompted Wollenweber & Hochapfel (1949) to view Wilson's (1914) new combination with doubt.

Wollenweber & Hochapfel (1949) adopted the binomial *Vermicularia graminicola* Westendorp for the maize anthracnose organism which Böhning & Wallner (1936) had identified as *C. graminicolum* (Ces.) Wils. in accordance with Wilson's (1914) findings.

Wilson (1914) had examined the cotype material of *Vermicularia graminicola* Westend., but found that its poor condition precluded an opinion as to its identity. He regarded material issued under the same name by Allescher, Schnabl and by Roumeguere as representative of "true *Vermicularia*" and consequently did not list the latter binomial, *V. graminicola* Westend., as a synonym of *C. graminicolum.*

Le Beau (1950) tested 593 isolates of *Colletotrichum* from 18 different grass host species for pathogenicity to sorghum and sugarcane. Three distinct groups were found. Isolates from sugarcane were highly pathogenic to sugarcane but rarely to sorghum. Isolates from sorghum, Johnson grass, Sudan grass, *Erianthus* and broom corn were non-pathogenic on sugarcane but mostly highly pathogenic on sorghum. The few other isolates from the remaining 13 grass species were not pathogenic to either sorghum or sugarcane.

Arx (1957a) grouped 35 grass anthracnose fungi together under the binomial *Colletotrichum graminicola* (Ces.) Wilson, including *C. falcatum* Went. and *Vermicularia graminicola* West. He (Arx, 1957a) cited both Cesati's (1852) and Wilson's (1914) form of the specific epithet incorrectly, as *Dicladium graminicola* Ces. and *Colletotrichum graminicola* (Ces.) Wils. instead of *D. graminicolum* and *C. graminicolum* respectively. The gramatically correct form of the specific epithet is, as used by Arx (1957a), "*graminicola*" because '-icola' is an invariable Latin substantive (Hawksworth, 1974) and must be treated in the same way for all genders even though the generic name is masculine or neuter (Stearn, 1973).

As Arx (1957a) regarded *C. falcatum* and *C. graminicola* as being conspecific, he considered the teleomorph of *C. falcatum, Glomerella tucumanensis* (Speg.) Arx & Müller, to be the teleomorph of the whole graminicolous *Colletotrichum* complex. This fungus had been regarded as *Physalospora tucumanensis* Speg. by Carvajal & Edgerton (1944), but transferred to *Glomerella* by Arx & Müller (1954).

Arx's (1957a & b) opinions regarding *C. graminicola* and *C. falcatum* did not receive unanimous support. Tarr (1962) conceded that the conidia of some strains of *C. graminicola* cannot be distinguished from those of *C. falcatum* and that it was consequently probably best to regard them as different pathogenic races of the same species. Tarr (1962), however, maintained that established usage and the fact that a teleomorph was known only for *C. falcatum* justified the separation of the two species.

Mordue (1967b & c) and Sutton (1968) distinguished between *C. graminicola* and *C. falcatum* on the grounds of conidium and appressorium morphology. The conidia of *C. graminicola* are regarded as being falcate or spindle shaped, while those of *C. falcatum* are sickle shaped (Mordue, 1967c). Appressoria of *C. graminicola* are described as obovate, pyriform or elliptical to irregular, while those of *C. falcatum* are broadly clavate, rarely becoming tapered at the apex, irregular or lobed (Sutton, 1968). Sutton (1968) therefore concluded that *C. graminicola* and *C. falcatum* are distinct species and was of the opinion that *C. graminicola* consists of at least two dissimilar taxa.

Politis & Wheeler (1972) reported finding the *Glomerella* teleomorph of *C. graminicola.* On the basis of Sutton's (1968) conclusions, Politis (1975) described it as *Glomerella graminicola* Politis, distinguishing it from *G. tucumanensis,* the teleomorph of *C. falcatum,* by morphological and pathogenic differences.

Sutton (1980) separated the graminicolous *Colletotrichum* representatives regarded by Arx (1957a & b) as *C. graminicola* (Ces.) Wils. into the following four taxa on the grounds of conidium and appressorium morphology as well as host specificity:
C. caudatum (Sacc.) Pk.; *C. falcatum* Went. on *Saccharum* spp.; *C. sublineolum* P. Henn. on *Sorghum* spp. and *C. graminicola* (Ces.) Wilson on *Zea* spp.

The graminicolous isolates examined in the present study may be divided into three groups according to Sutton's (1980) key: *C. graminicola* from *Zea, C. sublineolum* from *Sorghum* and a group of isolates from various other hosts which do not fit into any of the four taxa recognised by Sutton (1980). As these isolates were variable as regards conidium and appressorium dimensions and shape – characters used by Sutton (1980) to distinguish the respective taxa – and as no cross-inoculation tests were carried out in the present study, they were placed in *C. graminicola* (Ces.) Wils. *sensu* Arx (1957a, 1970) *pro parte. C. falcatum* West. is recognised as a separate species on the evidence presented by Le Beau (1950), Mordue (1967b & c), Sutton (1968, 1980) and Politis (1975).

C. graminicola is characterized by its relatively broad, falcate conidia which taper gradually to an acute apex and truncate base. In culture colonies are usually in brownish or purplish gray shades, often growing in a distinctive radially stranded pattern termed "dendritic" (Mordue, 1967b). Conidiomata are often not distinct but spread along these radial strands.

C. dematium and *C. graminicola,* both species with curved conidia, may be distinguished by the shorter, narrower conidia with rounded rather than acute apices of the former. In addition, the setae and conidiomata formed by *C. dematium* are more robust and larger than those formed by *C. graminicola* (Table 1).

6.5.3 *Colletotrichum crassipes* (Speg.)Arx, *Verh. Akad. Wet. Amst.* 51: 77 (1957)
Gloeosporium crassipes Speg., *Ampel. ital.* 405 (1878)

17 synonyms are listed by Arx (1957b) and an additional two by Sutton (1980).

Culture description

Cultures on MSA attain a diameter of 45 to 58 mm in seven days. Colony margins are entire, marginal zone closely, thinly appressed, Mouse Gray to Seashell Pink. The central zone is woolly or woolly alternating with concentric farinaceous zones, Dark Mouse Gray to Deep Mouse Gray (Fig. 6A). The reverse, marginal zone is Vinaceous-Buff to Light Drab, becoming Dark Mouse Gray or Chaetura Drab to Deep Mouse Gray in the centre.

On CDY colonies attain a diameter of 50 to 58 mm in seven days. Margins are entire, marginal zone closely appressed, Pale Mouse Gray to Drab-Gray or Ecru-Drab, becoming downy, Hair Brown. The central zone is cottony to woolly in the centre, Benzo Brown to Mouse Gray or Dark Quaker Drab (Fig. 6A). Reverse, marginal zone is Deep Olive-Buff to Warm Buff, becoming Chaetura Drab to Hair Brown, central portion Fuscous.

Conidiomata on both MSA and CDY are somewhat stromatically thickened, pulvinate, dark with robust black setae projecting above the cream-coloured or orange-tinged conidial masses, formed in concentric bands.

Morphology in culture

Conidiomata setose, pulvinate, becoming more stromatic and darker in pigmentation with increasing age (Fig. 6B); 135 - 325 μm in diameter on MSA and 170 - 350 μm on CDY.

Conidiogenous cells robust, broadly clavate, hyaline to pale brown,borne on branching conidiophores (Figs. 6C; 7A); 12 - (15,6) - 19 x 5,5 - (6,1) - 6,5 μm on MSA and 8,5 - (13,3) - 21 x 5,5 - (6,4) - 8 μm on CDY.

Conidia straight, broad cylindrical, obtuse apices, bases with truncate attachment point (Figs. 6D, E; 7B; 8A); 14 - (20,8) - 28,5 x 5,5 - (6,8) - 7,5 μm on MSA, mostly 18 - 24 x 7 - 7,5 μm, and 17 - (25,0) - 33 x 5,0 - (6,3) - 7 μm on CDY, mostly 23 - 27 x 6 - 6,5 μm.

Appressoria obovoid to clavate but deeply and irregularly lobed, brown to medium brown, unicellular, septate or in chains (Figs. 6F; 7B); 10 - (14, 7) - 24 x 6 - (7,8) - 13 μm.

Setae robust, subulate, dark brown to black, scattered on the branching conidiophores (Fig. 6B; 7A); 85 - (125) - 170 x 5 - (6,6) - 8 μm and 1 - (3) - 4 septate on MSA, 48 - (90) - 160 x 6 - (7,8) - 11 μm and 1 - (2) - 4 septate on CDY.

Morphology on host material

On host tissue acervuli are large, dark, stromatic with erect, subulate black setae projecting above the cream-coloured to pinkish conidial masses.

Conidia are broad cylindrical with obtuse apices, measuring 15 - (21,0) - 30 x 5,5 - (6,4) - 7,5 μm.

No teleomorph has been described in association with the anamorph although Arx (1957a) notes the presence of sterile perithecial initials in one of the isolates he examined. This phenomenon also occurred in the isolates in the present study.

Lesions caused by *C. crassipes* are variable in size and appearance, brown to reddish brown, often with a dark perimeter, round to elongate or irregular. It is polyphagous (Arx, 1957a) occurring as a pathogen or as a saprobe, causing leaf or stem spot and fruit rot.

Specimens examined

PREM 45774 on *Psidium guajava* leaf, Nelspruit, 25th May 1978;
PREM 45833 on *Bixa* sp. leaf, Burgers Hall Research Station E. Tvl, 23rd May 1978.

Comment

The description and dimensions given above largely correspond with those given by Arx (1957a, b & c, 1970), Stephan (1967a) and Sutton (1980). Arx (1957a, b & c, 1970) described *C. crassipes* as having glabrous or only sparsely setose conidiomata, while those formed by the isolates in this study had abundant setae. This corresponds with the description of *C. grossulariae* Jacz. (De Jaczewski, 1906), regarded by Arx (1957a) as a synonym of *C. crassipes,* and with that given by Sutton (1980).

There is some evidence that *C. crassipes* may be a form of the variable polyphage, *C. gloeosporioides* Penz., anamorph of *Glomerella cingulata* (Stonem.) Sp. & Schr. Chilton, Lucas & Edgerton (1945) noted an anamorphic strain of *G. cingulata* which produced unusually broad conidia. Arx (1957a & c) described inocculation experiments with an isolate of *C. crassipes* on young *Phaseolus vulgaris* plants in which the conidia of successive reisolations gradually decreased in size until those of the 5th reisolation resembled those of *C. lindemuthianum.* Arx (1957a) regarded the latter species as a host specific form of *C. gloeosporioides.*

In the present study, forms of *C. gloeosporioides* transitional to *C. crassipes* were examined. These had broader conidia and larger, more lobed appressoria than those of *C. gloeosporioides* This phenomenon has also been described by Stephan (1967a). In the multivariate phenetic analyses performed on the taxonomic data in this study (see Section 6.6), these transitional isolates were commonly placed in close association with the *C. crassipes* isolates.

C. crassipes is characterized by broad, straight cylindrical conidia and by large, deeply lobed appressoria (Tables 1 & 3).

6.5.4 *Colletotrichum coccodes* (Wallr.) Hughes, *Can. J. Bot.* 36: 754 (1958)
Chaetomium coccodes Wallr., *Fl. Crypt. Germ.* 2: 265 (1833)
Vermicularia atramentaria Berk. & Br., *Ann. Mag. Nat. Hist.* 5: 378 (1850)
Colletotrichum atramentarium (Berk. & Br.) Taubenh., *Mem. N. Y. Bot. Gdn.* 6: 549 (1916)

A list of 13 additional synonyms is given by Arx (1957a) under the name *C. atramentarium.*

Culture description

Colonies on MSA attain a diameter of 35 to 45 mm in seven days. Colony margins are entire to somewhat irregular, sometimes slightly submerged. The marginal zone is closely, thinly appressed, Drab-Gray to Pinkish Buff, becoming subfelty to cottony towards the centre, Pale Mouse Gray to Chaetura Drab or Chaetura Black, alternating with coalescing farinaceous concentric zones (Fig. 9A). The reverse marginal zone is Olive -Buff to Pale Pinkish Buff, becoming Vinaceous-Cinnamon towards the centre of the colony, alternating with Chaetura Black concentric zones. Slight segmentation was present in some isolates which formed areas with abundant aerial mycelium and sclerotia.

Colonies on CDY attain a diameter of 38 to 50 mm in seven days. Colony margins are entire, sometimes slightly submerged. The marginal area is closely, thinly appressed to downy, Buff-Pink to Pale Drab-Gray, becoming cobwebby to floccose, Vinaceous-Cinnamon to Light Mouse Gray, alternating with farinaceous concentric bands of Blackish Mouse Gray (Fig. 9A). The reverse marginal zone is Buff-Pink to Olive-Buff, becoming Vinaceous-Cinnamon towards the centre of the colony, banded with Olivaceous Black to Blackish Mouse Gray concentric zones. Slight segmentation similar to that on MSA also occurred.

Colony appearance is usually dominated by the formation of abundant spherical, black microsclerotia which frequently develop into conidiomata, becoming setose and producing conidiogenous cells. Conidiomata which do not originate from sclerotia are pulvinate, only slightly stromatically thickened, with slender erect dark brown to black setae projecting above the orange conidial masses.

Morphology in culture

Conidiomata astromatic to stromatically thickened, pulvinate, to globose and darkly pigmented when developing from microsclerotia, setose (Fig. 9B, G), 75 - (255) - 435 μm in diameter on MSA and 85 - (235) - 385 μm on CDY.

Conidiogenous cells cylindrical, slightly tapered towards the apex, hyaline to pale brown (Figs. 8B, C, D; 10A), 9 - (15,6) - 22 x 2,5 - (3,2) - 4,5 μm on MSA and 9 - (15,7) - 30 x 2,5 - (3,7) - 5,5 μm on CDY, borne on sparsely branched conidiophores. Percurrent proliferations sometimes occur (Fig. 8E).

Conidia narrow cylindrical, tapering somewhat towards both the rounded apices and truncate bases (Figs. 8D, E; 9C; 10B), 16 - (19,2) - 22 x 2,5 – (3,6) - 4,5 μm on MSA, mostly 19 x 3 μm, and 14 - (18,6) - 24 x 2,5 - (3,6) - 4,5 μm, mostly 18 x 3 μm, on CDY.

Appressoria obovoid to irregularly lobed, medium brown (Figs. 9D; 10C), 8,5 - (13,9) - 19,5 x 5 - (6,9) - 11,5 μm.

Setae straight, subulate, slightly swollen at the base, dark brown (Figs. 9B; 10A), 50 - (130) - 255 x 3 - (4,8) - 8 μm and 1 - (4) - 11 septate on MSA, 50 - (110) - 225 x 4 - (5,1) - 7 μm and 1 - (4) - 8 septate on CDY, scattered throughout the conidiomata on branching conidiophores.

Microsclerotia spherical to subspherical or somewhat elongated, black (Fig. 9E, F, G), 150 - (280) - 330 μm in diameter on MSA and 105 - (230) - 330 μm on CDY, frequently becoming setose and developing conidiogenous cells.

Morphology on host material

On host tissue acervuli are pulvinate to globose, black, originating as microsclerotia which become setose and develop conidiogenous cells, 145 - (170) - 250 μm diameter.

Conidia long cylindrical, tapering towards the apices and truncate bases, sometimes somewhat constricted in the middle, 15 - (17,8) - 22 x 3 - (3,6) - 5 μm.

Setae erect, subulate, black, 50 - (85) - 265 x 4 - (7,8) - 22 μm and 1 - (2) - 5 septate, scattered on the conidiomata and projecting above the orange conidial masses.

No teleomorph was found in this study.

Lesions formed by *C. coccodes* are usually characterized by the presence of numerous submerged black microsclerotia which are often formed in concentric rings.

Specimens examined

PREM	45384	on *Solanum tuberosum* tubers, Kouebokkeveld, 7th February 1977;
PREM	45824	on *Capsicum frutescens* fruit, Magaliesburg, 10th February 1977;
PREM	45739	on *Capsicum frutescens* stem, Magaliesburg, 14th February 1977;
PREM	45834	on *Tribulus terrestris* leaflets, Middelburg C. Prov., July 1978;
PREM	45745	on débris, Middelburg C. Prov., 16th August 1978;
PREM	45372	on *Ipomoea batatas* stem, Roodeplaat Tvl., 18th April 1977.

Comment

The description and dimensions given above correspond with those given by Arx (1957a), Chesters & Hornby (1965a), Simmonds (1965), Mordue (1967a) and Sutton (1980).

Arx (1957a & b) examined Saccardo's type material of *Colletotrichum phomoides* (Sacc.) Chester, the binomial most frequently applied to this fungus, and found that it represents a *Phomopsis* sp. Arx (1957a & b) also ascertained that the binomial had been applied equally as frequently to the anamorph of *Glomerella cingulata, Colletotrichum gloeosporioides*. He (Arx, 1957a) therefore proposed the adoption of the combination *C. atramentarium* (Berk. & Br.) Taubenh.

Hughes (1958) investigated the type material of *Chaetomium coccodes* Wallr. on potato tubers and found that it is identical to the fungus known as *Colletotrichum atramentarium*. He concluded that on the grounds of priority the correct name for the fungus was *Colletotrichum coccodes* (Wallr.) Hughes. This was accepted by Arx (1970).

C. coccodes is a widespread, mainly saprobic polyphage (Arx, 1957a). It is also a relatively unspecialized pathogen (Mordue, 1967a) which attacks a wide range of hosts from different families, the majority in the Cucurbitaceae, Leguminosae and Solanaceae, causing a variety of disease conditions (Chesters & Hornby, 1965b).

Chesters & Hornby (1965a) described cultures varying in pigmentation, size of sclerotia and conidia as well as in the amount of aerial mycelium produced. *C. coccodes* is characterized both on infected host tissue and in culture by the formation of abundant small, black microsclerotia. Its conidia are typically straight cylindrical, relatively long and narrow (Table 1), tapering somewhat towards the rounded apices and truncate bases.

6.5.5 *Colletotrichum destructivum* O' Gara, *Mycologia* 7: 37 (1915)
Colletotrichum sativum Horn., *Phytopathology* 42: 670 (1952)

Culture description

Colonies on MSA reaching a diameter of 40 to 60 mm in seven days. The margins even, marginal zone closely, thinly appressed, Pale Olive-Buff or Seashell Pink, sometimes with Olive segments, becoming downy to floccose towards the farinaceous central zone, Light Cinnamon-Drab with concentric zones of Benzo Brown or Chaetura Drab (Fig. 11A, B). The reverse, marginal area is Pale Olive-Buff or Salmon Color, becoming Grayish Olive or Wood Brown with concentric zones of Chaetura Drab.

On CDY, colonies reach a diameter of 40 to 58 mm in seven days. The margins are even to slightly irregular, the marginal zone closely, thinly appressed, Vinaceous-Buff, becoming subfelty to farinaceous towards the centre, Dark Grayish Olive to Wood Brown, sometimes with Fuscous segments (Fig. 11A, B). Reverse, marginal zone Cream-Buff to Pale Pinkish Buff, becoming Dark Grayish Olive or Fuscous, sometimes with Wood Brown segments towards the centre.

Conidiomata occur both as continuous, non-stromatic farinaceous zones in the centre of the colonies as well as flat, slightly stromatic conidiomata towards the marginal zones. Slender brown, rather sparse setae project above pale orange conidial masses.

Morphology in culture

Conidiomata astromatic or stromatic, pulvinate, somewhat flattened, pale to dark brown (Fig. 11C), measuring 65 - (195) - 640 μm in diameter on MSA and 50 - (160) - 575 μm on CDY where they are more frequently stromatic.

Conidiogenous cells phialidic, narrowly obclavate, tapering towards the apex, hyaline to pale brown, formed on branching conidiophores (Fig. 12A).

They are 8 - (17,9) - 22 x 2,5 - (3,4) - 4,5 µm on MSA and 10 - (17,0) - 24 x 2,5 - (3,8) - 4,5 µm on CDY. Percurrent proliferations sometimes occur (Fig. 8F).

Conidia narrow cylindrical, slightly unilaterally tapered towards the rounded apex and truncate base (Figs. 11D, E; 12B). On MSA they are 12 - (15,7) - 22,5 x 2,5 - (3,1) - 4,5 µm, mostly 14 - 16 x 3 µm, and on CDY 12,5 - (16,5) - 26,5 x 2,5 - (3,1) - 4,5 µm, mostly 15 - 16 x 3 µm.

Appressoria ovate to irregularly lobed, pale to medium brown, unicellular or septate (Figs. 11G, F; 12C), 6 - (9,7) - 15 x 4,5 - (6,1) - 10 µm.

Setae slender, straight but frequently flexuous, subulate, medium brown, variable in length (Figs. 11B; 12A), 45 - (105) - 195 x 3,5-(5,2) - 11 µm and 2 - (3) - 7 septate on MSA; 42 - (90) - 205 x 4 - (5,3) - 7 µm, 1 - (3) - 6 septate on CDY. They are scattered in the conidiogenous areas or in the conidiomata, borne on conidiophore branches.

Morphology on host material

On host tissue acervuli are small, often consisting of two or three setae only, in a cluster of conidiogenous cells, formed close together to constitute effuse patches on infected material. Conidial masses are usually unobtrusive.

Conidia narrow cylindrical, unilaterally tapered, 11 - (18,1) - 22,5 x 2,5 - (3,0) - 4 µm.

Setae slender, subulate with somewhat swollen bases, medium brown, 45 - (100) - 160 x 3 - (6,6) - 15 µm and 1 - (3) - 5 septate.

No teleomorph has been found associated with the anamorph in this study.

C. destructivum causes pale brown to dark brown elongated lesions on stems and leaves of infected plants, which develop "shepherd's crook" symptoms (Tiffany & Gilman, 1954).

Specimens examined

PREM 45364 on *Trifolium africanum* leaf, Cedara, 6th April 1977;
PREM 45816 on *Trifolium repens* leaf, Cedara, 6th April 1977;
PREM 45817 on *Trifolium pratense* stem, Cedara, 7th April 1977;
PREM 45773 on *Trifolium africanum* leaf, Cedara, 6th April 1977;
PREM 45748 on *Tribulus terrestris* leaflet, Middelburg C. Prov., 30th May 1979;
PREM 45746 on *Trifolium repens* leaf, Stellenbosch, 23rd March 1978.

Comment

The description and dimensions given above correspond generally with those given by O'Gara (1915), Horn (1952), Tiffany & Gilman (1954) and Arx (1957a), although the conidium dimensions given by Horn (1952) are slightly larger. Sutton (1980) does not include *C. destructivum* in his list of *Colletotrichum* species, but does include *C. higginsianum* Sacc. *apud* Higgins, regarded by Arx (1957a) as a synonym of *C. gloeosporioides. C. higginsianum* has conidia which are very similar in shape to those of *C. destructivum.*

Tiffany & Gilman (1954) report the teleomorph of *C. destructivum* to be *Glomerella glycines* (Hori) Lehman & Wolf, distinguished from *Glomerella cingulata* (Stonem.) Sp. & Schr. by its larger asci and ascospores. Arx & Müller (1954), however, regard *G. glycines* as a large spored form of the variable species, *G. cingulata.*

The variability of culture characteristics in *C. destructivum* has been reported by Chilton (1943) and by Tiffany & Gilman (1954). Chilton (1943) obtained 57 distinct culture types from 14 original isolates from *Trifolium* spp. These differed in growth rate, colour, zonation, presence or absence of setae and the amount of mycelium produced.

Tiffany & Gilman (1954) reported sclerotial isolates, characterized by the formation of a subsurface mat of white mycelium and numerous black sclerotia. The conidium dimensions and photographs provided, however, indicate that these may have been isolates of *C. coccodes. C. destructivum* cultures frequently do produce aggregations of dark mycelium, but these are not as compact as those of *C. coccodes,* or as prevalent. Both *C. coccodes* and *C. destructivum* have narrow cylindrical conidia, tapering towards the ends, but conidia of the latter tend to be narrow and shorter (Table 1), often unilaterally tapered.

C. destructivum occurs mainly as a pathogen on members of the Leguminosae, especially *Medicago sativa* and *Trifolium* spp., but has been reported as a pathogen of dodder (Leach, 1958) and may also be saprobic. It is distinguished by a combination of growth and morphological characteristics. In the central colony zone little aerial mycelium is produced and an almost continuous layer of conidiogenous cells, with scattered setae and small conidial masses, is formed. This phenomenon was noted by Tiffany & Gilman (1954) and also occurs on host tissue.

The characteristic unilateral tapering of the conidia is more prevalent in some isolates. It has not been mentioned in previous descriptions, although photographs presented by Tiffany & Gilman (1954) clearly illustrate this shape.

6.5.6 *Colletotrichum musae* (Berk. & Curt.) Arx, *Verh. Akad. Wet. Amst.* 51: 107 (1957)

Myxosporium musae Berk. & Curt., *Grevillea* 3: 13 (1874)
Gloeosporium musarum Cke. & Mass., *Grevillea* 16: 3 (1887)

Culture description

Cultures on MSA are effuse, spreading rapidly to diameters of 70 to 80 mm in seven days. Margins are entire, marginal zones thinly, closely appressed, Buff-Pink, becoming closely farinaceous in broad, coalescing bands in the centre of the colony, Chestnut-Brown to Orange-Cinnamon alternating with thinly cottony Orange-Cinnamon aerial mycelium (Fig. 13A). The reverse is Buff-Pink in the marginal zone, becoming Light Cinnamon-Drab towards the Orange-Cinnamon central zone.

On CDY colonies reach a diameter of 75 to 90 mm in seven days. The margins are slightly irregular, the marginal zones cobwebby, Buff-Pink becoming thinly cottony over farinaceous concentric zones of conidiomata in the centre of the colony, Vinaceous-Cinnamon (Fig. 13A). The reverse is similar in colour.

Little aerial mycelium is formed but conidium formation is prolific. Dark submerged aggregations of mycelium sometimes occur, frequently forming conidiomata.

Morphology in culture

Conidiomata astromatic to stromatic, pulvinate, pale to dark brown, extremely variable in size, glabrous (Fig. 13B); closely scattered over the centre of the colony or formed in coalescing concentric zones.

Conidiogenous cells phialidic, cylindrical, tapering slightly towards the apex (Figs. 8G; 14A), arising from branching conidiophores in loosely structured conidiomata, or singly in the aerial mycelium; 6 - (12,2) - 21,5 x 2 - (3,1) - 3,5 µm on MSA and 6 - (13,1) - 24 x 2 - (3,3) - 4 µm on CDY; frequently proliferating percurrently (Fig. 13C).

Conidia variable but mostly straight, short cylindrical to clavate or ellipsoidal, ends obtuse (Figs. 13D; 14B); 9 - (12,2) - 17 x 3 - (4,3) - 5 µm on MSA, mostly 12 x 4,5 µm, and 9 - (13,7) - 20 x 4 - (4,6) - 7 µm on CDY, mostly 13 x 4 µm.

Appressoria obovoid to irregular in shape, pale to medium brown (Figs. 13E, F; 14C), 8 - (10,9) - 15,5 x 6 - (7,4) - 10,5 µm.

Morphology on host material

On the host, acervuli are mostly rather small, pulvinate, pale to dark brown, glabrous, often formed in concentric rings, producing pale pink conidial masses.

Conidia short cylindrical with obtuse ends, 7 - (13,6) - 22 x 3 - (4,5) - 6 µm.

No teleomorph has been found in association with the anamorph with certainty.

Infected fruit develop small brown to black lesions which spread and coalesce as the fruit ripens, later turning the whole fruit black.

Specimens examined

PREM 45380 on *Musa* sp. fruit, Port St. Johns, 11th February 1977;
PREM 45825 on *Musa* sp. fruit, purchased Pretoria, March 1978;
PREM 45835 on *Musa* sp. fruit, Nelspruit, 23rd May 1978.

Comment

The description given above corresponds with those of Arx (1957a & c), Elarosi (1960), Simmonds (1965), Mordue (1970), Quimio (1976, 1977) and Sutton (1980).

This fungus was originally named *Myxosporium musae* Berk. & Curt. by Berkely (1874), but the subsequently applied binomial, *Gloeosporium musarum* Cke. & Mass. (Cooke, 1887), became more generally used. With Arx's (1957a) extension of the delimitation of *Colletotrichum* to include forms with glabrous conidiomata, the combination *Colletotrichum musae* (Berk. & Curt.) Arx was adopted.

C. musae is one of the most important and widely distributed causes of disease in ripening and ripe bananas (Mordue, 1970). It is characterized in culture by its fast growth rate with prolific conidium production, glabrous conidiomata and sparse aerial mycelium. These characteristics are relatively constant. Conidial shape is variable, broad cylindrical to elliptical or irregular.

6.5.7 *Colletotrichum orbiculare* (Berk. & Mont.) Arx, *Verh. Akad. Wet. Amst.* 51: 112 (1957)

Gloeosporium orbiculare Berk. & Mont., *P. Portug. Welw.* 7 (1853)
Colletotrichum lagenarium (Pass.) Ell. & Halst., *Bull. Torrey bot. Cl.* 20: 250 (1893)

Culture description

Colonies on MSA spreading fairly rapidly, reaching a diameter of 40 to 45 mm in seven days. Colony margin entire, marginal zone closely thinly appressed, colourless to Pinkish Buff, becoming subfelty alternating with coalescing farinaceous concentric bands of conidiomata towards the centre, Chaetura Drab to alternating bands of Olivaceous Black to Benzo Brown (Fig. 15A). Reverse, marginal zone colourless to Light Grayish Olive, becoming Deep Grayish Olive alternating with concentric zones of Olivaceous Black to Deep Quaker Drab in the central zone.

Colonies on CDY reach a diameter of 35 to 40 mm in seven days. Colony margins are entire, marginal zone closely, thinly appressed, colourless to Cinnamon-Buff, becoming finely, closely farinaceous in the central zone, Olive-Brown to Army Brown (Fig. 15A). Reverse, marginal zone colourless becoming Hair Brown to Chaetura Drab in the centre.

Conidiomata are initially astromatic, covered with large pale orange masses from which scattered slender, erect dark brown setae project. They are formed in the central colony zone, either scattered or in broad concentric bands.

Morphology in culture

Conidiomata pulvinate, becoming slightly stromatic and darkening from pale to dark brown with age, setose (Fig. 15B).

Conidiogenous cells phialidic, narrow cylindrical to subcylindrical, hyaline to pale brown (Figs. 15C; 16A), 10 - (11,7) - 14 x 4,5 - (5,1) - 5,5 µm on MSA and 8 - (16,6) - 23 x 4 - (4,9) - 6 µm on CDY where they tend to become thicker walled and darker with age. They are borne on branching conidiophores.

Conidia cylindrical, tapered to the truncate base, apex obtuse (Figs. 15D, E, F; 16 B), 15 - (16,9) - 19 x 4 - (4,2) - 5 µm on MSA, mostly 17 x 4 µm, and 15 - (20,2) - 22 x 3,5 (4,2) - 5 µm on CDY, mostly 21 x 4 µm.

Appressoria mostly clavate or ovoid to globose, rarely irregular, pale to medium brown (Figs. 15G; 16C); 6,5 - (9,3) - 16 x 5,5 - (6,8) - 10 µm.

Setae abundant, slender, subulate, straight to somewhat flexous, medium to dark brown (Figs. 15B; 16A); 80 - (120) - 150 x 4 - (5,0) - 6,5 µm on MSA and 1 - (2)- 4 septate, 80 - (115) - 170 x 4,5 - (5,6) - 6,5 µm on CDY and 1 - (2) - 4 septate; scattered on the branched conidiophores and projecting above the orange conidial masses.

Morphology on host material

On host tissue, acervuli are somewhat stromatic, flattened, pale to dark brown, with abundant long erect, subulate black setae projecting above the orange conidial masses, 65 - (115) - 195 x 4 - (5,7) - 7 µm and 1 - (2) - 4 septate.

Conidia long cylindrical with obtuse ends, 17 - (19,5) - 23 x 4 - (4,4) - 5,5 µm.

No teleomorph has been found in association with the anamorph with certainty.

C. orbiculare causes leafspot and anthracnose of fruit. Leafspots are often 2 to 4 mm in diameter, pale brown to grey. Lesions on fruit first become visible as brownish discolourations of the epidermis which enlarge to several centimeters in diameter, becoming sunken, wrinkled and darker with the development of concentric rings of acervuli.

Specimens examined

PREM 45826 on *Cucurbita pepo* (pumpkin) fruit, purchased Pretoria, 20th March 1978;
PREM 45827 on *Cucurbita pepo* (butternut) fruit, purchased Pretoria, 19th April 1978;
PREM 45750 on *Cucurbita pepo* (pumpkin) fruit, Nylstroom, 10th August 1978.

Comment

The description of *C. orbiculare* given above agrees with those of Arx (1957a), Simmonds (1965) and Sutton (1980).

According to Arx (1957a), the valid name for this species is *C. orbiculare* (Berk. & Mont.) Arx. Although the binomial *C. lagenarium* (Pass.) Ellis & Halst. has been commonly applied, *C. orbiculare* has precedence on the basis of prior publication.

There is little in general culture appearance to separate this species from *C. gloeosporioides.* With regard to morphology, the setae of *C. orbiculare* are usually longer than those of *C. gloeosporioides, C. coccodes* and *C. destructivum* (Table 2), and the conidia broader than those of *C. coccodes* and *C. destructivum*, often longer (Table 1), their ends obtuse and not tapered. Sclerotia are not produced.

6.5.8 *Colletotrichum gloeosporioides* (Penz.) Penz. & Sacc., *Fung. Agrum.* 2: 6 (1882)
Vermicularia gloeosporioides Penz.,*Michelia* 2: 450 (1880)
Teleomorphosis: *Glomerella cingulata* (Stonem.) Spauld. & Schrenk, *Science* ser. 2, 17: 751 (1903)

Arx (1957a) lists almost 600 synonyms for the anamorph and Arx & Müller (1954) list 120 synonyms for the teleomorph.

Culture description

Colony growth rate on MSA ranges from 35 to 65 mm in seven days. Margins are entire to sinuate or irregular. The marginal zone is closely appressed, white to Seashell Pink or Olive-Gray to Olive-Buff, becoming cottony to woolly or subfelty towards the centre, or farinaceous with the development of conidiomata. The colour of the central zone ranges from Salmon-Buff alternating with concentric zones of Flesh Ocher, to Light Mouse Gray alternating with Deep Mouse Gray, or Olive-Gray to Dark Grayish Olive, sometimes with scattered patches of white to Light Olive-Gray mycelium (Fig. 17 A - E).

The reverse, marginal zone is Olive-Gray to Olive-Buff, or Seashell Pink, becoming Salmon-Buff alternating with concentric zones of Flesh Ocher to Cinnamon-Rufous, or Dark Mouse Gray to Chaetura Drab becoming Drab to Chaetura Drab or Deep Mouse Gray in the centre.

Colonies on CDY attain a diameter of 40 to 75 mm in seven days. Margins are mostly entire but sometimes irregular, marginal zones cobwebby to closely, thinly appressed, colourless to white or sometimes Light Olive-Gray, becoming cottony to woolly or farinaceous, the latter often in alternating concentric zones. The colour of the central zone varies from Vinaceous-Pink alternating with concentric zones of Orange-Cinnamon, Mouse Gray in the centre, to Flesh Pink or Apricot Orange with Mouse Gray to Pale Pinkish Cinnamon overlaying aerial mycelium, or Mouse Gray alternating with concentric zones of Drab, to Dark Mouse Gray in the centre (Fig. 17 A - E).

The reverse, marginal zone is Warm Buff or Pinkish Buff to Pale Ochraceous-Salmon, becoming Ochraceous-Salmon alternating with concentric zones of Apricot Orange, or Warm Buff to Salmon-Buff, or alternating concentric zones of Light Drab and Blackish Mouse Gray in the central zone.

Conidiomata are variable in appearance and position. They may be stromatic or astromatic, glabrous or setose with abundant, well-developed or scattered, small setae, formed in concentric bands or scattered in the central colony zone.

Morphology in culture

Conidiomata very variable, ranging from small, astromatic to pulvinate stromatic structures, pale brown becoming dark brown with increasing age, often darker around the perimeter; setose (Figs. 18A; 19A2) or glabrous (Fig. 19A1).

Conidiogenous cells phialidic, cylindrical to subcylindrical, light to medium brown, closely clustered on branching conidiophores in the conidiomata but frequently found singly or in small groups in the aerial mycelium, relatively undifferentiated from the sterile hyphae (Fig. 19A1). They are 6 - (18,7) - 44 x 1,5 - (2,7) - 5 µm on MSA and 6 - (18,9) - 38 x 2 - (2,8) - 55 µm on CDY, occasionally proliferating percurrently (Fig. 18C).

Conidia short cylindrical, obtuse apices, tapering slightly to a truncate base, sometimes somewhat constricted in the centre (Fig. 19B1 - 4). On MSA they are 10 - (15,9) - 23 x 3 - (4,4) - 5 µm, mostly 13 - 14 x 4 µm, means of individual isolates ranging from 12,7 - 20,7 x 3,9 - 4,2 µm. On CDY they are 9 - (14,2) - 24 x 2,5 - (4,2) - 7 µm, mostly 15 x 4 µm, means of individual isolates ranging from 14,4 - 15,8 x 4,0 - 4,3 µm.

Appressoria mostly obovoid, occasionally subglobose to irregular, medium brown (Fig. 18D; 19C1 - 4), measuring 6 - (10,2) - 20 x 4,5-(6,6) - 9 µm, means ranging from 8,3 - 12,6 x 6,4 - 6,9 µm.

Setae formed in some isolates and not in others, frequently found either only on the host or only on certain agar media and not on others, relatively short and narrow, acicular, straight to somewhat flexuous (Figs. 18A; 19A2); measuring 35 - (80) - 160 x 3 - (4,6) - 7 µm, 1 - (3) - 6 septate on MSA, 27 - (80) - 143 x 3,5 - (5,0) - 9 µm, 1 - (3) - 5 septate on CDY.

Perithecia of the *Glomerella cingulata* teleomorph are formed in cultures of some *C. gloeosporioides* isolates, frequently not developing to maturity but remaining as sterile initials.

Mature perithecia single to caespitose, superficial or immersed, globose to ovoid or ampulliform, usually pale brown but also darker, often with silvery hairs on the apical portion. On MSA they measure 225 - (405) - 500 x 175 - (304) - 375 µm and on CDY, 310 - (370) - 510 x 230 - (265) - 310 µm.

Asci clavate to ellipsoidal, pedicillate, mostly eight-spored. Ascospores hyaline, ellipsoidal to narrowly clavate, both ends rounded or slightly tapered, straight or curved, one-celled, smooth walled, 14 - (15,9) - 18 x 4 - (4,9) - 6 µm on MSA and 12 - (15,0) - 17 x 4 - (4,8) - 6 µm on CDY.

Morphology on host material

Acervuli on host tissue are very variable in size, pigmentation and amount of stromatic thickening, develop pulvinately rupturing the outer epidermis walls and cuticle either by a single split or splitting it into three or four irregular flaps. Acervuli range from small astromatic structures to large discs of stromatic tissue, pale to dark brown, often darker and thicker around the perimeter, glabrous or setose.

Setae usually sparse, relatively short, often submerged in the pale pink to pale orange conidial masses, acicular, medium brown, 30 - (72) - 135 x 2 - (5,2) - 11 µm and 1 - (2) - 6 septate.

Conidia straight cylindrical, sometimes slightly clavate, obtuse apices, base truncate 9,5 - (14,8) - 20 x 3 - (5,0) - 6,5 µm.

Glomerella cingulata, the teleomorph of *Colletotrichum gloeosporioides,* is frequently found in association with this species on host tissue. Perithecia are extremely variable in size, shape and growth habits, either single or caespitose; erumpent, developing intra- or sub-epidermally, dark brown to black, covered with erect silvery hyphae (Fig. 18F, G), mostly 150 - 350 x 100 - 300 µm.

Asci are clavate to ellipsoidal (Fig. 18G), 45 - 75 x 15 - 20 µm, mostly eight-spored, uniseriate. Ascospores are straight or falcate, ellipsoidal or narrowly clavate, ends rounded or slightly tapered, hyaline (Fig. 18H, I), 12 - 18 x 4,5 - 6 µm. Paraphyses visible in young perithecia but disintegrate with age.

The *Colletotrichum* anamorph of *Glomerella cingulata* (Stonem.) Sp. & Schr., *C. gloeosporioides* Penz. & Sacc., is an ubiquitous polyphage. It occurs as a saprobe on senescent plant material or as a pathogen on an extensive host range, causing a wide variety of disease symptoms including leaf and stem spot, dieback and fruit rot.

Leaf spots vary from small dark, punctiform lesions a millimetre of two in diameter, to large pale to dark brown spreading and coalescing necrotic areas. On average they are 3 - 5 mm in diameter, pale brown to gray in the center with a dark perimeter, sometimes surrounded by a chlorotic border.

Stem lesions are usually pale orange-brown to dark brown, sunken, dark bordered areas, elongating along the length and often spreading and coalescing to girdle the stem. This results in the death of the distal stem portion.

Fruit infections are most conspicuous as ripe rots. Lesions are initially pale brown to black spots which later enlarge and coalesce. Concentric rings of acervuli and pink conidial masses are often visible.

Specimens examined

PREM 45383 on *Citrus maxima* fruit, Pretoria, 16th April 1974;
PREM 45375 on *Citrus maxima* fruit, purchased Johannesburg, Feb. 1977;
PREM 45378 on *Mangifera indica* fruit, purchased Pretoria, March 1977;
PREM 45812 on *Combretum erythrophyllum* leaf, Johannesburg, 10th March, 1977;
PREM 45365 on *Mangifera indica* fruit, Nylstroom, 25th March 1977;
PREM 45818 on *Erythrina humeana* leaf, Pretoria, 6th April 1977;
PREM 45819 on *Citrus limonia* leaf, Johannesburg, 13th May 1977;
PREM 45371 on *Persea americana* fruit, Pretoria, 16th May 1977;
PREM 45828 on *Cussonia spicata* leaflet, Pretoria, 13th May 1977;
PREM 45829 on *Citrus reticulata* fruit, Zeerust, 12th July 1977;
PREM 45830 on *Citrus sinensis* leaf, Zeerust, 12th July 1977;
PREM 45831 on *Mangifera indica* fruit, purchased Pretoria, Jan. 1978;
PREM 45836 on *Citrus reticulata* twigs, Nelspruit, 23rd May 1978;
PREM 45837 on *Mangifera indica* leaf, Nelspruit, 23rd May 1978;
PREM 45838 on *Mangifera indica* twigs, Nelspruit, 23rd May 1978;
PREM 45839 on *Sclerocarya caffra* leaf, Nelspruit, 23rd May 1978;
PREM 45840 on *Coffea arabica* twigs, Burgers Hall Exp. Station, E. Tvl., 23rd May 1978;
PREM 45840 on *Passiflora edulis* twigs, Burgers Hall Exp. Station, E. Tvl., 23rd May 1978;
PREM 45841 on *Passiflora edulis* fruit, Burgers Hall Exp. Station, E. Tvl., 23rd May 1978;
PREM 45843 on *Manihot esculenta* leaf, Burgers Hall Exp. Station, E. Tvl., 23rd May 1978;
PREM 45844 on *Zingiber officinale* leaf, Burgers Hall Exp. Station, E. Tvl., 23rd May 1978;
PREM 45845 on *Piper nigrum* leaf, Burgers Hall Exp. Station, E. Tvl., 23rd May 1978;
PREM 45846 on *Thea sinensis* leaf, Sabie, 23rd May 1978;
PREM 45847 on *Persea americana* fruit, Nelspruit, 25th May 1978;
PREM 45848 on *Persea americana* leaves, Nelspruit, 25th May 1978;
PREM 45849 on *Citrus limonia* twigs, Nelspruit, 25th May 1978;
PREM 45850 on *Adinia microcephala* var. *galpini* leaf, Nelspruit Botanical Gardens, 25th May 1978;
PREM 45851 on *Bauhinia galpini* leaf, Nelspruit Botanical Gardens, 25th May 1978;
PREM 45852 on *Pelargonium transvaalense* leaves, Nelspruit Botanical Gardens, 25th May 1978;
PREM 45853 on *Carica papaya* fruit, Nelspruit, 22nd Aug. 1978;
PREM 45854 on *Malus* sp. fruit, Langkloof, 9th May 1979.

Comment

The above descriptions agree generally with those given by Simmonds (1965), Stephan (1967a & b), Mordue (1971a), Hindorf (1973b) and Sutton (1980).

The confusion surrounding the genera *Vermicularia, Colletotrichum* and *Gloeosporium* is most strongly reflected in the *C. gloeosporioides* complex as the result of its variable conidiomatal structure and frequent absence of setae. Penzig (1883) first described this species as *Vermicularia gloeosporioides,* but it was transferred subsequently (Penzig, 1885) to *Colletotrichum gloeosporioides.* It was characterized by straight cylindrical conidia with rounded ends, measuring, 16 - 18 x 4 - 6 µm. Shear & Wood (1913) found *C. gloeosporioides* to be a very variable species and referred strains from 34 hosts to it. Burger (1921) regarded it as a polymorphic species made up of a number of culturally distinct strains. Small (1926) also observed that many morphologically similar conidial forms, described as separate species, with a proved connection with *Glomerella cingulata* should be grouped in a single species, namely *C. gloeosporioides.* Baker, Crowdy & McKee (1940) came to a similar decision as regards anthracnose fungi from tropical fruits.

The name *Gloeosporium fructigenum* Berk. has been used for this variable fungus by Southworth (1891b), Wollenweber & Hochapfel (1949) and Böhni (1949). Saccardo (1884) described the conidia of *C. gloeosporioides* (Penz.) Penz. & Sacc. as being straight cylindrical with rounded ends, 16 - 18 x 4 - 6 µm, and those of *C. fructigenum* Berk. as somewhat curved, oblong to cylindrical, 20 - 30 x 5 - 6 µm. Arx (1957a) included *C. fructigenum* and 593 other binomials in the synonomy of *C. gloeosporioides*, a name which he adopted out of convenience, not because it was the oldest applicable.

Arx (1957a) also distinguished several pathogenic forms of *C. gloeosporioides* on the basis of their host specificity and distinctive culture characteristics. Arx (1957c) conceded that *C. gloeosporioides* and its various forms were neither morphologically nor biologically sharply divided. These forms were retained under their original names as they have no certain connection with *Glomerella cingulata* teleomorphs (Arx, 1957a) and also for the convenience of pathologists (Arx, 1957c).

Gorter (1956, 1962) investigated the heterogenous group of fungi causing anthracnose of *Olea europaea.* He doubted whether all could be regarded as *Gloeosporium olivarum* Alm. (d'Almeida, 1899), as they varied greatly in culture characteristics and conidium size. Gorter (1962) distinguished two groups. Firstly a *"Glomerella-Colletotrichum"* group, associated with a *Glomerella* teleomorph and characterized by conidia with a width modus equal or larger than 5 µm. Secondly, a *"Gloeosporium"* group characterized by narrower, more pointed conidia with a width modus of less than 5 µm, not associated with a teleomorph.

As Edgerton (1915) had already designated the latter group *Gloeosporium fructigenum*, Gorter (1962) also adopted this name for the chromogenic South African anthracnose fungus, which fell into this group, naming it *G. fructigenum* f. *chromogenum*. Gorter (1962) did not uphold Arx's (1957a) opinion that *G. fructigenum* is a synonym of *C. gloeosporioides*, but agreed that the olive anthracnose fungus identified as *G. fructigenum* f. *chromogenum* could be named *Colletotrichum fructigenum* (Berk.) Vassilj. f. *chromogenum* in accordance with Arx's (1957a & b) findings regarding the genus *Gloeosporium*.

Sutton (1980) emphasised that *Colletotrichum gloeosporioides* shows excessive variation and indicated that forms could probably be differentiated by a combination of cultural characters, morphology, host range and pathogenicity. He gave Mordue (1971a) as reference for a full description of *C. gloeosporioides*. Mordue (1971a) expressed the opinion that detailed studies of the taxa in the suggested synonomies of Arx & Müller (1954) and Arx (1957a) may reveal that many are distinct.

The heterogeneity of *C. gloeosporioides sensu* Arx has also been noted by Simmonds (1965) and Hindorf (1970, 1973a, b, c, 1974). Although culture characteristics vary greatly in all respects, groups based on similarities in colour and texture may be discerned (Baker, Crowdy & McKee, 1940; Stephan, 1967b; Hindorf, 1973b).

The *C. gloeosporioides* isolates in the present study are best characterized by their relatively short, straight cylindrical to broadly ellipsoidal or somewhat clavate conidia with obtuse ends and truncate attachment point. Conidia are generally narrower than 5 µm, seldom exceeding 6 µm, mostly measuring 10 - (15) - 24 x 3 - (4,5) - 6 µm (Table 1). Appressoria are smooth in outline not lobed as those of *C. crassipes*. Setae are not always present.

6.5.9 *Colletotrichum lindemuthianum* (Sacc. & Magn.) Br. & Cav., *Funghi Parass.* 50 (1889)
Gloeosporium lindemuthianum Sacc. & Magn., *Michelia* 1: 128 (1880)
Gloeosporium socium Sacc., *Bull. trimest. Soc. mycol. Fr.* 12: 71 (1896)

Culture description

Colonies on MSA relatively slow-growing, reaching a diameter of 20 to 30 mm in seven days. Margins entire,marginal zone closely appressed, white to Vinaceous-Buff, becoming downy to subfelty in the centre, at first Dark Grayish Olive to Olivaceous Black, later farinaceous and Light Cinnamon-Drab with the development of conidiomata in the central zone (Fig. 20A). Reverse, Pale Ochraceous-Salmon marginal zone and Olive-Gray to Chaetura Black central zone.

Colonies on CDY reach a diameter of 15 to 20 mm in seven days. The margins are irregular, marginal zone submerged, Pale Pinkish Cinnamon, becoming downy or subfelty towards the coarsely farinaceous centre, Buff-Pink to Mouse Gray (Fig. 20A). Reverse, marginal zone Pale Ochraceous-Salmon becoming Ochraceous-Salmon and then Dark Mouse Gray in the central zone.

Conidiomata on both MSA and CDY are mostly pulvinate, darkly pigmented with erect black setae projecting above the pinkish conidial masses, scattered in the central portion of the colony. Occasionally a few submerged black sclerotia are formed.

Morphology in culture

Conidiomata pulvinate, darkly pigmented, becoming somewhat stromatic with increasing age (Fig. 20B); 125 - (300) - 450 µm in diameter on MSA and 150 - (340) - 550 µm on CDY.

Conidiogenous cells phialidic, long cylindrical, hyaline to pale brown, borne on branching conidiophores (Fig. 21A1); 12,5 - (17,5) - 25 x 3 - (3,2) - 4 µm on MSA and 10 - (17) - 24 x 3 - (3,5) - 5 µm on CDY.

Conidia straight, short cylindrical, apices obtuse and bases slightly tapered and truncate (Figs. 20C; 21B1); 10 - (11,8) - 13 x 3 - (3,8) - 4 µm on MSA and 10 - (12,7) - 19 x 3 - (4,0) - 5 µm on CDY, on both media mostly 12 x 4 µm.

Appressoria globose to ovoid or clavate, seldom irregular in shape, pale to medium brown (Figs. 20D; 21C1); 5,5 - (6,2) - 7 x 5 - (5,2) - 6 µm.

Setae numerous, long, slender, subulate, dark brown to black (Figs. 20B; 21A1); 80 - (145) - 280 x 3,5 - (5,0) - 7 µm on MSA, 2 - (4,0) - 9 septate, 75 - (125) - 235 x 3,5 - (4,9) - 7 µm and 2 - (3,0) - 7 septate on CDY, borne on the branching conidiophores scattered between the conidiogenous cells.

Morphology on host material

On host tissue acervuli are generally pulvinate, dark, sometimes glabrous but mostly setose, 150 to 250 µm in diameter. Setae slender, erect to somewhat flexuous, subulate, dark brown to black, scattered over the acervuli, 45 - (85) - 155 x 3 - (4,4) - 7 µm and 1 - (3) - 6 septate. Conidia short cylindrical, 9 - (10,4) - 18 x 3 - (4,5) - 5 µm, salmon in mass.

No teleomorph has been found in association with the anamorph in this or previous studies.

C. lindemuthianum is primarily a pathogen of *Phaseolus* spp., especially *P. vulgaris.* Lesions on infected pods or seeds characteristically circular, 2 to 5 mm in diameter, consisting of a pale to dark brown sunken necrotic centre, where pink conidial masses are usually visible, and a dark edge becoming reddish brown towards the outside of the lesion. In badly infected pods the lesions may coalesce giving the pods a gnarled appearance. Infected seed may be prevented from germinating or may give rise to seedlings with typical anthracnose lesions on the cotyledons.

Specimens examined

PREM 45877 on *Phaseolus vulgaris* "Black Turtle" pod, Koster, 4th March 1977;
PREM 45370 on *Phaseolus vulgaris* pod, Roodeplaat, 15th April, 1977;
PREM 45855 on *Phaseolus vulgaris* pod, Dendron, 11th July 1978;
PREM 45856 on *Phaseolus vulgaris* pod, Potchefstroom, 1978.

Comment

The description given above corresponds with those of Arx (1957a), Tiffany & Gilman (1954), Mordue (1971b), Kulshrestha *et al.* (1976) and Sutton (1980).

C. lindemuthianum shows a high degree of variability (Mordue, 1971b), but Schaffnit & Böhning (1925) found that the ranges of conidial dimensions on culture media always stay within those found on the natural host. A number of pathogenic races have been distinguished in *C. lindemuthianum* (Barrus, 1918; Burkholder, 1923; Frandsen, 1953; Yerkes & Ortiz, 1956; Yerkes, 1958), on the grounds of differential pathogenicity. According to Arx (1957a) this number is limited only by the number of fungus isolates used and the number of bean cultivars tested.

C. lindemuthianum is morphologically similar to *C. gloeosporioides* and *C. trifolii* but may be distinguished in culture by a slower growth rate and darker pigmentation of its colonies. Its setae are usually larger and more prominent than those of the other two species (Table 2).

6.5.10 *Colletotrichum trifolii* Bain & Essary, *J. of Mycol.* 12: 193 (1906)

Culture description

Colonies on MSA grow relatively slowly, reaching a diameter of 35 to 40 mm in seven days. The margins are sinuate, marginal zone closely appressed, Pale Olive-Buff, becoming subfelty alternating with concentric farinaceous bands towards the centre, Dark Olive becoming Mouse Gray to Blackish Mouse Gray (Fig. 20E). Reverse, marginal zone Pale Olive-Buff becoming Iron Gray and Dark Olive-Gray in alternating concentric zones in the centre.

On CDY colonies reach a diameter of 25 to 35 mm in seven days. They are frequently radially folded. Margins are irregular, marginal zone closely appressed, Cartridge Buff, coming farinaceous, Hair Brown towards the central zone which is Cinnamon-Buff alternating with Light Cinnamon-Drab segments, Benzo Brown in the very centre (Fig. 20E). Reverse, marginal zone Cartridge Buff, becoming Chaetura Drab to Chaetura Black in segments, alternating with segments of Benzo Brown to Hair Brown in the central zone.

Conidiomata on both MSA and CDY are usually pulvinate, dark brown, setose, formed in concentric bands. Scattered black submerged sclerotia are also sometimes formed.

Morphology in culture

Conidiomata are small, irregular in size, pulvinate, brown to black (Fig. 20F), measuring 100 to 250 μm in diameter on MSA and 150 to 300 μm on CDY. Scattered sclerotia-like aggregations of submerged mycelium also occur.

Conidiogenous cells are phialidic, robust, cylindrical, hyaline becoming pale brown (Fig. 21A2); 17 - (21,4) - 28 x 4 - (4,1) - 4,5 µm on MSA and 11 - (17,5) - 24 x 4 - (4,5) - 5 µm on CDY, arising from branched conidiophores.

Conidia short cylindrical, relatively broad, both ends obtuse (Figs. 20G; 21 B2); measuring 9,5 - (10,9) - 12 x 4 - (4,1) - 4,5 µm on MSA, mostly 11 x 4 µm, and 10 - (12,1) - 14 x 3,5 - (4,0) - 4,5 µm on CDY, mostly 12 x 4 µm.

Appressoria ovate to obovoid, pale to medium brown (Figs. 20H; 21 C2), measuring 7 - (9,5) - 17 x 5,5 - (6,6) - 9,5 µm.

Setae relatively short and robust, subulate, dark brown (Figs. 20F; 21 A2); 55 - (75) - 100 x 4 - (4,9) - 7 µm on MSA, 1 - (2) - 3 septate, and 55 - (70) - 90 x 4,5 - (5,4) - 8,5 µm, 1 - (1) - 2 septate on CDY, scattered on the branched conidiophores.

Morphology on host material

On host tissue acervuli are small, slightly stromatic, pulvinate, pale to dark brown, 100 to 250 µm in diameter, with scattered setae. Conidia broad cylindrical, ends obtuse, 11 - (14,6) - 18 x 4 - (5,2) - 6 µm. Setae relatively short, often hidden by the pale pink conidial masses, subulate, dark brown, 50 - (70) - 95 x 4 - (5,6) - 8 µm, 1 - (2) - 3 septate.

No teleomorph was found in association with the anamorph.

Colletotrichum trifolii Bain & Essary is a pathogen mainly of *Medicago* and *Trifolium* spp., causing characteristic diamond-shaped brown lesions on the stems, and pale to dark brown, round to irregular lesions on the leaves and petioles.

Specimens examined

PREM 45813 on *Glycine max* pod, Buffelspoort, 14th March 1977;
PREM 45857 on *Medicago sativa* stem, Bethlehem, 14th March 1979.

Comment

The description and dimensions given above correspond with those given by Bain & Essary (1906), Tiffany & Gilman (1954) and Arx (1957a & c).

C. trifolii was originally described as a pathogen of *Medicago sativa* Bain & Essary (1906) and has subsequently been applied mainly in this sense. However, it is similar to *C. lindemuthianum* both in culture characteristics and morphology, and both fungi are pathogenic to members of the Leguminosae. Sutton (1980) does not include *C. trifolii* in his list of *Colletotrichum* species, but extends the host range of *C. lindemuthianum* to include *Medicago sativa.*

Isolates regarded as *C. trifolii* in this study were slightly faster growing than those of *C. lindemuthianum* in culture, predominantly in olive green shades, with somewhat shorter (Table 2) and sparser setae. However, in the multivariate phenetic analyses of morphological and culture characteristics (Section 6.6), *C. trifolii* and *C. lindemuthianum* were constantly grouped together, indicating their close similarity.

Further morphological and culture studies together with host range tests may show that *C. trifolii* and *C. lindemuthianum* differ significantly only in host specialization and that *C. trifolii* must consequently be regarded as a synonym of *C. lindemuthianum.*

6.5.11 *Colletotrichum fructigenum* (Berk.) Vassil., *Fungi imperfecti parasitica* 2: 296 (1950)
Gloeosporium fructigenum Berk., *Gard. Chron.,* 247 (1856)

6.5.12 *Colletotrichum fructigenum* f. sp. *chromogenum* Gorter, *Bothalia* 7: 777 (1962)

Culture description

Non-chromogenic form:
Colonies on MSA reach a diameter of 45 to 50 mm in seven days. Margins entire, marginal zones downy, Pale Mouse Gray, becoming densely woolly and somewhat chrystalline towards the centre, with alternating zones of Light Mouse Gray and Deep Mouse Gray (Fig. 22A). Reverse, marginal zone Pale Olive-Buff becoming Deep Grayish Olive in the central zone, alternating with concentric zones of Benzo Brown.

On CDY, colonies also reach a diameter of 45 to 50 mm in seven days. Margins are also entire, marginal zones downy, white, but becoming cottony, somewhat chrystalline, to thickly felty in the centre, Pale Olive-Gray to Olive-Gray, Light Olive-Gray in the extreme centre (Fig. 22A). Reverse, Pinkish Buff to Neutral Red, paling slightly in the marginal zone.

Chromogenic form:
Colonies of the chromogenic form are slower-growing on MSA, reaching a diameter of 35 to 45 mm in seven days. Margins are also entire and marginal zones downy, but Pallid Quaker Drab to Seashell Pink, becoming aggregated woolly and somewhat chrystalline towards the centre, Light Grayish Vinaceous to Hydrangea Pink or Rhodonite Pink to Deep Hellebore Red, Pale Mouse Gray in the extreme centre (Fig. 22B). Reverse, marginal zone Pallid Quaker Drab or Pale Pinkish Cinnamon to Light Buff, becoming Hydrangea Red to Pomegranate Purple in the central zone, or becoming Neutral Red.

Colonies of the chromogenic form are also slower-growing than those of the non-chromogenic form on CDY, reaching a diameter of 35 to 40 mm in seven days. Margins are sinuate to irregular, marginal zones downy, Light Ochraceous-Salmon or Hydrangea Pink, becoming cottony with a somewhat chrystalline appearance, to felty in the central zone, Pinkish Vinaceous or alternating concentric zones of Light Ochraceous-Salmon to Vinaceous-Cinnamon and Orange-Cinnamon (Fig. 22B). Reverse, marginal zone Ochraceous-Salmon to Cartridge Buff, becoming Neutral Red in the central zone, or becoming Orange-Cinnamon which darkens to Deep Brownish Vinaceous in the centre.

Conidiomata of both strains on both media are small, slightly stromatic, pulvinate to somewhat cupulate, scattered in the central area and frequently concealed under the aerial mycelium. The dense aerial mycelium of both the chromogenic and non-chromogenic strains of this species has a chrystalline appearance, due to the formation of small conidial masses.

Morphology in culture

Non-chromogenic form:
Conidiomata relatively small, scattered, astromatic to slightly stromatic, pulvinate to somewhat cupulate with increasing age, pale to dark brown, frequently darker around the perimeter, glabrous or sparsely setose. On MSA they are 100 - (205) - 300 µm in diameter and on CDY, 250 - (330) - 400 µm.

Conidiogenous cells phialidic, cylindrical to subcylindrical or narrowly obclavate, hyaline to pale brown (Fig. 23 A1), measuring 15 - (16,8) - 17,5 x 2,5 - (2,7) - 3 µm on MSA and 13 - (16,5) - 17 x 2,5 - (2,6) - 3,5 µm on CDY, borne either directly on the hyphae in the aerial mycelium or on branching conidiophores which form conidiomata.

Conidia straight fusiform (Figs. 22E; 23 B1), measuring 10 - (12,9) - 15 x 3 - (3,2) - 3,5 µm, mostly 12 - 13 x 3 µm on MSA, and 9 - (11,4) - 13 x 3 - (3,5) - 4 µm, mostly 11 - 12 x 3,5 µm on CDY. Frequently, especially in slide culture, conidia form secondary phialoconidia on germination and not appressoria (Fig. 23 B1).

Appressoria sparse, mostly obovoid but ovoid to irregularly lobed, unicellular or septate, often formed in chains (Fig. 23 C1); 7,5 - (10,6) - 15 x 5 - (6,2) - 8 µm.

Setae very sparse, usually concealed under conidial masses, robust, subulate, dark brown frequently with paler basal cells; 40 - (55) - 75 x 3 - (3,9) - 5 µm on MSA, 0 - (0) - 2 septate, absent on CDY.

Chromogenic form:
Conidiomata (Fig. 22C), conidiogenous cells, conidia, appressoria and setae similar in form, colour and origin to the above description.

Conidiogenous cells (Figs. 22D; 23 A2) measure 7,5 - (11,5) - 18 x 2,5 - (2,7) - 4 µm on MSA and 8 - (12,6) - 17 x 2,5 - (2,9) - 3,5 µm on CDY.

Conidia (Figs. 22F, G, H; 23 B2) measure 8 - (12,8) - 15,5 x 3 - (3,6) - 4 µm on MSA, mostly 12 - 13 x 3,5 µm, and 9 - (12,7) - 15 x 3 - (3,3) - 4,5 µm on CDY, mostly 12 x 3 - 3,5 µm.

Appressoria (Figs. 22 I; 23 C2) measure 7,5 - (9,6) - 15 x 5 - (6,1) - 7,5 µm.

Setae (Figs. 22C; 23 A2) on MSA measure 30 - (45) - 75 x 3,5 - (3,9) - 4,5 µm, 0 - (0) - 1 septate, while on CDY they measure 20 - (35) - 45 x 3,5 - (4,1) - 4,5 µm and are also 0 - (0) - 1 septate.

Morphology on host material

On host tissue acervuli are small, pulvinate, glabrous, pale to dark brown, rupturing the epidermis with a single split through which the pale to bright orange conidial masses are exuded.

Conida fusoid to ellipsoidal, 10,5 - (12,5) - 14 x 3 - (3,3) - 4 µm in the non-chromogenic form and 13 - (14,5) - 17 x 3,5 - (3,9) - 4,5 µm in the chromogenic form.

No teleomorph has been found in association with the anamorph.

Both isolates of *C. fructigenum* in this study were obtained from lesions on cultivated *Fragaria* sp. plants, causing leaf and petiole spot and girdling the runners. Lesions on the leaves were 2 - 3 mm in diameter, pale brown with a reddish border. On petioles and runners the lesions were pale to dark brown, elongate, spreading and coalescing. Of the two chromogenic isolates studied,one was that found by Gorter (1956, 1962) to cause anthracnose of *Olea europaea* fruit and the other was saprobic on *Grewia monticola* leaves.

Specimens examined

C. fructigenum f. sp. *fructigenum*
PREM 45858 on *Fragaria* sp. stolon, Roodeplaat Tvl., 15th Sep. 1978;
PREM 45777 on *Fragaria* sp. stolon, Cullinan, 7th March 1979.
CBS 295.67 on *Fragaria* sp., Australia.

C. fructigenum f. sp. *chromogenum*
PREM 45379 on *Olea europaea* fruit, W. Cape Prov., 1941;
PREM 45776 on *Grewia monticola* leaf, Nelspruit Botanical Gardens, 25th May 1978.

Comment

The descriptions given above correspond with those of *C. fructigenum* f. sp. *fructigenum* and *C. fructigenum* f. sp. *chromogenum* given by Gorter (1962) and also with those of *C. acutatum* given by Simmonds (1965), Hindorf (1973b), Kulshrestha *et al.* (1976), Dyko & Mordue (1979) and Sutton (1980).

In 1962, Gorter described *C. fructigenum* f. sp. *chromogenum,* separating it from *C. gloeosporioides* Penz. *sensu* Arx (1957a) because of the narrower, more pointed conidia of *C. fructigenum,* its distinguishing culture characteristics and the fact that no *Glomerella cingulata* teleomorph had been connected with it. Gorter (1962) regarded *Gloeosporium limetticolum* Clausen and *G. olivarum* Alm. as forms of *C. fructigenum,* not as synonyms of *C. gloeosporioides* as did Arx (1957a).

Gorter (1962) noted that the characteristics which he used to distinguish *C. fructigenum* had already been pointed out by other workers. Shear & Wood (1913) had observed that the chromogenic strain of *C. gloeosporioides* produced abundant conidia in the aerial mycelium when grown in culture; Andes & Keitt (1950) had stated that the chromogenic strain — as well as all strains with narrow, pointed conidia – do not produce perithecia. This was also noted by Ramsey, Smith & Heiberg (1951).

Simmonds (1965) described *C. acutatum* causing fruit rot in Australia. He characterized this species by its relatively small conidia with pointed ends, measuring 8,3 - (11,1) - 14,4 x 2,5 - (3,1) - 4,0 µm. The formation of conidia throughout the aerial mycelium in culture, giving it a chrystalline appearance, and the formation of scattered, poorly developed setae were also noted, together with the occurance of morphologically identical bright pink isolates. Simmonds (1965) observed that this species of *Colletotrichum* was not one of the 11 recognised by Arx (1957a), but admitted the possibility that it had been described before. However, the lack of detail in older descriptions, together with the custom of quoting extremes in size and not means, precluded accurate comparisons (Simmonds, 1965).

Simmonds (1965) also noted that the temperature reactions of the Queensland *C. acutatum* isolates closely resembled those of isolates considered by Edgerton (1915) to be *Gloeosporium fructigenum*. He (Simmonds, 1965) regarded the two organisms as being distinct, however, on the grounds of the larger conidium dimensions usually attributed to *G. fructigenum.* Arx (1970) accepted Simmonds' (1965) description of *C. acutatum* and included it in his list of *Colletotrichum* species.

According to Dyko & Mordue (1979), *C. acutatum* Simmonds was a *nomen invalidum* as Simmonds (1965) had not designated a type specimen. The name was validated in 1968 when Simmonds designated a holotype.

Hindorf (1970, 1973a, b, c) identified *C. acutatum* from coffee plants. He described the isolates in culture as being pink initially, becoming wine red with increasing age and forming only scattered setae. The isolates were characterized by the constant form and size of the conidia, which were straight, ellipsoid, tapered and pointed at both ends, 9,5 - (12,1) - 14,9 x 2,7 - (3,4) - 4,1 µm. Appressoria were small with a smooth outline, 6,6 x 5,9 µm. Setae, when present, averaged 50 x 3,5 µm.

Dyko & Mordue (1979) describe the conidia of *C. acutatum* as being straight, fusiform, 8 - 16 x 2,5 - 4 µm, and the appressoria as clavate to obovate, margins smooth, measuring 6,5 - 11 x 4,5 - 7,4 µm. According to Dyko & Mordue (1979) setae are not formed in culture, but are present in some collections on the natural substrate where they measure 46,5 - 85 x 3 - 4 µm. They (Dyko & Mordue, 1979) distinguish *C. acutatum* from

C. gloeosporioides by the former's orange to pink colony colour and by its fusiform conidia, also noting that no perithecia have been reported for *C. acutatum*.

Peredo, Osario & Santamaria (1979) recorded a new pathogen of *Pinus radiata* seedlings in Chile, namely *Colletotrichum acutatum* f. sp. *pinea*. The identification of both orange and grey cultures as *C. acutatum* was confirmed by Arx (Peredo *et al.*, 1979).

From the dimensions and descriptions given in the present study and by Gorter (1962), Simmonds (1965), Arx (1970), Hindorf (1973b), Dyko & Mordue (1979) and Sutton (1980), it would appear that the fungi designated *C. fructigenum* (Berk.) Vassilj. by Gorter (1962) and *C. acutatum* by Simmonds (1965) are very similar.

A CBS culture (CBS 295.67) of *C. acutatum* from strawberries closely resembled the non-chromogenic form described above, both in culture characteristics and in morphology. Conidia measured 10 - (12,8) - 15 x 3 - (3,7) - 4 µm on MSA and 8 - (12,4) - 15,5 x 3 - (3,6) - 4 µm on CDY. It would, therefore, appear that *C. fructigenum sensu* Gorter (1962) and *C. acutatum* Simmonds are conspecific.

Considerable confusion has surrounded the oldest valid name apparently applicable to this fungus, *C. fructigenum* Berk., since its inception (Stoneman, 1898b; Böhni, 1949; Arx, 1957a). It is suggested, therefore, that the name *C. acutatum* Simmonds be adopted.

It is characterized by its chrystalline-textured colonies in culture and by its relatively small (Table 1), fusoid conidia.

6.6 RESULTS OF MULTIVARIATE PHENETIC ANALYSES

6.6.1 Cluster analyses

Single linkage (SL) cluster analysis of the selected OTU's resulted in the formation of long straggly clusters (Fig. 24) as pointed out by Sneath & Sokal (1973). The only distinct low-level cluster present was that of two *C. graminicola* OTU's (numbers 17 &28, Appendix 4). The cophenetic correlation coefficient was 0,733.

In the complete linkage (CL) analysis, there was a distinct clustering of OTU's into groups (Fig. 25) but the cophenentic correlation coefficient was only 0,558. OTU groups distinguished were *C. dematium; C. graminicola; C. crassipes*, with a transitional *C. gloeosporioides* OTU (24, Appendix 4) in the same cluster, and a loose grouping of *C. fructigenum* OTU's (14 & 21, Appendix 4). *C. trifolii* and *C. lindemuthianum* (OTU's 23 & 15) were clustered together with a *C. gloeosporioides* OTU (number 12), while *C. coccodes, C. destructivum* and other *C. gloeosporioides* OTU's were intermingled.

In the average linkage (AL) cluster analyses the following results were obtained. Both the correlation (Fig. 26) and distance (Fig. 27) phenograms obtained in the UPGMA analysis produced clusters similar to those produced in the CL analysis. Cophenetic correlation coefficients were 0,709 and 0,781 respectively.

In the WPGMA (Fig. 28) AL analysis, with a cophenetic correlation coefficient of 0,733, good groupings of morphologically and culturally similar OTU's were produced. *C. dematium* and *C. graminicola* OTU's were placed in two distinct clusters; *C. crassipes* OTU's were placed together, in the same cluster as two OTU's intermediate between *C. crassipes* and *C. gloeosporioides* (numbers 13 & 24); *C. lindemuthianum* and *C. trifolii* were clustered together, with a morphologically similar *C. gloeosporioides* OTU (number 12). *C. musae* (OTU 2) was relatively distinct, although placed in association with OTU's of the *C. gloeosporioides* complex. The *C. fructigenum* OTU's, however, were not placed in close association with each other, and the *C. destructivum* and *C. coccodes* OTU's were interspersed, as in the SL, CL and UPGMA analyses.

The cophenetic correlation coefficient of the UPGMC AL cluster analysis was only 0,529 and the clusters produced were irregular, often uniting divergent OTU's. Clusters corresponding to those formed in the other analyses were those formed by the *C. graminicola* and *C. crassipes* OTU's, and by *C. lindemuthianum* and *C. trifolii.* Two *C. coccodes* OTU's (Numbers 7 & 18) also formed a distinct cluster.

6.6.2 Ordinations and MST

Two ordinations were performed, one with 20 OTU's and one with 28. For the first ordination, eight OTU's (2, 4, 10, 12, 13, 17, 24 & 28, Appendix 5) with missing characters (Table 4) were discarded. Almost 75% of the variation in this study was explained by the first five components (Table 5), the first accounting for 24,89% of the total variation.

Characters loading most heavily on this component, in decreasing order of importance, were numbers 18, 7, 15, 20, 19 and 12 (Appendix 5), a combination of texture and seta characteristics. This variation is illustrated in Figure 30. *C. crassipes* OTU's (9, 27) *C. dematium* OTU's (6, 8, 22), both species having large robust, darkly pigmented setae, were placed to the left of axis 1 while *C. fructigenum* OTU's, having few or no setae were placed to the right, with intermediate OTU's inbetween.

The second component accounted for 19,01% of the total variation, loaded most heavily by characters 23 and 16, followed by 24 and 10 (Table 5, Appendix 5). This was a combination of conidium width, presence of perithecia, appressorium shape and the colour of conidial masses. The separation of OTU's along the second principal axis is illustrated in Figure 30. Here *C. crassipes* OTU's (numbers 9 & 27), having characteristically very broad conidia and deeply lobed, irregular appressoria, were completely isolated from the other OTU's.

The third and fourth components accounted for 11,7% and 9,2% of the total variation respectively. Characters loading most heavily on factor three were numbers 3 and 21 (Table 5; Appendix 5), marginal zone colour, above and conidium shape. The fourth factor was loaded most heavily by characters 2 and 4 (Table 5; Appendix 5), colony colour, both above and reverse. This is illustrated in the ordination diagrams (Fig. 31 & 32). Along axis 3, groups were not clearly separated, although OTU's with light or hyaline colony margins and cylindrical conidia were placed towards the right of the diagram, while those with darker colony margins and narrower, broader or curved conidia were placed towards the left. Along axis 4 (Fig. 32), the paler colonies were placed towards the lower part of the diagram, while the darker colonies were placed towards the upper portion.

The fifth component accounted for 8,58% of the variation. Character 26 (Table 5; Appendix 5), appressorium width, loaded most heavily on this component, followed by characters 1 and 8, growth rate and nature of margin. Fig. 31 illustrates the placing of OTU's with relatively broad appressoria and colonies with a relatively fast growth rate and entire margins, towards the top of axis 5. OTU's with relatively narrow appressoria, slow growth rates and irregular colony margins were placed towards the lower portion of the axis, while the intermediate OTU's were distributed between the two extremes.

In the second ordination 28 OTU's were included but characters 12, 13, 14 and 19 (Appendix 5 were excluded as they were absent in some OTU's (Table 4) and characters 2 and 25 were excluded because they were shown to be highly correlated with numbers 4 and 26 respectively (Fig. 33). Characters 18 and 20 (Appendix 5) were also excluded because they were both relatively highly correlated (Fig. 33) and were also absent from some OTU's (Table 4).

The first five factors in this ordination explained almost 70% of the total variation. The first factor accounted for 21,59% of the variation. Characters loading most heavily on this component were, in decreasing order, numbers 17, 23, 5 and 16 (Table 6; Appendix 5). They represented presence or absence of setae, conidium width, colony reverse centre colour and the presence or absence of perithecia in culture. This is illustrated in Fig. 34, where the *C. crassipes* OTU's and other OTU's having only scattered setae, broad conidia, perithecial initials in culture and a relatively dark coloured colony centre reverse, were placed on one end of axis 2. On the other end of this axis was *C. dematium,* having abundant setae, narrow conidia and no perithecial initials.

The second component accounted for 16,84% of the total variation. Characters 7,15 and 3 (Appendix 5) loaded most heavily on this component, representing texture of the marginal colony zone, conidia formed predominantly from mycelial side branches or not, and the colour of the colony marginal zone, above. The third component accounted for 11,06% of the total variation, loaded most heavily by characters 11, 21 and 22, namely the presence or absence of conidiomata and conidium shape and length (Appendix 5). This is illustrated in Fig. 35 where, along the second axis, OTU's with downy marginal zones, forming conidia in the aerial mycelium, were placed to the right, while those with submerged to closely appressed marginal zones, not forming conidia in the aerial mycelium, were placed to the left.

Along axis 3 (Fig. 35 & 36), OTU's not forming conidiomata or with very broad, curved or fusoid conidia were placed towards the upper section in Fig. 35, to the right in Fig. 36. Those OTU's with conidiomata and cylindrical conidia were placed towards the lower portion of the axis in Fig. 35 and to the left in Fig. 36.

The fourth component accounted for 10,40% of the total variation. Character 24, appressorium shape, mainly loaded this component, followed by 27 and 26, presence or absence of sclerotia and appressorium width (Appendix 5) respectively. Fig. 36 illustrates the distribution of OTU's with broad or irregular appressoria and which form sclerotia to a greater or lesser extent, along the lower portion of axis 4. OTU's forming obovoid to clavate, narrower appressoria and not forming sclerotia, were placed towards the upper part of the axis.

The fifth component accounted for 9,56% of the variation. Characters loading most heavily on this component were numbers 1 and 4, growth rate and colour of the colony reverse, central zone. The ordination diagram, Fig. 37, reflects the placement of OTU's with a relatively fast growth rate and light colony colour, towards the upper part of axis 5, while those with a slower growth rate and darker colony colour were placed towards the lower portion of the axis.

In the 28 OTU ordination and MST, the strongest links between OTU's were found within the *C. dematium, C. graminicola* and *C. crassipes* groups, and also between the *C. trifolii* and *C. lindemuthianum* OTU's.

7. DISCUSSION AND CONCLUSIONS

7.1 MULTIVARIATE PHENETIC ANALYSES

Multivariate phenetic analyses were performed in order to establish whether a practical species-grouping of South African collections of *Colletotrichum* could be obtained using an objective evaluation of certain easily observed morphological and culture characteristics. Moss *et al.* (1977) favour the use of ordination techniques in taxonomic studies rather than cluster analyses as the latter tend to impose structure not necessarily present in the data. However, they suggest the use of several methods of analyses to enable as comprehensive an exploration of the data matrix structure possible.

This was done in the present study. Comparable clusters were produced by the CL together with the UPGMA average linkage analyses, principal component analysis and MST. The only clusters produced in the WPGMA phenogram comparable to groups produced by other methods, were the *C. graminicola* and *C. crassipes* groupings, together with the association of *C. trifolii* and *C. lindemuthianum* OTU's. However, the UPGMC (Fig. 29) produced the only phenogram to cluster two *C. coccodes* OTU's together, namely numbers 7 and 18 (Appendix 4). Little or poor grouping of OTU's was obtained in the SL and UPGMC methods.

Characters which proved to be discriminatory were the presence or absence of setae; conidium width together with conidium shape, length and whether they are produced mainly from conidiomata or from hyphal side-branches; presence or absence of perithecia and texture and colour of marginal zones in culture. Other contributing factors were appressorium shape and width, presence or absence of sclerotia and conidiomata, colony growth rate and colour of the colony reverse, central zone.

Characters which proved to be relatively unimportant in distinguishing between groups were the colour and texture of the colony central zone; presence or absence and nature of zonation and the nature of colony margins in culture, and the colour of conidial masses.

The methods employed were largely successful in distinguishing taxa OTU clusters corresponding with the following species were obtained in most of the analyses: *C. dematium*, *C. graminicola*, *C. crassipes* and *C. fructigenum*. The phenetically similar *C. trifolii* and *C. lindemuthianum* OTU's were also grouped together. OTU's representing *C. coccodes* and *C. destructivum* were,however, interspersed, with the exception of *C. coccodes* OTU's

7 and 18 (Appendix 4) linked in the MST (Figs. 34 - 37) and UPGMC (Fig. 29). This may have resulted from their phenetic similarity or from the use of insufficient characters to discriminate between them. *C. musae* was placed in a relatively distinct position in the SL (Fig. 24), UPGMA distance phenogram (Fig. 27), WPGMA (Fig 28), UPGMC (Fig. 29) and the 28 OTU ordination (Figs 34 - 37), while *C. orbiculare* appeared relatively distinct only in the UPGMA correlation phenogram (Fig. 26).

The phenetic heterogeneity within the group of OTU's designated as *C. gloeosporioides* (10, 11, 12, 13 and 24, Table 4, Appendix 4) was clearly illustrated in all the analyses performed. OTU's 10, 11, and 13 were mostly placed in a relatively distinct position, although OTU 13 was frequently loosely associated with *C. crassipes*. OTU 24, however, was constantly clustered with the *C. crassipes* OTU's. The placing of these transitional forms (OTU's 13 and 14) of *C. gloeosporioides* with *C. crassipes* OTU's illustrated the postulated connection between the two species. The position of OTU 11 varied, frequently being close to *C. destructivum* OTU 25 (Figs. 25, 27 & 28), while OTU 12 was constantly placed in the same cluster as the *C. trifolii* and *C. lindemuthianum* OTU's (numbers 23 & 15).

Two problem placings were those of OTU's 3 and 26 (Appendix 4). Number 3, isolated from *Beta vulgaris* leaves, was characterized by conidia similar in shape to those of *C. graminicola*. Number 26, isolated from grass seeds, was characterized by conidia and conidiomata bearing a strong resemblance to those of *C. dematium*. In all the analyses performed in this study, OTU 3 was placed in a relatively distinct position. It may, therefore, possibly be regarded as a separate taxon. On the other hand, it may be found to fit into *C. dematium* or *C. graminicola* if the variability of these taxa is examined in more detail. OTU 26, however, was placed in association with *C. graminicola* OTU's in most of the analyses and may consequently be regarded as a representative of that species.

The predominant clustering pattern obtained with these multivariate statistical analyses may be regarded as an accurate interpretation of the data matrix structure. These methods appear to provide a valuable tool for the exploration of taxonomic data and the evaluation of their contribution to the delimitation of taxa.

7.2 GENERAL TAXONOMY

The purpose of the present study was to report on the culture characteristics of a variety of South African collections of *Colletotrichum,* the development and morphology of conidiogenous cells, conidia, setae and appressoria and their usefulness in the taxonomy of the genus. Various statistical methods were employed to obtain a more objective evaluation of the groupings made by traditional taxonomic methods and an indication of the contribution of the selected characters to the delineation of these groups.

Earlier workers, including Edgerton (1908, 1913), Burger (1921), Ashby (1931), Baker, Crowdy & McKee (1940), Chilton (1943), Chona & Hingorani (1950), Ramsey, Smith & Heiberg (1951), Frandsen (1953), Arx (1957c), Chesters & Hornby (1965a), Stephan (1967a), Mishra & Prasad (1975) and Quimio(1976), found culture characteristics to be very variable within individual species of *Colletotrichum.* However, Sutton (1973) pointed out that Arx (1957a) applied culture characteristics successfully in the separation of *Colletotrichum* species. This was possible as, despite the cultural variability, sufficient relatively constant characteristics occur to assist the distinguishing of several taxa. In the present study, certain culture characters were constantly associated with various species: *C. dematium* formed concentric rings of large dark, stromatic conidiomata with long black setae in culture; *C. graminicola* often developed in a dendritic pattern, forming radially elongated, coalescing conidiogenous areas; *C. coccodes* was the only species to form abundant black microsclerotia, in concentric rings or scattered throughout the colony; *C. destructivum* formed large conidiogenous zones with scattered relatively small setae and limited production of conidial masses; *C. musae* was characterized by its fast growth rate, effuse colonies and glabrous conidiomata, while *C. lindemuthianum* grew relatively slowly, forming dark, almost black colonies with a pale marginal zone and *C. fructigenum* was characterized by the abundant production of conidial masses in the aerial mycelium, giving its colonies a chrystalline appearance. Because of their constant association, these characters allowed the rapid recognition of the different species in culture. The differences were also significant in the interspecific differentiation of taxa when applied in the multivariate statistical analyses. Much of the total variation in the principal component analyses was contributed to by the following culture characteristics: texture and colour of marginal zones; colour of the central zone, reverse; colony growth rate and presence or absence of perithecia, conidiomata and sclerotia. These characters are relatively constant and are consequently of use in the distinguishing of species.

Traditionally, the most discriminatory morphological criteria in *Colletotrichum* have been the Saccardoan characteristics of conidium shape and size, with emphasis on shape and width. This is evident in the keys to species formulated by previous workers (Arx, 1957a; Quimio, 1976; Sutton, 1980) and in the present study, with species separation based on the presence of straight or curved conidia. Average measurements were found to have more value in the identification of taxa than the ranges or extremes listed in most descriptions as these tend to overlap between species. These results support the conclusions of Wollenweber & Hochapfel (1949).

Morgan-Jones (1971) pointed out that little attention had been paid to conidium ontogeny or conidiophore structure in *Colletotrichum*. In the present study, conidiogenous cells were found to be morphologically similar in the species studied, irrespective of whether they were present as discrete cells or incorporated into more or less complex conidiomata. There were no constantly associated discriminatory tendencies. Conidium ontogeny was constantly phialidic with occasional percurrent proliferation being observed. Conidiogenous cells can, therefore, not be used as specific diagnostic criteria. However, an important characteristic in distinguishing *C. fructigenum* from the other species in the present study was found to be whether conidiogenous cells are produced mainly in conidiomata or mainly in the aerial mycelium in culture.

Sutton (1962) indicated the possibility of using appressorial characteristics in the identification of *Colletotrichum* species. In the present study, *C. crassipes* alone could be characterized by its appressoria which were very large and deeply lobed. Appressorial dimensions and shape in other species were found to be very variable, precluding their use as taxonomic criteria. This agrees with the report by Simmonds (1965).

Seta production is variable and controlled by environmental factors in many species (Schaffnit & Böhning, 1925; Frost, 1964; Chahal, 1978). They are often formed only on certain substrates in *C. gloeosporioides* (Stephan, 1969b). Despite this their presence and relative abundance, or absence, was found to be a primary discriminatory characteristic in the multivariate phenetic analyses in the present study. Setal ontogeny, however, was found to be similar in all species examined and together with length, septation and width did not prove to be discriminatory.

Emphasis on pathogenicity and host specificity previously lead to the description of hundreds of morphologically similar *Colletotrichum* species whose number Arx (1957a & b) attempted to reduce by using culture characteristics and morphology in culture as distinguishing characters. Pathogenicity tests were not carried out in the present study. Extensive investigation of the occurrence of physiological strains in *Colletotrichum* is necessary, however, from a plant pathological viewpoint, especially in the large, variable species such as *C. dematium, C. graminicola* and *C. gloeosporioides.* This has also been noted by Arx (1957a) and Sutton (1962, 1980).

Multivariate analyses were employed in the present study to determine whether the traditional taxonomic groupings could be supported statistically by using certain easily observed phenological characters. The result is consequently a relatively objective phenetic comparison which indicates the readily identifiable groups in the data matrix and evaluates the contribution of various characters to their separation.

The isolates of *C. dematium, C. graminicola, C. crassipes, C. fructigenum, C. musae* and *C. lindemuthianum* together with *C. trifolii,* emerged as distinct groups. Characters which contributed most to their identification were the presence or absence of setae; conidium size and shape together with loci of production; appressorium shape and width; presence or absence of perithecia, sclerotia and conidiomata plus texture and colour of colony margins in culture and colony growth rate.

C. gloeosporioides, C. coccodes and *C. destructivum* isolates, however, were constantly interspersed and did not emerge as distinct entities on the basis of the characters employed in the statistical analyses. This indicated the necessity for further investigation of these groups, especially *C. gloeosporioides* whose heterogeneity was clearly illustrated.

As the exemplar approach (Sneath & Sokal, 1973) was employed in selecting representatives for inclusion in the statistical analyses, intraspecific variation could not be evaluated and errors may have resulted from the choice of aberrant OTU's (Moss *et al.*, 1977). However, valuable information was obtained as regards the discriminatory value of characters, and traditional groupings were largely supported.

The statistical analyses confirmed Gorter's (1956, 1962) division of *C. gloeosporioides sensu* Arx (1957a) into two groups. The isolates which agreed with *C. fructigenum* (Gorter, 1962) appear to be identical to *C. acutatum*, described by Simmonds (1965). Simmonds (1965) had noted that Arx (1957a) did not include a *Colletotrichum* species which fitted the description of this fungus, in his key. As older descriptions are extremely brief and lack data on culture characteristics or other modern criteria such as conidium ontogeny, and as culture comparisons of old type material are precluded, Simmonds (1965) described this fungus as a new species. Although the name *C. fructigenum* has priority over that of *C. acutatum* Simmonds, it appears to be more expedient to conserve Simmonds' (1965) binomial against *C. fructigenum* (Berk.) Vassilj. *sensu* Gorter (1962), especially when the confusion surrounding the latter name is considered (Southworth, 1891b; Böhni, 1949; Arx, 1957a).

The statistical analyses also drew attention to the striking morphological and cultural similarities between *C. lindemuthianum* and *C. trifolii*, constantly grouping them together. *C. lindemuthianum* has traditionally been considered host specific to *Phaseolus* spp. and *C. trifolii* to *Medicago* and *Trifolium* spp., all three host species being leguminous, but Sutton (1980) extended the host range of *C. lindemuthianum* to include *Medicago sativa* and did not mention *C. trifolii* in his key to *Colletotrichum* species. Arx (1957a, 1970) regarded these two species as being host specific forms of *C. gloeosporioides*, together with *C. musae* and *C. orbiculare*. As no teleomorphs had been associated with them, however, as opposed to *C. gloeosporioides*, Arx (1957a, 1970) did not make formal combinations but retained them under their original names. *C. lindemuthianum*, *C. trifolii*, *C. musae* and *C. orbiculare* should be regarded as separate taxonomic species as they are morphologically and culturally relatively distinct. *C. lindemuthianum* and *C. trifolii* may be considered to be two physiological forms of the same fungus, in which case the older name, *C. lindemuthianum*, should apply for this taxon.

Despite the considerable amount of attention to which the genus *Colletotrichum* has been subjected over the past century, its taxonomic state remains confused. Arx (1957a, 1970) regarded most *Colletotrichum* species as being very variable, consequently setting them wide boundaries. Sutton (1980), in contrast, placed more emphasis on smaller morphological differences and on host specificity and pathogenicity, especially in *C. dematium* and *C. graminicola sensu* Arx (1957a). The results of the present study, however, support Arx's (1957a) views of these species.

One of the justifications of fungal taxonomy is its necessity in applied mycology (Johnson, 1968). Consequently it is often utilitarian and classifications tend to change both with increasing knowledge and with changes in their purpose (Talbot, 1971). The morphological characters commonly used for species description are not always associated with the cultural, physiological and pathogenic variability which has been demonstrated in fungi (Johnson, 1968). However, species should be distinguished by well-marked discontinuities in characters as far as possible of the same order (Hawksworth, 1974), and it is generally accepted that these characters be morphological at the species level in fungi and physiological at lower levels only.

In order to establish where the intrageneric discontinuities in *Colletotrichum* lie, large numbers of isolates of each currently recognised taxonomic species must be examined, both morphologically and pathogenically, to ascertain the boundaries of their variability, and compared with type material as far as possible. The consideration of characters displayed in pure culture together with the traditional morphological taxonomic characters and the application of statistical methods of evaluating these data, would significantly contribute to a sound basis for a more stable classification of *Colletotrichum* species.

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9. REFERENCES

AINSWORTH, G.C. (1971). *Ainsworth & Bisby's Dictionary of the Fungi,* 6th ed. Kew: Commonwealth Mycological Institute.

AKAI, S. & ISHIDA, N. (1968). An electron microscopic observation on the germination of conidia of *Colletotrichum lagenarium. Mycopathologia et Mycologia Applicata* 34, 337 - 345.

ALLESCHER, A. (1901). Fungi imperfecti: Hyalin-sporige Sphaerioideen. In *Rabenhorst's Kryptogamen-Flora von Deutschland, Oesterreich und der Schweiz,* Abt. VI. Leipzig: Eduard Kummer.

ALLESCHER, A. (1903). Fungi imperfecti: Gefärbt-sporige Sphaerioideen, Nectrioideen, Leptostromaceen, Excipulaceen und Familien der Ordnung der Melanconieen. In *Rabenhorst's Kryptogamen-Flora von Deutschland, Oesterreich und der Schweiz,* Abt. VII. Leipzig: Eduard Kummer.

ANDERBERG, M.R. (1973) *Cluster Analysis for Applications.* New York: Academic Press.

ANDERSON, T.F. (1951). Techniques for the preservation of three-dimensional structure in preparing specimens for the electron microscope. *Transactions of the New York Academy of Science* 13, 130.

ANDES, J.O. & KEITT, G.W. (1950). Variability of *Glomerella cingulata* (Stonem.) Sp. & Schr. from apples. *Phytopathology* 40: 915 - 925.

ARX, J.A. von. (1957a). Die Arten der Gattung *Colletotrichum* Corda. *Phytopathologische Zeitschrift* 29: 413 - 468.

ARX, J.A. von. (1957b). Revision der zu *Gloeosporium* gestellten Pilze. *Proceedings Koninklyke Nederlandse Akademie van Wetenschappen,* Serie C, 51, 1 - 153.

ARX, J.A. von. (1957c). Kultur- und Infektionsversuche mit einigen *Colletotrichum*-Arten. *Tijdschrift over Planteziekten* 63, 171 - 190.

ARX, J.A. von. (1970). A Revision of the Fungi classified as *Gloeosporium. Bibliotheca Mycologia,* Band 24. Lehre: J. Cramer.

ARX. J.A. von & MÜLLER, E. (1954). Die Gattungen der Amerosporen Pyrenomyceten. *Beiträge zu Kryptogamenflora der Schweiz* II. Bern: Büchler & Co.

ASHBY, S.F. (1931). *Gloeosporium* strains. *Tropical Agriculture* 8, 322 - 325.

ATKINSON, G.F. (1891). Anthracnose of cotton. *Journal of Mycology* 6, 173 - 178.

BAIN, S.M. & ESSARY, S.H. (1906). A new anthracnose of Alfalfa and Red Clover *Journal of Mycology* 12, 192 - 193.

BAKER, R.E.D., CROWDY, S.H. & McKEE, R.K. (1940). A review of latent infections caused by *Colletotrichum gloeosporioides* and allied fungi. *Tropical Agriculture* 17, 128 - 132.

BARNES, G.L. (1972). Differential pathogenicity of Oklahoma isolates of *Colletotrichum orbiculare. Plant Disease Reporter* 56, 35 - 38.

BARRUS, M.F. (1918) Varietal susceptibility of beans to strains of *Colletotrichum lindemuthianum. Phytopathology* 8, 589 - 614.

BERKELY, M.J. (1874). Notices of North American Fungi. *Grevillea* 3, 1 - 17.

BINYAMINI, N. & SCHIFFMAN-NADEL, M. (1972) Latent infection in Avocado fruit due to *Colletotrichum gloeosporioides. Phytopathology* 62, 592 - 594.

BLAKEMAN, J.P. & BRODIE, I.D.S. (1977). Competition for nutrients between epiphytic micro-organisms and germination of spores of plant pathogens on beetroot leaves. *Physiological Plant Pathology* 10, 29 - 42.

BLAKEMAN, J.P. & HORNBY, D. (1966). The persistence of *Colletotrichum coccodes* and *Mycosphaerella ligulicola* in soil, with special reference to sclerotia and conidia. *Transactions of the British mycological Society* 49, 227 - 240.

BLAKEMAN, J.P. & PARBERY, D.G. (1977). Stimulation of appressorium formation in *Colletotrichum acutatum* by phylloplane bacteria. *Physiological Plant Pathology* 11, 313 - 325.

BÖHNI, E. (1949). Untersuchungen über die Bitterfäule an Kirschen. *Phytopathologische Zeitschrift* 15, 333 - 375.

BÖHNING, K. & WALLNER, F. (1936). Fusskrankheit und andere Schadingungen an Mais durch *Colletotrichum graminicolum* (Ces.) Wilson. *Phytopathologische Zeitschrift* 9, 99 - 110.

BROWN, G.E. (1975). Factors affecting postharvest development of *Colletotrichum gloeosporioides* in citrus fruits. *Phytopathology* 65, 404 - 409.

BROWN, G.E. (1977). Ultrastructure of penetration of ethylene degreened Robinson tangerines by *Colletotrichum gloeosporioides. Phytopathology* 67, 315 - 320.

BROWN, G.E. & BARMORE, C.R. (1977). The effect of ethylene on the susceptibility of Robinson tangerines to anthracnose. *Phytopathology* 67, 120 - 123.

BURGER, O.F. (1921). Variations in *Colletotrichum gloeosporioides. Journal of agricultural Research* 20, 723 - 736.

BURKHOLDER, W.H. (1923). The gamma strain of *Colletotrichum lindemuthianum* (Sacc. & Magn.) Br. & Cav. *Phytopathology* 13, 316 - 323.

CAMPBELL, W.A. (1938). The cultural characteristics of the species of *Fomes. Bulletin of the Torrey botanical Club* 65, 31 - 69.

CAMPBELL, W.P. & GRIFFITHS, D.A. (1974). Fine structure of sclerotial germination in *Colletotrichum coccodes. Transactions of the British mycological Society* 63, 19 - 25.

CARROLL, R.B., JONES, E.R. & SWAIN, R.H. (1977). Winter survival of *Colletotrichum trifolii* in Delaware. *Plant Disease Reporter* 61, 12 - 15.

CARVAJAL, F. & EDGERTON, C.W. (1944). The perfect stage of *Colletotrichum falcatum. Phytopathology* 34, 206 - 213.

CESATI, V. de. (1852). Klotzsch, herbarum vivum mycologicum, sistens fungorum per totam Germaniam crescentium collectionem perfectam. Cent. XVII. *Flora* 35, 398.

CHAHAL, S.S. (1978). Role of relative humidity and nutrients on seta formation in *Colletotrichum papayae* P. Henn. *Current Science* 47, 430 - 431.

CHESTERS, C.G.C. & HORNBY, D. (1965a). Studies on *Colletotrichum coccodes.* I. The taxonomic significance of variation in isolates from tomato roots. *Transactions of the British mycological Society* 48, 573 - 581.

CHESTERS, C.G.C. & HORNBY, D. (1965b). Studies on *Colletotrichum coccodes.* II. Alternative host tests and tomato fruit inoculations using a typical tomato root isolate. *Transactions of the British mycological Society* 48, 583 - 594.

CHILTON, S.J.P. (1943). Variations in sporulation of different isolates of *Colletotrichum destructivum. Mycologia* 35, 13 - 20.

CHILTON, S.J.P., LUCAS, G.B. & EDGERTON, C.W. (1945). Genetics of *Glomerella.* III. Crosses with a conidial strain. *American Journal of Botany* 32, 549 - 554.

CHILTON, S.J.P. & WHEELER, H.E. (1949a) Genetics of *Glomerella.* VI. Linkage. *American Journal of Botany* 36, 270 - 273.

CHILTON, S.J.P. & WHEELER, H.E. (1949b). Genetics of *Glomerella.* VII. Mutation and segregation in plus cultures. *American Journal of Botany* 36, 717 - 721.

CHONA, B.L. & HINGORANI, M.K. (1950). Mutation in *Colletotrichum falcatum* Went., the causal organism of sugar-cane red rot. *Phytopathology* 40, 221 - 227.

CHONA, B.L. & SRIVASTAVA, D.N. (1960). Variations in *Colletotrichum falcatum* Went., the causal organism of red rot of sugar-cane. *Indian Phytopathology* 13, 58 - 65.

CLAUSEN, R.E. (1912). A new fungus concerned in wither tip of varieties of *Citrus medica. Phytopathology* 2, 217 - 234.

C.M.I. (1968). *Plant Pathologist's Pocketbook.* Kew: Commonwealth Mycological Institute.

COLE, G.T. & SAMSON, R.A. (1979). *Patterns of development in conidial Fungi.* London: Pitman Publ. Co.

COOKE, M.C. (1887). New Australian Fungi. *Grevillea* 16, 1 - 6.

CORDA, A.C.I. (1831 - 1832). *Sturm's Deutschlands Kryptogamen Flora.* Nürnberg. Vol. 3.

CORDA, A.C.I. (1837). *Icones fungorum hucusque cognitorum.* Vol. 1. Prague.

DABINET, P.E. & WELLMAN, A.M. (1978). Numerical taxonomy of certain genera of Fungi Imperfecti and Ascomycotina. *Canadian Journal of Botany* 56, 2031 - 2049.

D'ALMEIDA, M.J.V. (1899). La Galla dos olives en Portugal. *Bulletin de la Société Mycologique de France* 15, 90 - 94.

DE JACZEWSKI, M.A. (1906). *Alternaria grossulariae* n. sp. et *Colletotrichum grossulariae* n. sp. *Bulletin de la Société Mycologique de France* 22, 121 - 124.

DESMAZIÈRES, J.B.H.J. & MONTAGNÈ, J.C.F. (1849). Quaterzieme notice sur les plantes cryptogames récemment decauvertes en France. *Annales des sciences naturelles,* sér. 3: 11, 295.

DICKSON, B.T. (1925). *Colletotrichum* v *Vermicularia. Mycologia* 17, 213 - 217.

DIEDICKE, H. (1913). Noch einige "Leptostromaceen", die Nectrioideen, Excipulaceen und Melanconieen. *Annales Mycologici* 11 528 - 545.

DIPPENAAR, N.J. (1980). A taxonomic revision of the *monax-dolichura, luna-fumosa, glassi* and *zooden-poensis* complexes of Afrotropical *Crocidura* (Mammalia: Soricidae). Unpublished Ph.D. thesis, University of Natal.

DRIVER, C.H. & WHEELER, H.E. (1955). A sexual hormone in *Glomerella. Mycologia* 47, 311 - 316.

DUKE, M.M. (1928). The genera *Vermicularia* Fr. and *Colletotrichum* Cda. *Transactions of the British mycological Society* 13, 156 - 184.

DYKO, B.J. & MORDUE, J.E.M. (1979). *C.M.I. Descriptions of Pathogenic Fungi and Bacteria,* no. 630. Kew: Commonwealth Mycological Institute.

EDGERTON, C.W. (1908). The physiology and development of some anthracnoses. *Botanical Gazette* 45, 367 - 408.

EDGERTON, C.W. (1915). Effect of temperature on *Glomerella. Phytopathology* 5, 247 - 259.

EDGERTON, C.W., CHILTON, S.J.P. & LUCAS, G.B. (1945). Genetics of *Glomerella.* II. Fertilization between strains. *American Journal of Botany* 32, 115 - 118.

ELAROSI, H. (1960). *Gloeosporium* fruit rot of banana. *Transactions of the British mycological Society* 43, 681 - 687.

ELLIS, M.B. (1971). *Dematiaceous Hyphomycetes.* Kew: Commonwealth Mycological Society.

EMMETT, R.W. & PARBERY, D.G. (1975). Appressoria. In *Annual Review of Phytopathology* vol. 13 (ed. K.F. Baker, G.A. Zentmyer & E.B. Cowling), pp. 147 - 167. California: Annual Reviews Inc.

ERB, K., GALLEGLY, M.E. & LEACH, J.G. (1973). Longevity of mycelium of *Colletotrichum lindemuthianum* in hypocotyl tissue of resistant and susceptible bean cultivars. *Phytopathology* 63, 1334 - 1335.

EVERITT, B. (1974). *Cluster Analysis.* London: Heineman Educational Books Ltd.

FARLY, J.D. (1976). Survival of *Colletotrichum coccodes* in soil. *Phytopathology* 66, 640 - 641.

FIRMAN, I.D. & WALLER, J.M. (1977). Coffee berry disease and other *Colletotrichum* diseases of coffee. *Phytopathological Papers,* no. 20. Kew: Commonwealth Mycological Institute.

FRANDSEN, N.O. (1953). Zur physiologischen Spezialisierung von *Colletotrichum lindemuthianum. Zeitschrift für Pflanzenkrankheiten* 60, 113 - 125.

FRIES, E.M. (1825). *Systema orbis vegetabilis.* Lundae.

FRIES, E.M. (1849). *Summa vegetabilum Scandinaviae* 2 Uppsala.

FROST, R.R. (1964). Setae formation in *Colletotrichum* spp. *Nature,* London 201, 730 - 731.

GIBBS, J.N. (1969). Inoculum sources for coffee berry disease. *Annals of applied Biology* 64, 515 - 522.

GLAUERT, A.M. (1975). *Fixation, dehydration and embedding of biological specimens.* Amsterdam: North-Holland Publishing Co.

GOODE, M.J. (1958). Physiological specialization in *Colletotrichum lagenarium. Phytopathology* 48, 79 - 83.

GORTER, G.J.M.A. (1956). Anthracnose fungi of olives. *Nature*, London 178, 1129 - 1130.

GORTER, G.J.M.A. (1962). The identity of the fungus causing anthracnose of olives in South Africa. *Bothalia* 7, 769 - 778.

GORTER, G.J.M.A. (1977). Index of plant pathogens and the diseases they cause in cultivated plants in South Africa. *Scientific Bulletin of the Department of Agricultural Technical Services of South Africa,* no. 392.

GRIFFITHS, D.A. & CAMPBELL, W.P. (1972). Fine structure of conidial development in *Colletotrichum atramentarium. Transactions of the British mycological Society* 59, 483 - 489.

GROVE, W.B. (1918). New or noteworthy fungi. VI. *Journal of Botany* 56, 340 - 346.

GROVE, W.B. (1937). *British Stem and Leaf Fungi,* Vol. II. London: Cambridge University Press.

HANSON, E.W., MILLIRON, H.E. & CHRISTENSEN, J.J. (1950). The relation of the bluegrass billbug, *Calendra parvula* (Gyllenhal), to the development of basal stem rot and root rot of cereals and grasses in North-central United States. *Phytopathology* 40, 527 - 543.

HARTIGAN, J.A. (1975). *Clustering Algorithms.* New York: John Wiley & Sons.

HASSELBRING, H. (1906). The appressoria of the anthracnoses. *Botanical Gazette* 42, 135 - 142.

HAWKSWORTH, D.L. (1974). *Mycologist's Handbook.* Kew: Commonwealth Mycological Institute.

HAYAT, M.A. (1972). *Basic Electron Microscopy Techniques.* New York: Van Nostrand Reinhold Company.

HENNEBERT, G.L. & WERESUB, L.K. (1977). Terms for states and forms of fungi, their names and types. *Mycotaxon* 6, 207 - 211.

HINDORF, H. (1970). *Colletotrichum* spp. isolated from *Coffea arabica* L. in Kenya. *Zeitschrift für Pflanzenkrakheiten und Pflanzenschutz* 77, 328 - 331.

HINDORF, H. (1973a). *Colletotrichum*-Population auf *Coffea arabica* L. in Kenia. I. Eine Methode zur systematischen Trennung von Pilzpopulationen. *Phytopathologische Zeitschrift* 77, 97 - 116.

HINDORF, H. (1973b). *Colletotrichum* –Population auf *Coffea arabica* L. in Kenia. II. Qualitative und quantitative Unterschiede in der *Colletotrichum*-Population. *Phytopathologische Zeitschrift* 77, 216 - 234.

HINDORF, H. (1973c). *Colletotrichum*-Population auf *Coffea arabica* L. in Kenia. III. Verbreitung von *Colletotrichum*-Arten auf den einzelnen Organen des Kafeestrauches. *Phytopathologische Zeitschrift* 77, 324 - 338.

HINDORF, H. (1974). *Colletotrichum*-Arten aus dem Kaffeenanbaugebiet von Kiambu in Kenia. *Zeitschrift für Pflanzenkrankheiten und Pflanzenschutz* 81, 108 - 113.

HINDORF, H. & MUTHAPPA, B.N. (1974). A comparison of *Colletotrichum coffeanum* Noack from South India and Kenya. *Phytopathologische Zeitschrift* 80, 9 - 12.

HORN, N.L. (1952). A comparative study of two species of *Colletotrichum* on vetch. *Phytopathology* 42, 670 - 674.

HUGHES, S.J. (1958). Revisiones hyphomycetum aliquot cum appendice de nominibus rejiciendus. *Canadian Journal of Botany* 36, 727 - 836.

JARDINE, N. & SIBSON, R. (1971). *Mathematical Taxonomy.* London: John Wiley & Sons.

JENKINS, S.F., WINSTEAD, N.N. & McCOMBS, C.L. (1964). Pathogenic comparisons of three new and four previously described races of *Glomerella cingulata* var. *orbiculare. Plant Disease Reporter* 48, 619 - 622.

JOHNSON, T. (1968). Host specialization as a taxonomic criterion. In *The Fungi,* Vol. III (ed. G.C. Ainsworth & A.S. Sussman), pp. 543 - 556. New York: Academic Press.

KELLY, K.L. & JUDD, D.B. (1963). The ISCC-NBS method of designating colors and a dictionary of color names. Washington DC: National Bureau of Standards Circular no. 553.

KENDRICK, W.B. & PROCTOR, J.R. (1964). Computer taxonomy in the Fungi Imperfecti. *Canadian Journal of Botany* 42, 65 - 88.

KOZAR, F. & NETOLITZKY, H.J. (1978). Studies on hyphal development and appressorium formation of *Colletotrichum graminicola. Canadian Journal of Botany* 56, 2234 - 2242.

KULSHRESTHA, D.D., MATHUR, S.B. & NEERGAARD, P. (1976). Identification of seed borne species of *Colletotrichum. Friesia* 11, 116 - 125.

LAPP, M.S. & SKOROPAD, W.P. (1978a). Nature of adhesive material of *Colletotrichum graminicola* appressoria. *Transactions of the British mycological Society* 70, 221 - 223.

LAPP, M.S. & SKOROPAD, W.P. (1978b). Location of appressoria of *Colletotrichum graminicola* on natural and artificial barley leaf surfaces. *Transactions of the British mycological Society* 70, 225 - 228.

LEACH, C.M. (1958). A disease of dodder caused by the fungus *Colletotrichum destructivum. Plant Disease Reporter* 42, 827 - 829.

LEAKEY, C.L.A. & SIMBWA-BUNNYA, M. (1972). Races of *Colletotrichum lindemuthianum* and implications for bean breeding in Uganda. *Annals of applied Biology* 70, 25 - 34.

LE BEAU, F.J. (1950). Pathogenicity studies with *Colletotrichum* from different hosts on *Sorghum* and sugarcane. *Phytopathology* 40, 430 - 439.

LENNE, J.M. & PARBERY, D.G. (1976). Phyllosphere antagonists and appressorium formation in *Colletotrichum gloeosporioides. Transactions of the British mycological Society* 66, 334 - 336.

LONG, W.H. & HARSCH, R.M. (1918). Pure cultures of wood-rotting fungi on artificial media. *Journal of agricultural Research* 12, 33 - 82.

LUCAS, G.B. (1946). Genetics of *Glomerella.* IV. Nuclear phenomena in the ascus. *American Journal of Botany* 33, 802 - 806.

LUCAS, G.B. CHILTON, S.J.P. & EDGERTON, C.W. (1944). Genetics of *Glomerella.* I. Studies on the behaviour of certain strains. *American Journal of Botany* 31, 233 - 240.

LUKEZIC, F.L. (1974). Dissemination and survival of *Colletotrichum trifolii* under field conditions. *Phytopathology* 64, 57 - 59.

McGAHEN, J.W. & WHEELER, H.E. (1951). Genetics of *Glomerella.* IX. Perithecial development and plasmogamy. *American Journal of Botany* 38, 610 - 617.

McINTYRE, G.A. & RUSANOWSKI, C. (1975). Scanning electron microscope observations of the development of sporophores of *Colletotrichum atramentarium* (B. & Br.) Taub. on infected potato periderm. *American Potato Journal* 52, 269 - 275.

MERCER, P.C., WOOD, R.K.S. & GREENWOOD, A.D. (1971). Initial infection of *Phaseolus vulgaris* by *Colletotrichum lindemuthianum.* In *Ecology of Leaf Surface Micro-organisms* (ed. T.F. Preece & C.H. Dickinson), pp. 381 - 393. London: Academic Press.

MIEHLE, B.R. & LUKEZIC, F.L. (1972). Studies on conidial germination and appressorium formation by *Colletotrichum trifolii. Canadian Journal of Microbiology* 18, 1263 - 1269.

MISHRA, A. & PRASAD, N. (1975). Pathogenic and cultural variation in *Colletotrichum graminicolum* isolated from Sorghum. *Indian Journal of Mycology and Plant Pathology* 5, 5.

MISHRA, A. & SIRADHANA, B.S. (1979). Studies on the survival of sorghum anthracnose *(Colletotrichum graminicolum)* pathogen. *Philippine Agriculture* 62, 149 - 152.

MORDUE, J.E.M. (1967a). *C.M.I. Descriptions of Pathogenic Fungi and Bacteria,* no. 131. Kew: Commonwealth Mycological Institute.

MORDUE, J.E.M. (1967b). *C.M.I. Descriptions of Pathogenic Fungi and Bacteria,* no. 132. Kew: Commonwealth Mycological Institute.

MORDUE, J.E.M. (1967c). *C.M.I. Descriptions of Pathogenic Fungi and Bacteria,* no. 133. Kew: Commonwealth Mycological Institute.

MORDUE, J.E.M. (1970). *C.M.I. Descriptions of Pathogenic Fungi and Bacteria,* no. 222. Kew: Commonwealth Mycological Institute.

MORDUE, J.E.M. (1971a). *C.M.I. Descriptions of Pathogenic Fungi and Bacteria,* no. 315. Kew: Commonwealth Mycological Institute.

MORDUE, J.E.M. (1971b). *C.M.I. Descriptions of Pathogenic Fungi and Bacteria,* no. 316. Kew: Commonwealth Mycological Institute.

MORGAN-JONES, G. (1971). Conidium ontogeny in Coelomycetes. II. Some Melanconiales which possess phialides. *Canadian Journal of Botany* 49, 1931 - 1937.

MORGAN-JONES, G., NAG RAJ, T.R. & KENDRICK, B. (1972). Conidium ontogeny in Coelomycetes. IV. Percurrently proliferating phialides. *Canadian Journal of Botany* 50, 2009 - 2014.

MOSS, W.W., PETERSON, P.C. & ATYEO, W.T. (1977). A multivariate assessment of phenetic relationships within the feather mite family Eustathiidae (Acari). *Systematic Zoology* 26, 386 - 409.

NAG RAJ, T.R. & KENDRICK, B. (1975). A Monograph of *Chalara* and Allied Genera. Ontario: Wilfred Laurier University Press.

NAYLOR, V.D. & LEONARD, K.J. (1977). Survival of *Colletotrichum graminicola* in infected corn stalks in North Carolina. *Plant Disease Reporter* 61, 382 - 383.

NEGRU, A. (1960). Critical observations on some fungi species of the genera *Gloeosporium, Colletotrichum* and *Vermicularia. Revue de Biologie Academie Republique Populaire Roumaine* 5; 77 - 86.

NICHOLSON, R.L. & MORAES, W.B.C. (1980). Survival of *Colletotrichum graminicola:* Importance of the spore matrix. *Phytopathology* 70, 255 - 261.

NUTMAN, F.J. & ROBERTS, F.M. (1960). Investigations on a disease of *Coffea arabica* caused by a form of *Colletotrichum coffeanum* Noack. II. Some factors affecting germination and infection, and their relation to disease distribution. *Transactions of the British mycological Society* 43, 643 - 659.

O'GARA, P.J. (1915). New species of *Colletotrichum* and *Phoma. Mycologia* 7, 38 - 41.

OLIARI, L., VIEIRA, C. & WILKINSON, R.E. (1973). Physiologic races of *Colletotrichum lindemuthianum* in the state of Minas Geràs, Brazil. *Plant Disease Reporter* 57, 870 - 872.

PARBERY, D.G. & EMMETT, R.W. (1977). Hypotheses regarding appressoria, spores, survival and phylogeny in parasitic fungi. *Revue de Mycologie* 41, 429 - 447.

PAVGI, M.S. & SINGH, U.P. (1964). Parasitic fungi from North India. III. *Mycopathologia et Mycologia Applicata* 24, 355 - 361.

PAVGI, M.S. & SINGH, U.P. (1965). Parasitic fungi from North India. IV. *Mycopathologia et Mycologia Applicata* 27, 81 - 88.

PAVGI, M.S. & UPADHYAY, H.P. (1964). Parasitic fungi from North India. II. *Mycopathologia et Mycologia Applicata* 24, 347 - 354.

PENZIG, O. (1883). Repertorium. Fungi Agrumicoli *(Michelia* 11). *Hedwigia* 22, 73 - 77.

PENZIG, O. (1885). Note Micologiche, II. Contribuz. allo studio dei Funghi Agrumicoli. *Hedwigia* 24, 82 - 84.

PEREDO, H., OSARIO, M. & SANTAMARIA, A. (1979). *Colletotrichum acutatum* f. sp. *pinea,* a new pathogen of *Pinus radiata* in nurseries in Chile. *Plant Disease Reporter* 63, 121 - 122.

POLITIS, D.J. (1975). The identity and perfect state of *Colletotrichum graminicola. Mycologia* 67, 56 - 62.

POLITIS, D.J. (1976). Ultrastructure of penetration by *Colletotrichum graminicola* of highly resistant oat leaves. *Physiological Plant Pathology* 8, 117 - 122.

POLITIS, D.J. & WHEELER, H. (1972). The perfect stage of *Colletotrichum graminicola. Plant Disease Reporter* 56, 1026 - 1027.

POLITIS, D.J. & WHEELER, H. (1973). Ultrastructure of penetration of maize leaves by *Colletotrichum graminicola. Phytopathology* 63, 447.

PROCTOR, J.R. (1966). Some processes of numerical taxonomy in terms of distance. *Systematic Zoology* 15, 131 - 140.

QUIMIO, T.H. (1976). Variability in *Colletotrichum musae* (Berk. & Curt.) Arx and its significance in chemical control. *Philippine Phytopathology* 12, 40 - 50.

QUIMIO, T.H. (1977). Species of *Colletotrichum* in the *Philippines. Nova Hedwigia* 28, 543 - 553.

RAMSEY, G.B., SMITH, M.A. & HEIBERG, B.C. (1951). Anthracnoses of peaches. *Phytopathology* 41, 446 - 455.

RAYNER, R.W. (1970). *A mycological Colour Chart.* Kew: Commonwealth Mycological Institute.

RIDGWAY, R. (1912). *Color Standards and Color Nomenclature.* Washington: R. Ridgway.

RILEY, E.A. (1955). Tobacco anthracnose. II. Some physiological characteristics of the causal organism in relation to epidemiology. *Tropical Agriculture* 32, 150 - 155.

ROHLF, F.J. (1968). Stereograms in numerical taxonomy. *Systematic Zoology* 17, 246 - 255.

ROHLF, F.J., KISHPAUGH, J. & KIRK, D. (1972). *NT-SYS. Numerical Taxonomy System of Multivariate Statistical Programs.* New York: State University, Stony Brook.

SACCARDO, P.A. (1884). *Sylloge fungorum,* Vol. III. Padua: P.A. Saccardo.

SACCARDO, P.A. (1886). *Sylloge fungorum,* Vol. IV. Padua: P.A. Saccardo.

SCHAFFNIT, E. & BÖHNING, K. (1925). Die Brennfleckenkrankheit der Bohnen, eine monographische Studie auf biologischer Grundlage. *Centralblatt für Bakteriologie, Parasitenkunde und Infektionskrankheiten,* Abt. 2 63, 176 - 254, 360 - 438, 481 - 508.

SCHMIEDEKNECHT, M. (1957). Beitrag zur Morphologie und Cytologie von *Colletotrichum atramentarium* (B. & Br.) Taub. *Phytopathologische Zeitschrift* 29, 339 - 345.

SCHWINGHAMER, E.A. (1956). Physiologic specialization in *Colletotrichum linicolum. Phytopathology* 46, 300 - 305.

SHEAR, C.L. & WOOD, A.K. (1907). Ascogenous forms of *Gloeosporium* and *Colletotrichum. Botanical Gazette* 43, 259 - 266.

SHEAR, C.L. & WOOD, A.K. (1913). Studies of fungous parasites belonging to the genus *Glomerella.* United States Department of Agriculture, Bureau of Plant Industry Bulletin no. 252.

SIMMONDS, J.H. (1965). A study of the species of *Colletotrichum* causing ripe fruit rots in Queensland. *Queensland Journal of agricultural Science* 22, 437 - 459.

SIMMONDS, J.H. (1968). Type specimens of *Colletotrichum gloeosporioides* var. *minor* and *Colletotrichum acutatum. Queensland Journal of agricultural and animal Science* 25, 178.

SMALL, W. (1926). On the occurrences of a species of *Colletotrichum. Transactions of the British mycological society* 11, 112 - 137.

SMITH, R.W. & CROSSAN, D.F. (1958). The taxonomy, etiology and control of *Colletotrichum piperatum* (E. & E.). E. & H. and *Colletotrichum capsici* (Syd.) B. & B. *Plant Disease Reporter* 42, 1099 - 1103.

SNEATH, P.H.A. & SOKAL, R.R. (1973). *Numerical Taxonomy*. San Francisco: W.H. Freeman & Company.

SOKAL, R.R. & SNEATH, P.H.A. (1963). *Principles of Numerical Taxonomy.* San Francisco: W.H. Freeman & Company.

SOUTHWORTH, E.A. (1891a). Anthracnose of cotton. *Journal of Mycology* 6, 100 - 105.

SOUTHWORTH, E.A. (1891b). Ripe rot of grapes and apples. *Journal of Mycology* 6, 164 - 173.

STAPLES, R.C., LACCETTI, L. & YANIV, Z. (1976). Appressorium formation and nuclear division in *Colletotrichum truncatum. Archives of Microbiology* 109, 75 - 84.

STEARN, W.T. (1973). *Botanical Latin,* 2nd ed. Newton Abbott: David & Charles.

STEPHAN, B.R. (1966). Heterokaryose bei *Colletotrichum gloeosporioides* Penzig. *Naturwissenschaften* 53, 532 - 533.

STEPHAN, B.R. (1967a). Untersuchungen über die Variabilität bei *Colletotrichum gloeosporioides* Penzig in Verbindung mit Heterokaryose. I. Morphologische variabilität bei *C. gloeosporioides* Penz. *Zentralblatt für Bakteriologie, Parasitenkunde, Infektionskrankheiten und Hygiene* 121, 41 - 57.

STEPHAN, B.R. (1967b). Untersuchungen über die Variabilität bei *Colletotrichum gloeosporioides* Penzig in Verbindung mit Heterokaryose. II. Cytologische Grundlagen der Heterokaryose. *Zentralblatt für Bakteriologie, Parasitenkunde, Infectionskrankheiten und Hygiene* 121, 58 - 72.

STEPHAN, B.R. (1967c). Untersuchungen uber die Variabilität bei *Colletotrichum gloeosporioides* Penzig in Verbindung mit Heterokaryose. III. Versuche zum Nachweis der Heterokaryose. *Zentralblatt für Bakteriologie, Parasitenkunde, Infectionskrankheiten und Hygiene* 121, 73 - 83.

STEPHAN, B.R. (1968). Untersuchungen zum Nachweis der Heterokaryose bei *Colletotrichum gloeosporioides* Penzig unter Verwendung auxotropher Mutanten. *Zentralblatt für Bakteriologie, Parasitenkunde, Infektionskrankheiten und Hygiene* 122, 420 - 435.

STONEMAN, B. (1898). A comparative study of the development of some anthracnoses. *Botanical Gazette* 26, 69 - 120.

STRUBLE, F.B. & KEITT, G.W. (1950). Variability and inheritance in *Glomerella cingulata* (Stonem.) S. & S. from apple. *American Journal of Botany* 37, 563 - 567.

SUTTON, B.C. (1962). *Colletotrichum dematium* (Pers. *ex* Fries) Grove and *C. trichellum* (Fr. *ex* Fr .) Duke. *Transactions of the British mycological Society* 45, 222 - 232.

SUTTON, B.C. (1966). Development of fructifications in *Colletotrichum graminicola* (Ces.) Wils. and related species. *Canadian Journal of Botany* 44, 887 - 897.

SUTTON, B.C. (1968). The appressoria of *Colletotrichum graminicola* and *C. falcatum. Canadian Journal of Botany* 46, 873 - 876.

SUTTON, B.C. (1973). Coelomycetes. In *The Fungi,* vol. IV A (ed. G.C. Ainsworth, F.K. Sparrow & A.S. Sussman), pp. 513 - 582. New York: Academic Press.

SUTTON, B.C. (1977). Coelomycetes. VI. Nomenclature of generic names proposed for Coelomycetes. *Mycological Papers* no. 141. Kew: Commonwealth Mycological Institute.

SUTTON, B.C. (1980). *The Coelomycetes.* Kew: Commonwealth Mycological Institute.

SUTTON, B.C. & SELLAR, P.W. (1963). British records no. 67: *Colletotrichum typhae* H.C. Greene. *Transactions of the British mycological Society* 46, 459 - 462.

SWINBURNE, T.R. (1976). Stimulants of germination and appressoria formation by *Colletotrichum musae* (Berk. & Curt.). Arx in banana leachate. *Phytopathologische Zeitschrift* 87, 74 - 90.

TALBOT, P.H.B. (1971). *Principles of Fungal Taxonomy.* London: Macmillan Press.

TANI, M., ISHIDA, N. & FURASAWA, I. (1977). Effects of temperature and antibiotics on appressorium formation in spores of *Colletotrichum lagenarium. Canadian Journal of Microbiology* 23, 626 - 629.

TARR, S.A.J. (1962). *Diseases of Sorghum, Sudan Grass and Broom Corn.* Kew: Commonwealth Mycological Institute.

TAUBENHAUS, J.J. (1911). A study of some Gloeosporiums and their relation to a sweet pea disease. *Phytopathology* 1, 196 - 202.

TAUBENHAUS, J.J. (1912). A further study of some Gloeosporiums and their relation to a sweet pea disease. *Phytopathology* 2, 153 - 160.

TAYLOR, L.S. (1961). Aggregation, variance and the mean. *Nature*, London, 189, 732 - 735.

TIFFANY, L.H. (1951). Delayed sporulation of *Colletotrichum* from Soybean. *Phytopathology* 41, 975 - 985.

TIFFANY, L.H. & GILMAN, J.C. (1954). Species of *Colletotrichum* from Legumes. *Mycologia* 46, 52 - 75.

TODE, H.J. (1790). *Fungi Mecklenbergensis Selecti.* Vol. I. Luneberg.

TOWNSEND, B.B. & WILLETS, H.J. (1954). The development of sclerotia of certain fungi. *Transactions of the British mycological Society* 37, 213 - 221.

TU, J.C. (1980). The ontogeny of the sclerotia of *Colletotrichum coccodes. Canadian Journal of Botany* 58, 631 - 636.

VAN DER AA, H.A. (1978). A leaf spot disease of *Nymphaea alba* in the Netherlands. *Netherlands Journal of Plant Pathology* 84, 109 - 115.

VAN DER WESTHUIZEN, G.C.A. & HOLTZHAUSEN, M.A. (1980). *Alternaria helianthi* on sunflower in South Africa. *Phytophylactica* 12, 49 - 52.

VERWOERD, L. & DU PLESSIS, S.J. (1931). Descriptions of some new species of South African fungi and of species not previously recorded from South Africa. III. *South African Journal of Science* 28, 290 - 297.

VERWOERD, L. & DU PLESSIS, S.J. (1933). Descriptions of some new species of South African fungi and of species not previously recorded from South Africa. V. *South African Journal of Science* 30, 222 - 233.

WALKER, J. (1980). *Gaeumannomyces, Linocarpon, Ophiobolus* and several other genera of scolecospored ascomycetes and *Phialophora* conidial states, with a note on hyphopodia. *Mycotaxon* 11, 1 - 129.

WALKER, J.C. (1921). Onion smudge. *Journal of agricultural Research* 20, 685 - 722.

WALLER, J.M. (1972). Water-borne spore dispersal in coffee berry disease and its relation to control. *Annals of Applied Biology* 71, 1 - 18.

WARREN, H.L. (1977). Survival of *Colletotrichum graminicola* in corn kernels. *Phytopathology* 67, 160 - 162.

WELTY, R.E. & MUELLER, J.P. (1979). Occurrence of a highly virulent isolate of *Colletotrichum trifolii* on alfalfa in North Carolina U.S.A. *Plant Disease Reporter* 63, 666 - 670.

WHEELER, H.E. (1950). Genetics of *Glomerella.* VIII. A genetic basis for the occurrence of minus mutants. *American Journal of Botany* 37, 304 - 312.

WHEELER, H.E. (1954). Genetics and evolution of heterothallism in *Glomerella. Phytopathology* 44, 342 - 345.

WHEELER, H.E. & DRIVER, C.H. (1953). Genetics and cytology of a mutant, dwarf-spored *Glomerella. American Journal of Botany* 40, 694 - 702.

WHEELER, H.E., DRIVER, C.H. & CAMPA, C. (1959). Cross and self-fertilization in *Glomerella. American Journal of Botany* 46, 361 - 365.

WHEELER, H.E. & McGAHEN, J.W. (1952). Genetics of *Glomerella.* X. Genes affecting sexual reproduction. *American Journal of Botany* 39, 110 - 119.

WHEELER, H.E., OLIVE, L.S., ERNEST, C.T. & EDGERTON, C.W. (1948). Genetics of *Glomerella.* V. Crozier and ascus development. *American Journal of Botany* 35, 722 - 728.

WILSON, G.W. (1914). The identity of the anthracnose of grasses. *Phytopathology* 4, 106 - 112.

WOLLENWEBER, H.W. & HOCHAPFEL, H. (1949). Beitrage zur Kenntnis parasitärer und saprophytischer Pilze. VI. *Vermicularia, Colletotrichum, Gloeosporium* und ihre Beziehung zur Fruchtfäule. *Zeitschrift für Parasitenkunde* 14, 181 - 268.

YANG, S.J. & ELLINGBOE, A.H. (1972). Cuticle layer as a determining factor for formation of mature appressoria of *Erysiphe graminis* on wheat and barley. *Phytopathology* 62, 708 - 714.

YERKES, W.D. (1958). Additional new races of *Colletotrichum lindemuthianum* in Mexico. *Plant Disease Reporter* 42, 329.

YERKES, W.D. & ORTIZ, M.T. (1956). New races of *Colletotrichum lindemuthianum* in Mexico. *Phytopathology* 46, 564 - 567.

ZWILLENBERG, H.H.L. (1959). *Colletotrichum graminicola* (Ces.) Wilson auf Mais und verschiedenen anderen Pflanzen. *Phytopathologische Zeitschrift* 34, 417 - 425.

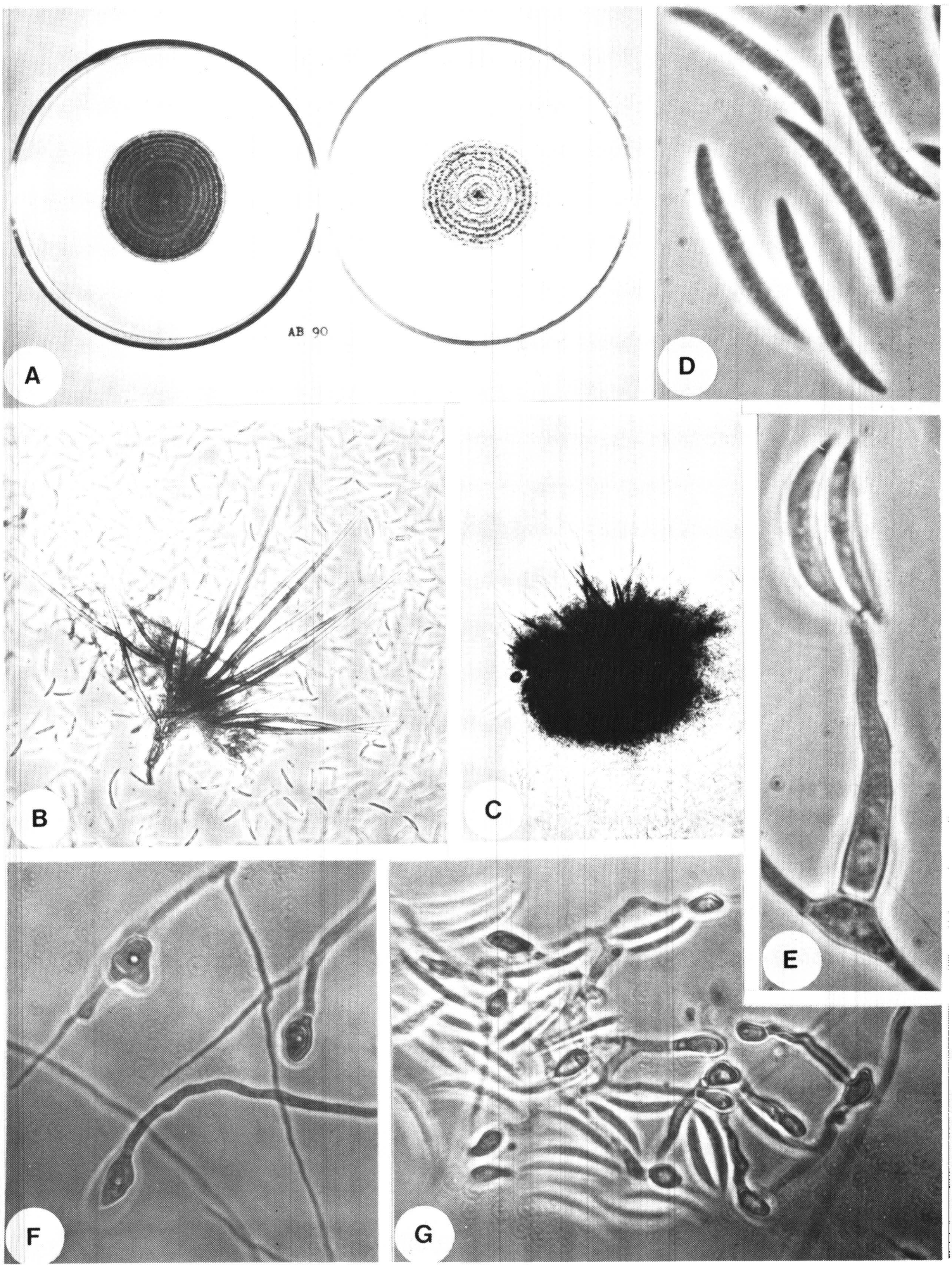

FIG. 1 C. **dematium,** *A. cultures of PREM 45751 on CDY (left) and MSA (right) at 10 days; B, unthickened conidioma of PREM 45751 x 100; C, stromatically thickened conidioma of PREM 45740 x 50; D, conidia of PREM 45751 x 1000, E, conidiogenous cell and conidia of PREM 45738 x 1 000; F, appressoria of PREM 45751 x 500; G, appressoria of PREM 45832 x 500.*

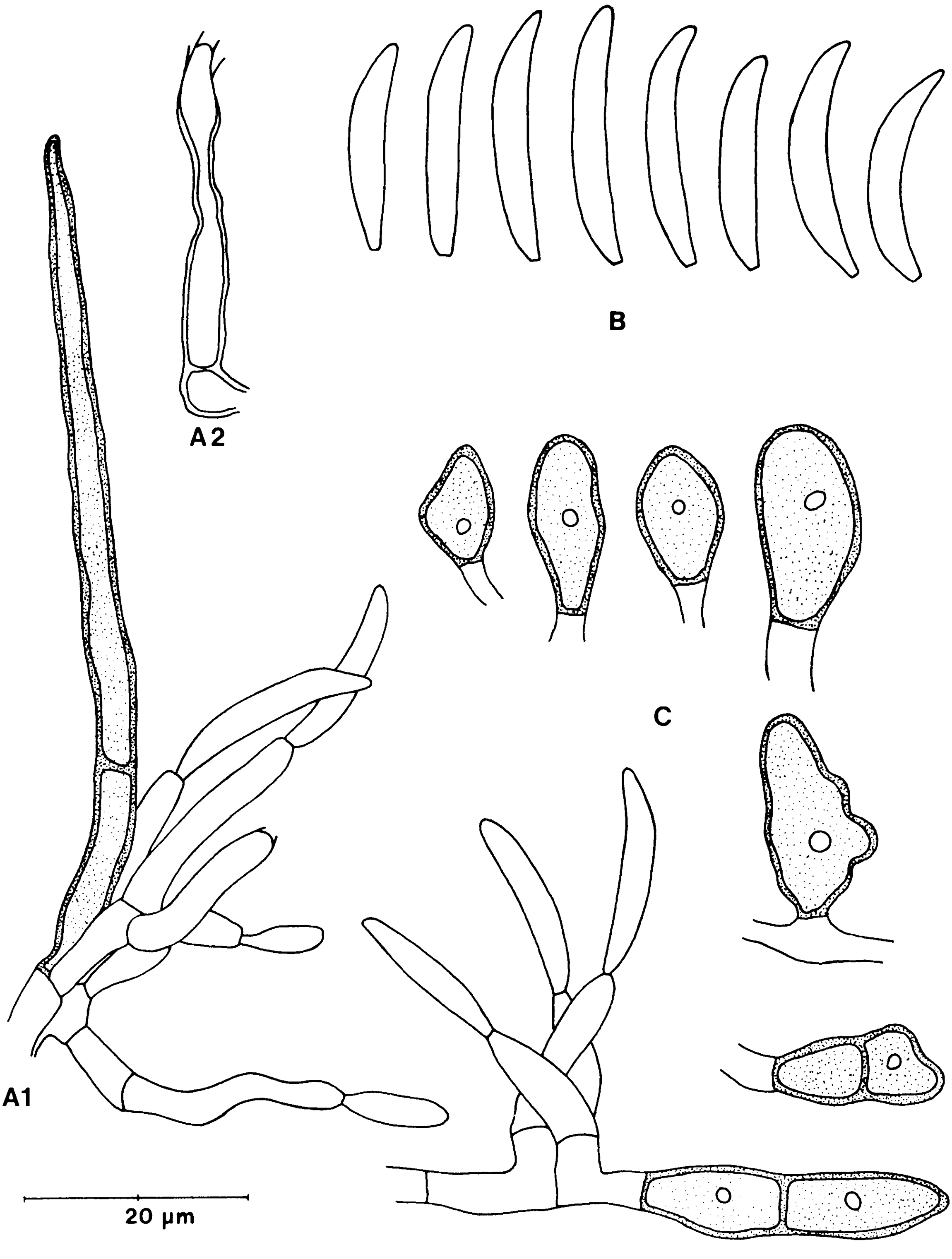

FIG. 2 **C. dematium**, *A1, seta and conidiogenous cells, PREM 45751; A2, percurrently proliferating conidiogenous cell, PREM 45738; B, conidia, PREM 45751, 45821; C, appressoria, PREM 45751, 45821, 45832.*

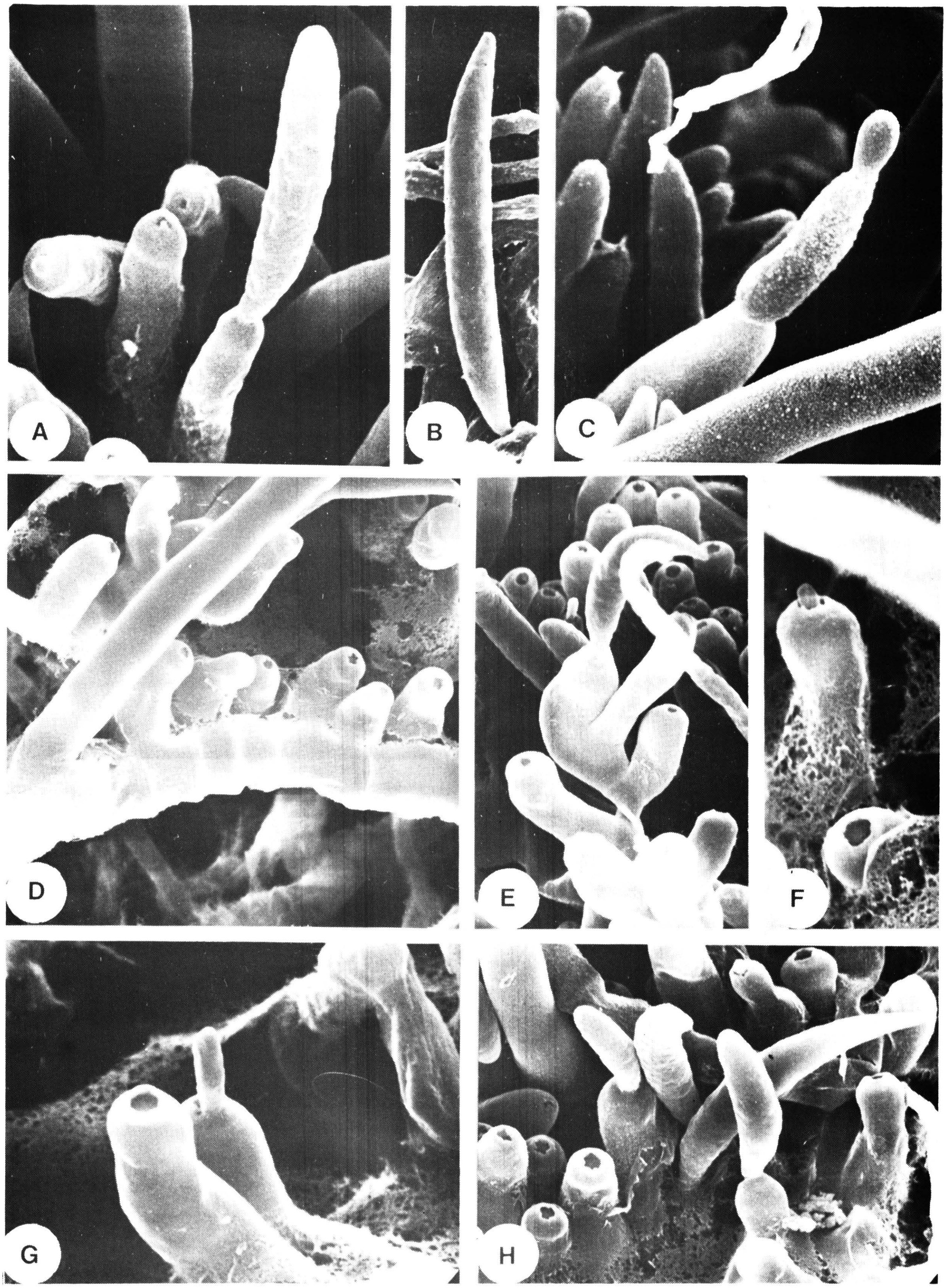

FIG. 3 *A, conidiogenous cells and conidium of* C. **dematium** *PREM 45832 x 6 000; B, conidium of* C. **dematium** *PREM 45740 x 4 800; C, percurrently proliferating conidiogenous cell of* C. **dematium** *PREM 45740 x 4 800; D, seta and conidiogenous cells of* C. **graminicola** *PREM 45749 x 2 600; E, branched conidiophore of* C. **graminicola** *PREM 45749 x 2 600; F, conidium initial of* C. **graminicola** *PREM 45749 x 6 000; G, conidiogenous cells and conidium initial of* C. **graminicola** *PREM 45749 x 6 000; H, conidia of* C. **graminicola** *PREM 45749 x 3 000 in various stages of development.*

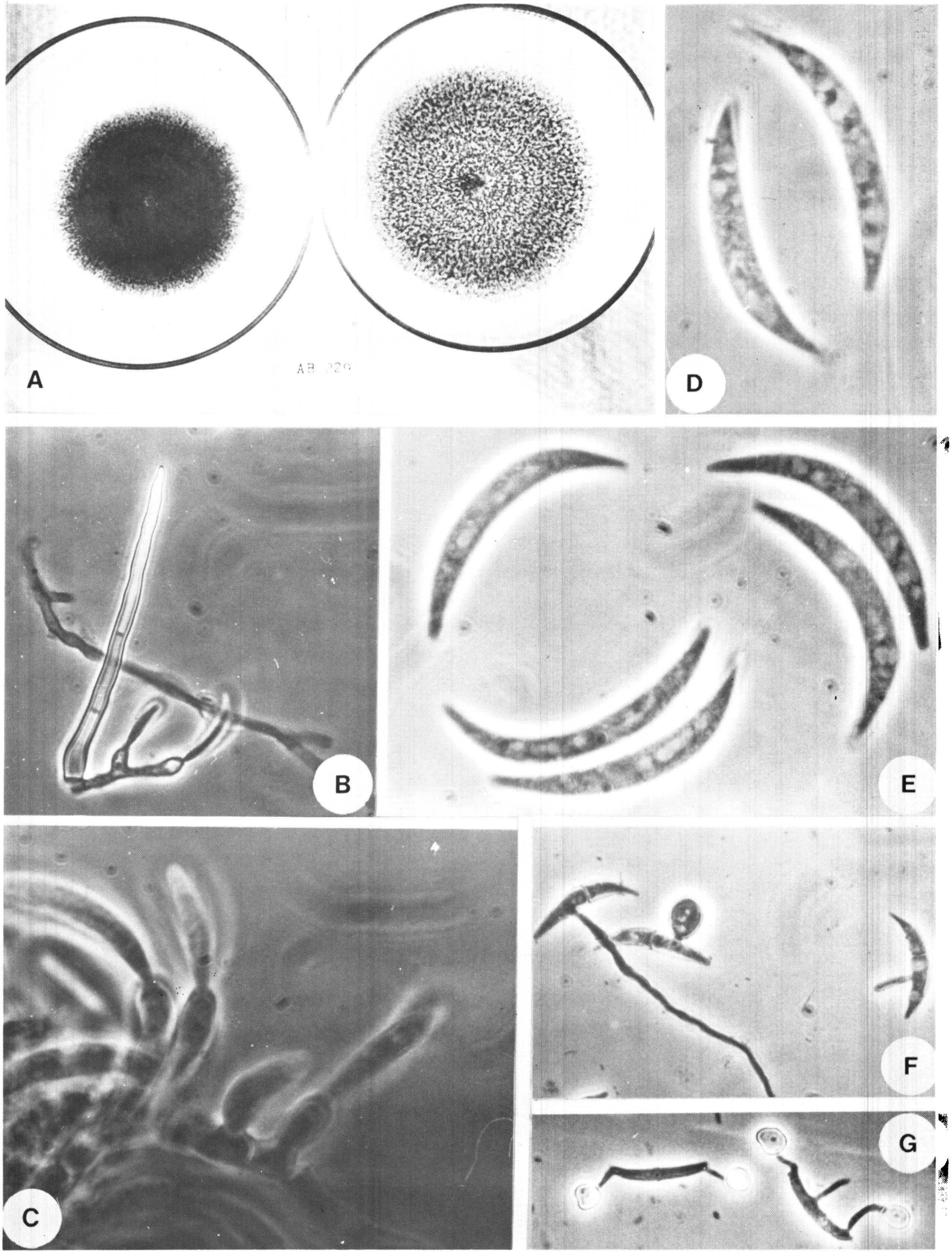

FIG. 4 **C. graminicola**, *A, cultures of PREM 45749 on CDY (left) and MSA (right) at 10 days; B, seta and conidiagenous cells of PREM 45747 x 400; C, conidiogenous cells of PREM 45747 x 1 000; D, conidia of PREM 45749 x 1 000; E, conidia of PREM 45747 x 1 000; F, germinating conidia of PREM 45822 x 400; G, germinating conidia of PREM 45832 x 400.*

FIG. 5 **C. graminicola**, *A, seta and conidiogenous cells, PREM 45747; B, conidia, PREM 45744, 45749, 45779; C, appressoria, PREM 45747, 45779.*

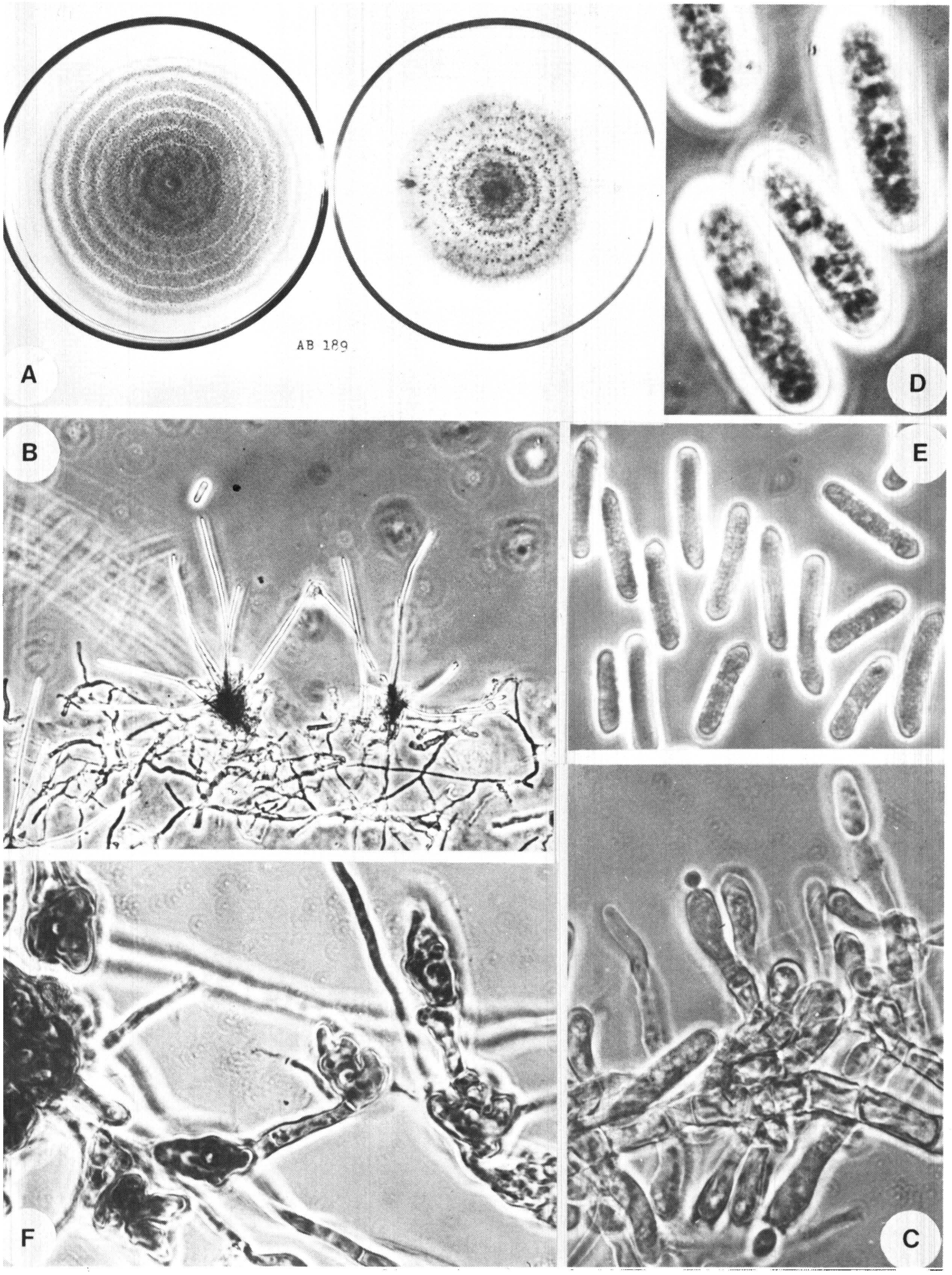

FIG. 6 C. **crassipes** *PREM 45774, A, cultures on CDY (left) and MSA (right) at 10 days; B, conidiomata x 100; C, conidiogenous cells x 1 000; D, conidia x 1 000; E, conidia x 400; F, appressoria x 500.*

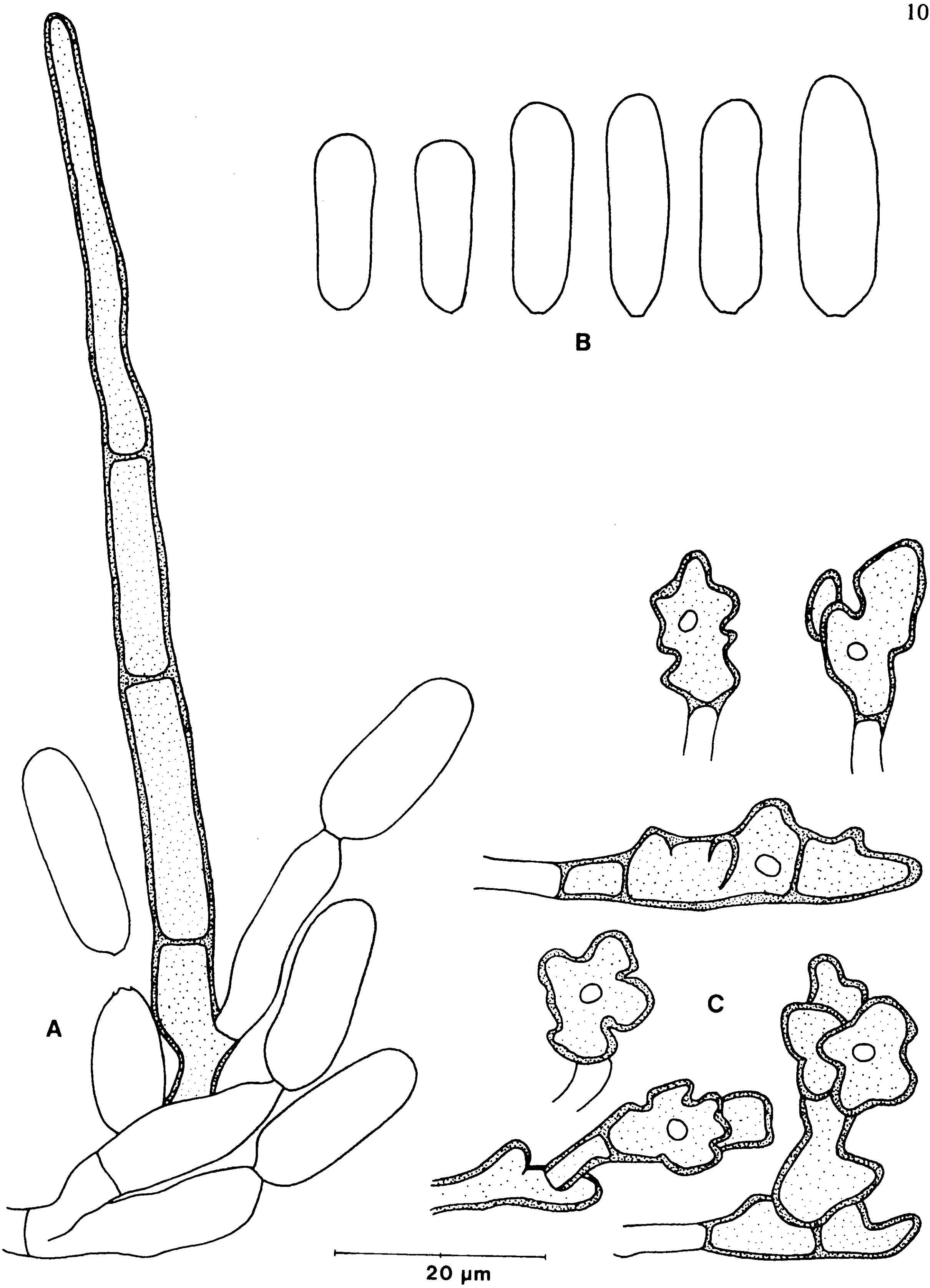

FIG. 7 C. **crassipes**, *A, seta and conidiogenous cells, PREM 45774; B, conidia, PREM 45774, 45833; C. appressoria, PREM 45774, 45833.*

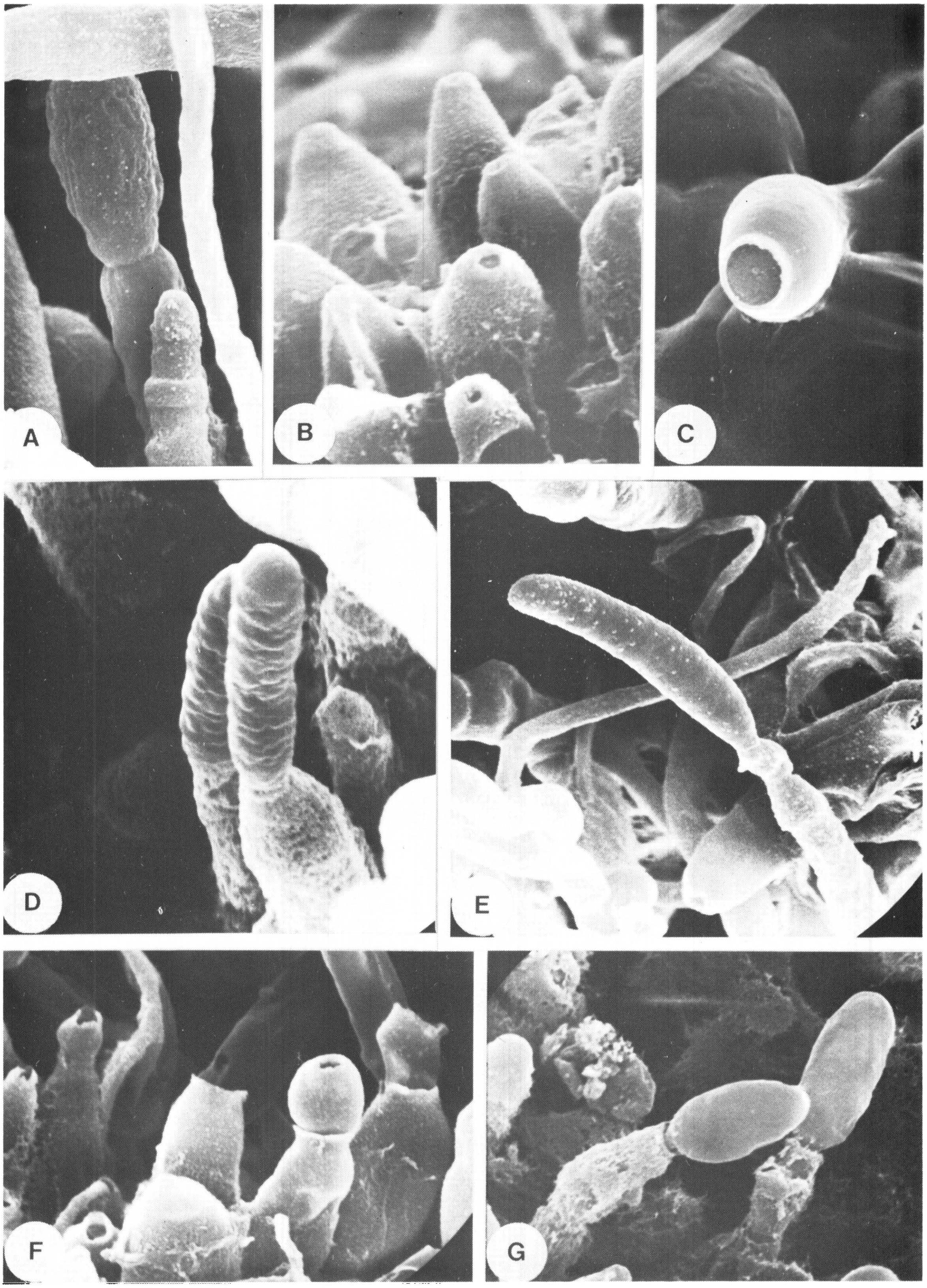

FIG. 8 *A, conidia and conidiogenous cells of* C. crassipes *PREM 45774 x 4 800; B, conidiogenous cells of* C. coccodes *PREM 45384 x 6 000; C. conidiogenous cell of* C. coccodes *PREM 45745 x 4 800 showing septal pore; D,* C. coccodes *PREM 45384 conidia and conidiogenous cells x 6 000; E,* C. coccodes *PREM 45745 percurrently proliferating conidiogenous cell x 4 800; F,* C. destructivum *PREM 45748 percurrently proliferating conidiogenous cell x 6 000; G,* C. musae *PREM 45380 conidiogenous cells and conidia x 4 800.*

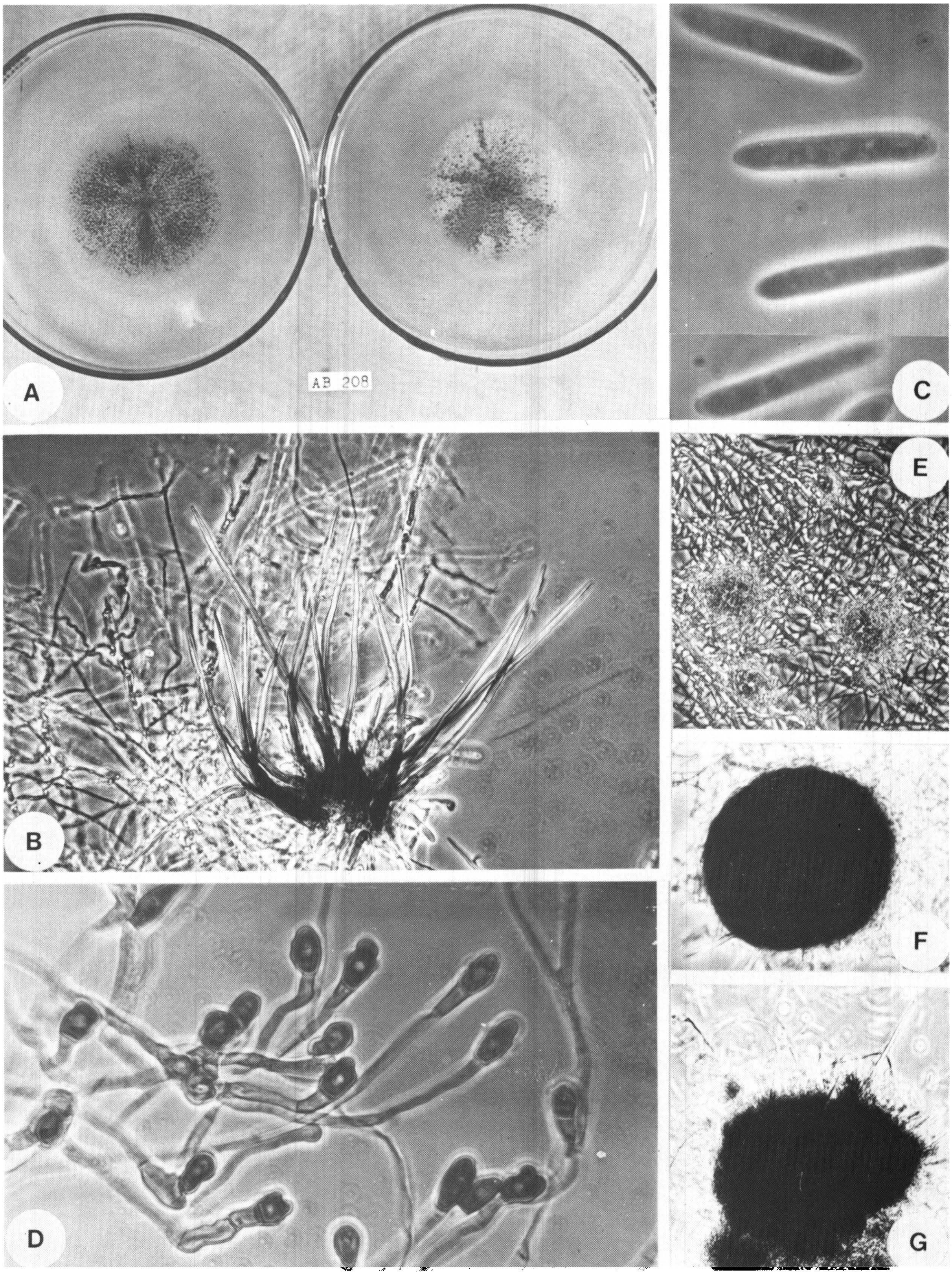

FIG. 9 **C. coccodes**, *A, cultures of PREM 45745 on CDY (left) and MSA (right) at 10 days; B, conidioma of PREM 45384 x 200; C,conidia of PREM 45739 x 1 000; D, appressoria of PREM 45739 x 500; E, sclerotium initials of PREM 45384 x 100; F, sclerotium of PREM 45824 x 100; G. conidioma formed by sclerotium of PREM 45384 x 100.*

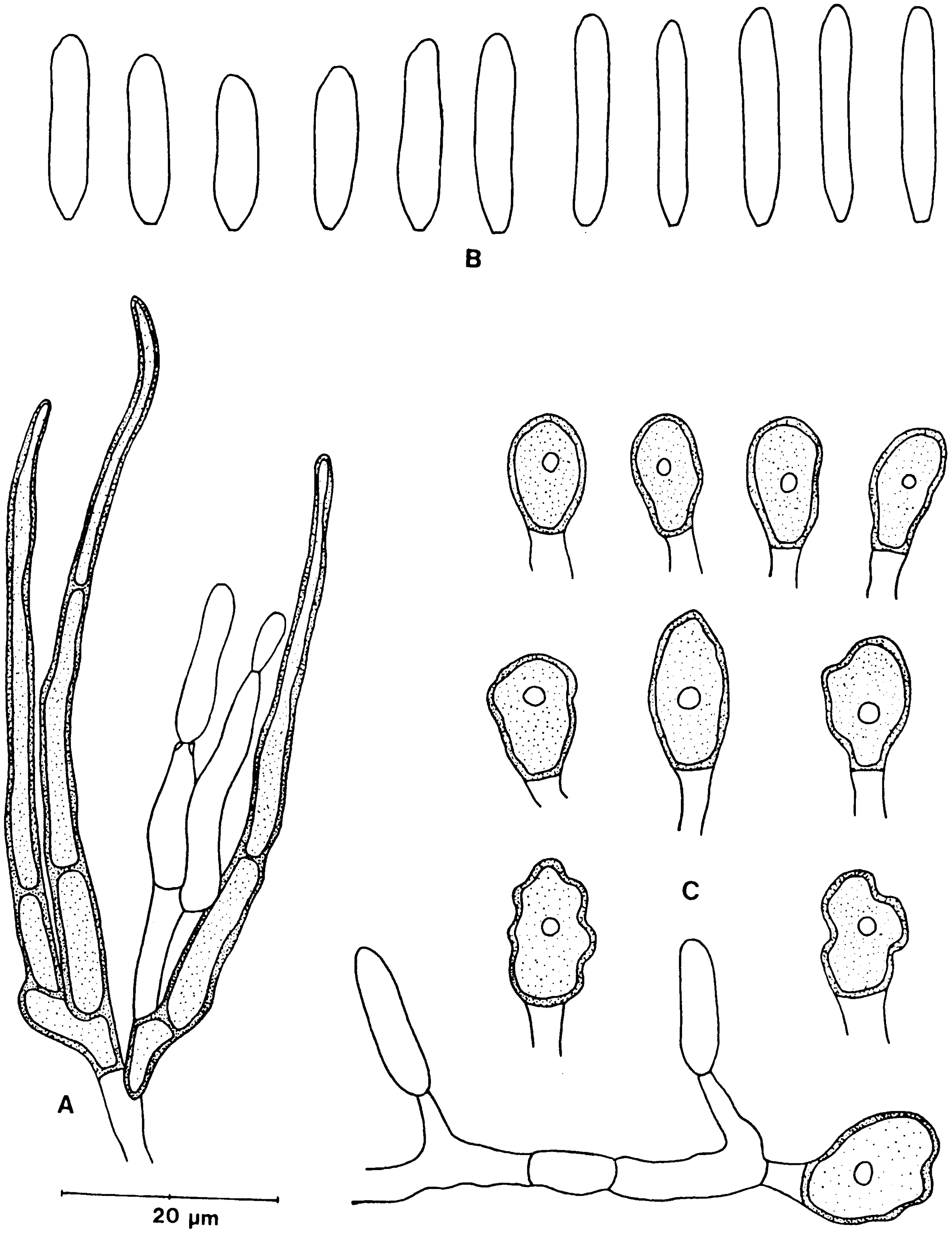

FIG. 10 C. coccodes, *A, setae and conidiogenous cells, PREM 45745; B, conidia, PREM 45384, 45739, 45745; C, appressoria, PREM 45739, 45745.*

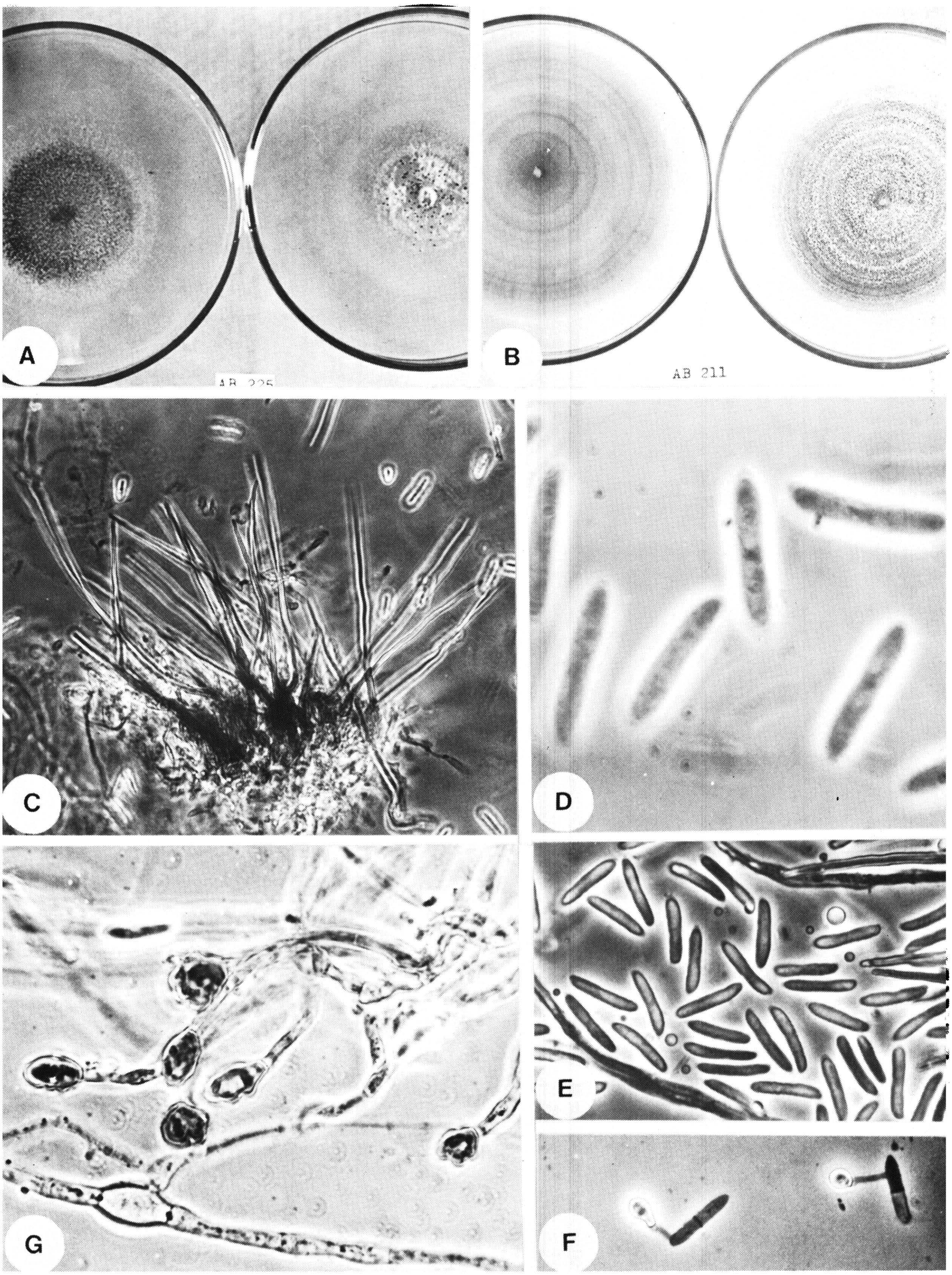

FIG. 11 **C. destructivum**, *A, cultures of PREM 45748 on CDY (left) and MSA (right) at 10 days; B, cultures of PREM 45746 on CDY (left) and MSA (right) at 10 days; C, conidioma of PREM 45748 x 200; D, conidia of PREM 45748 x 1 000; E, conidia of PREM 45748 x 400; F, germinated conidia of PREM 45364 x 400; G, appressoria x 500 of PREM 45748.*

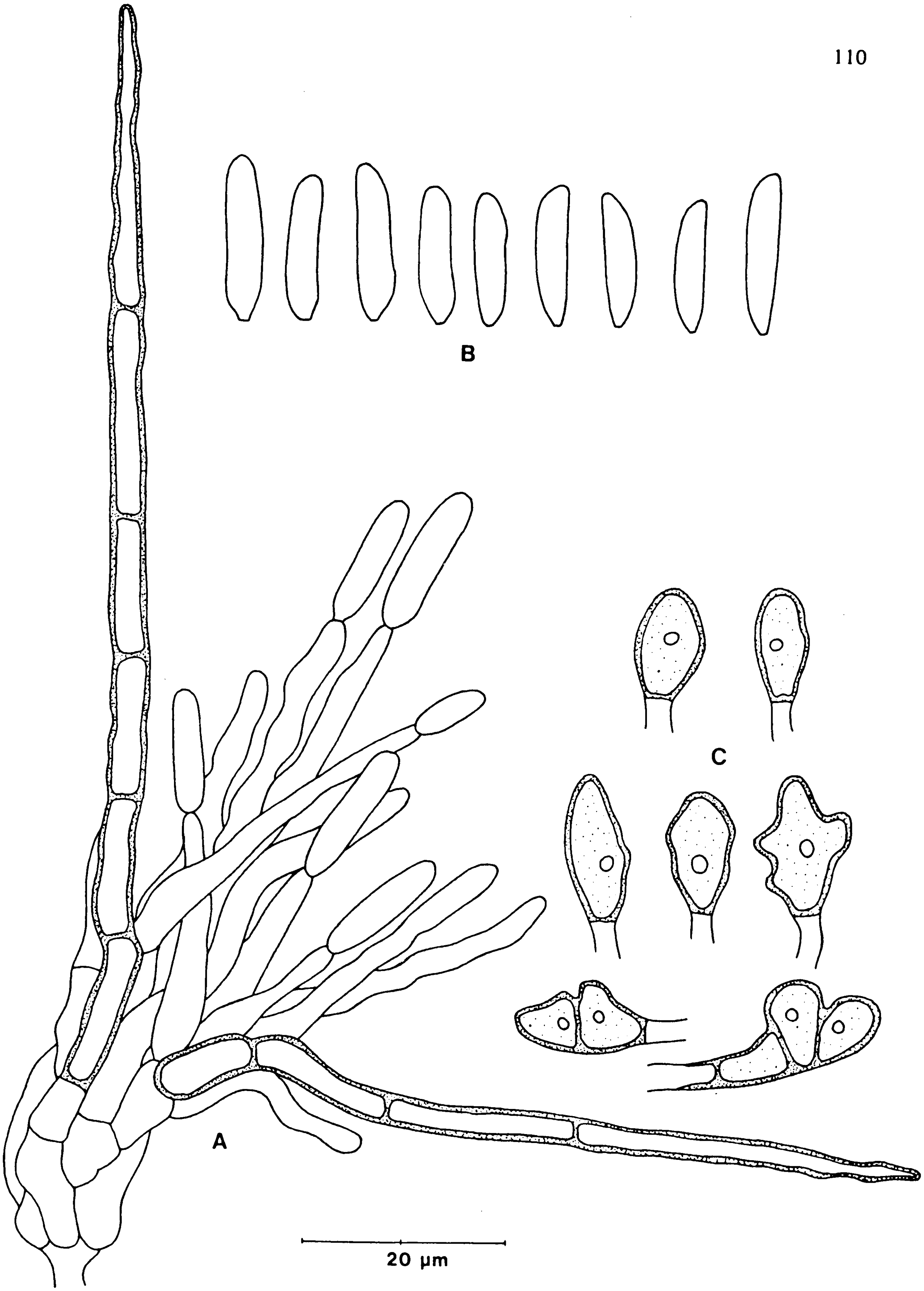

FIG. 12 **C. destructivum**, *A, setae and conidiogenous cells PREM 45746; B, conidia, PREM 45773, 45748; C, appressoria, PREM 45748, 45773.*

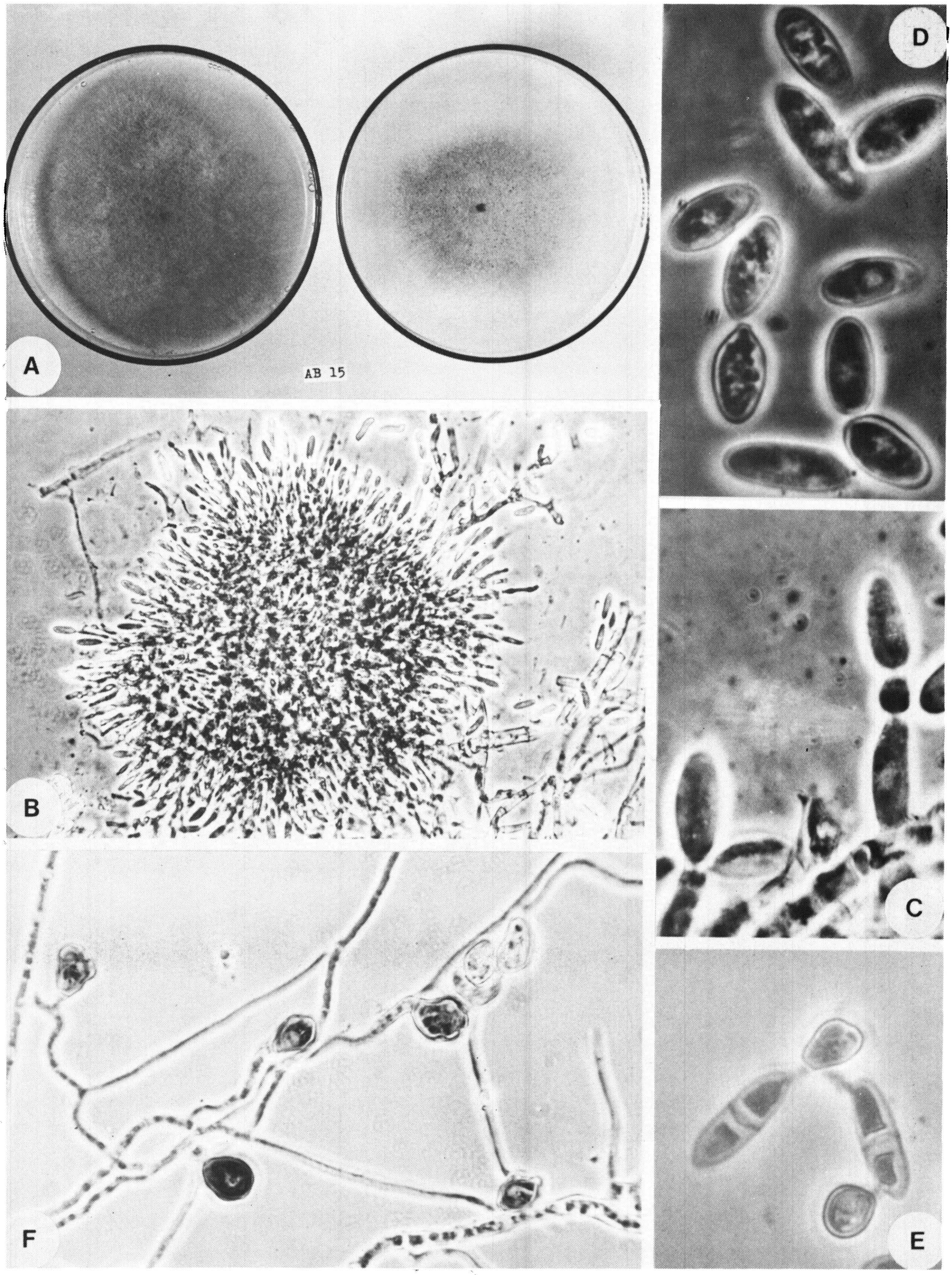

FIG. 13 C. musae *PREM 45380; A, cultures on CDY (left) and MSA (right) at 10 days; B, conidioma x 200; C, conidiogenous cell (left) and percurrently proliferating conidiogenous cell (right) x 1 000; D, conidia x 1 000; E, germinated conidia x 800; F, appressoria x 500.*

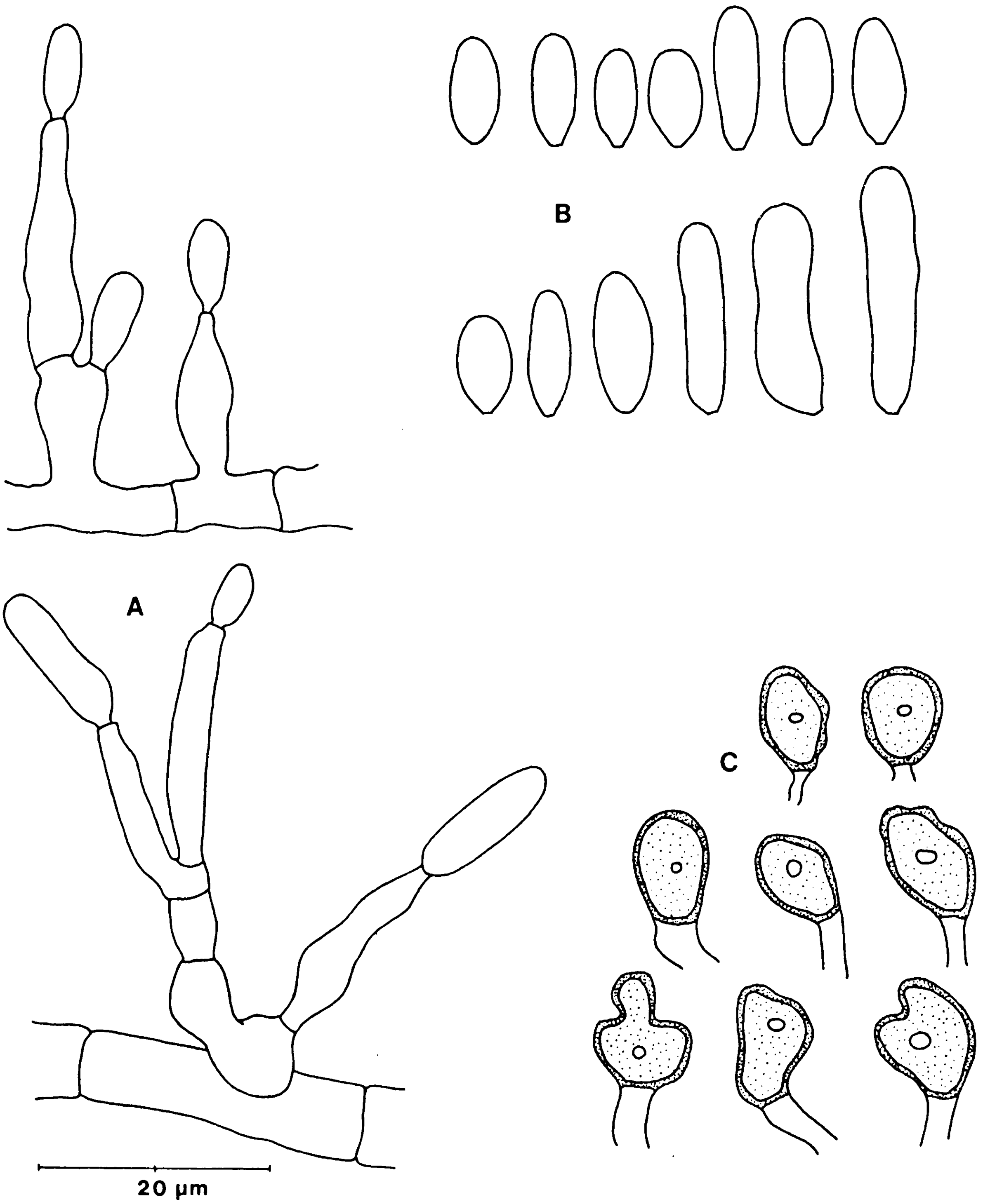

FIG. 14 C. musae, *PREM 45380, A, conidiogenous cells; B, conidia; C. appressoria.*

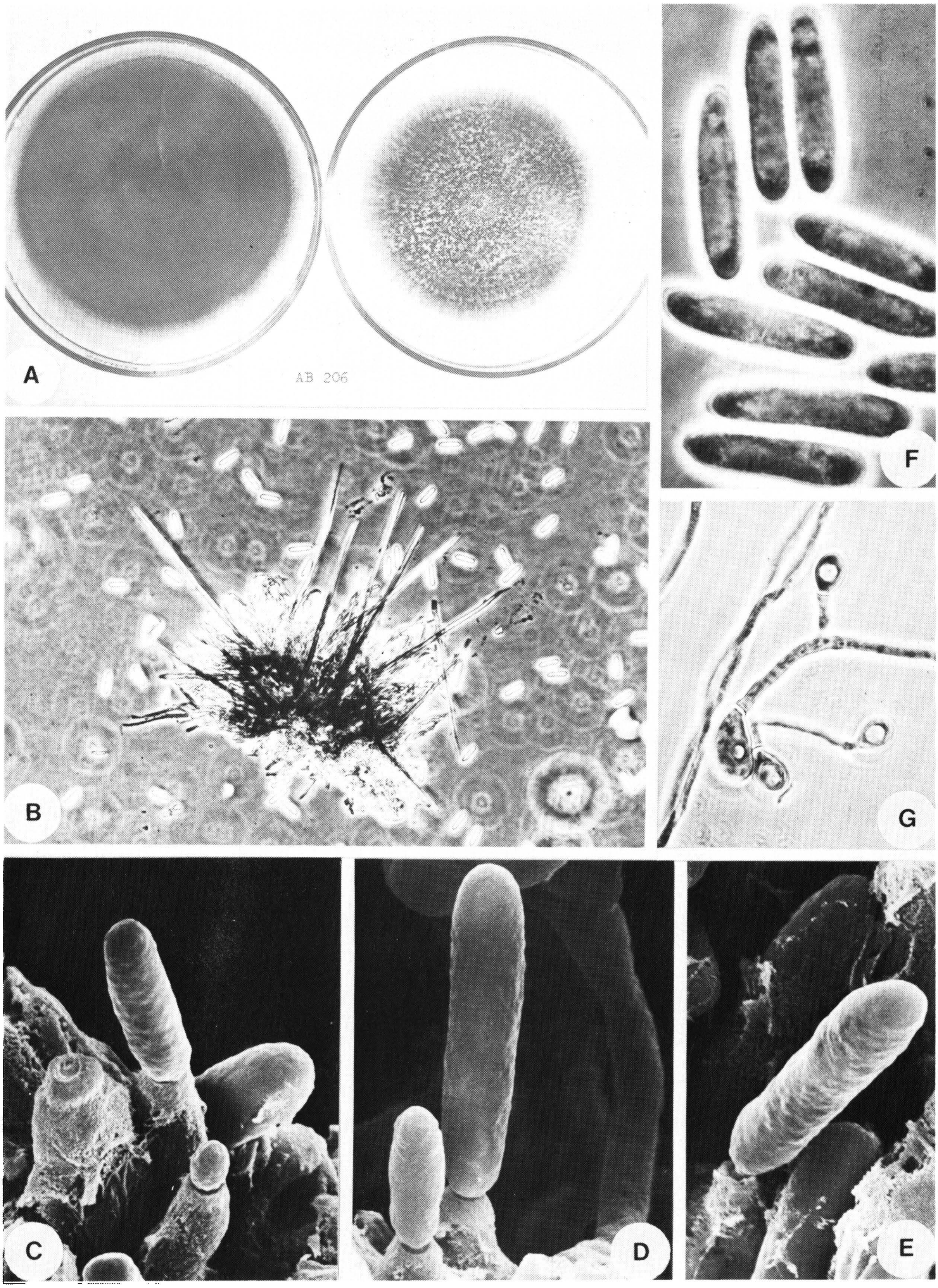

FIG. 15 **C. orbiculare** *PREM 45750, A, cultures on CDY (left) and MSA (right) at 10 days; B, conidioma x 100; C, conidia and conidiogenous cells x 4 800; D, conidia x 4 800; E, seceeding conidium x 4 800; F, conidia x 1 000; G, appressoria x 500.*

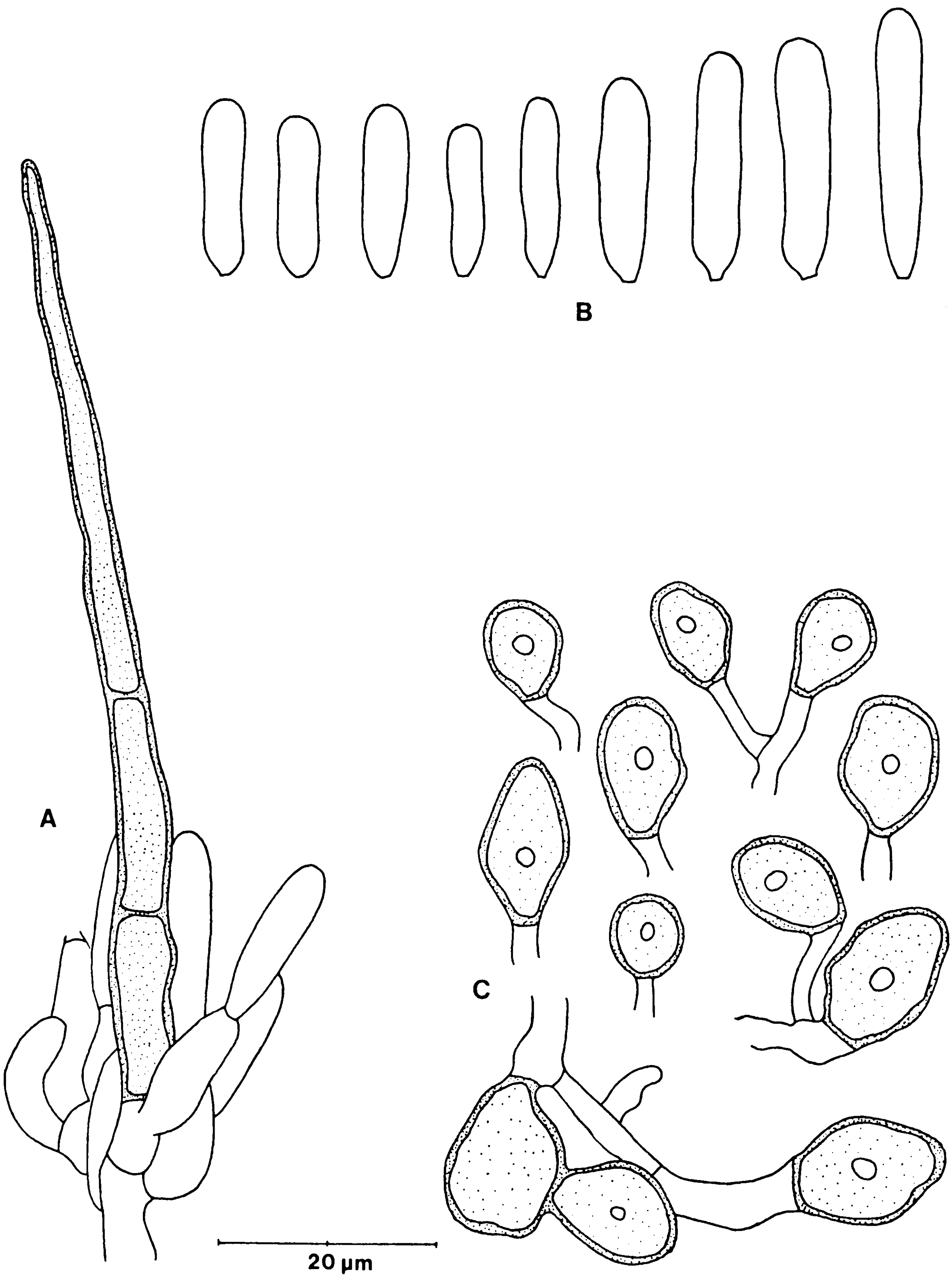

FIG. 16 C. orbiculare, *PREM 45750, A, seta and conidiogenous cells; B, conidia; C, appressoria.*

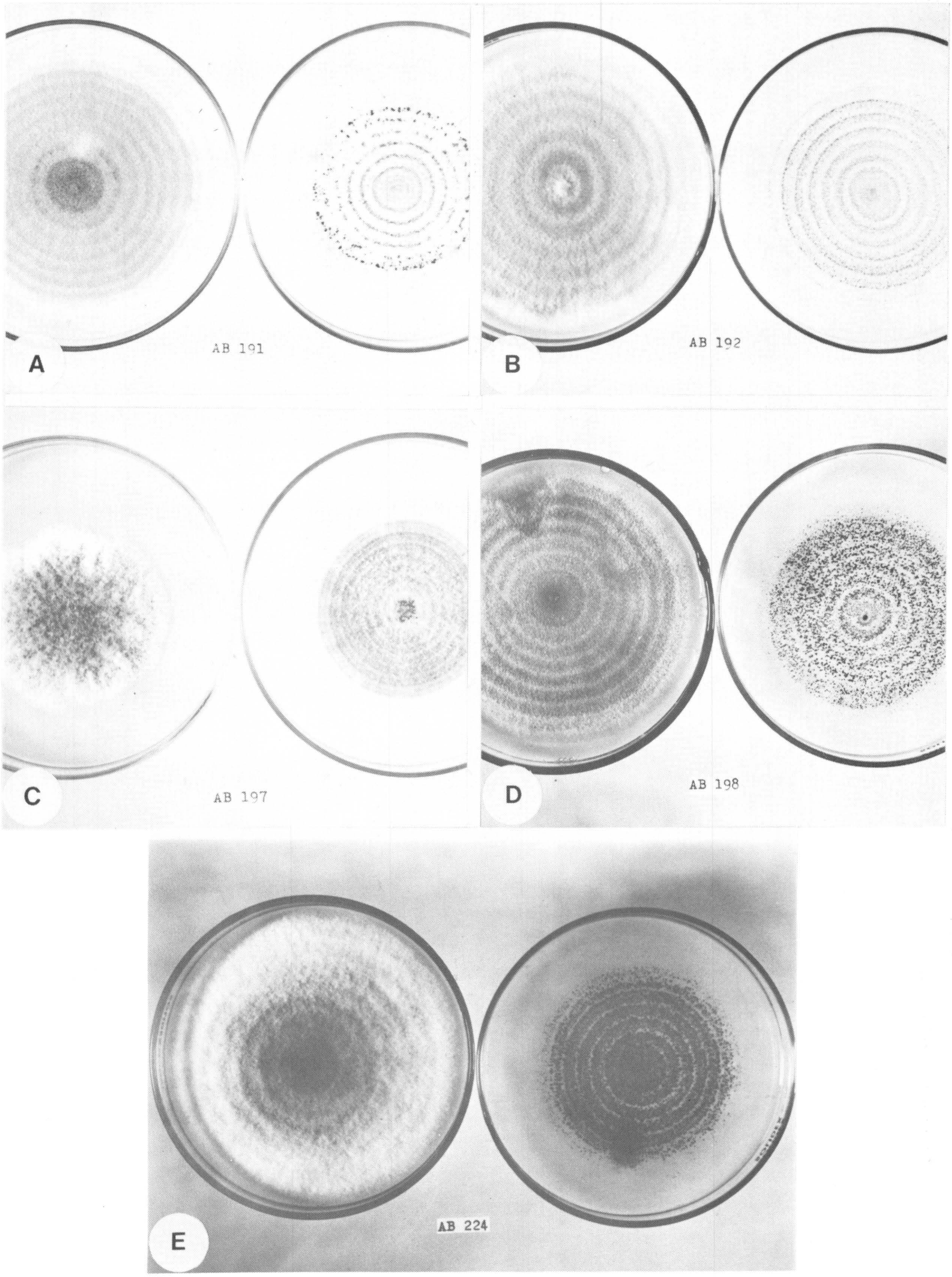

FIG. 17 C. **gloeosporioides** *cultures on CDY (left) and MSA (right) at 10 days; A, PREM 45741; B, PREM 45752; C, PREM 45775; D, PREM 45742; E, PREM 45778.*

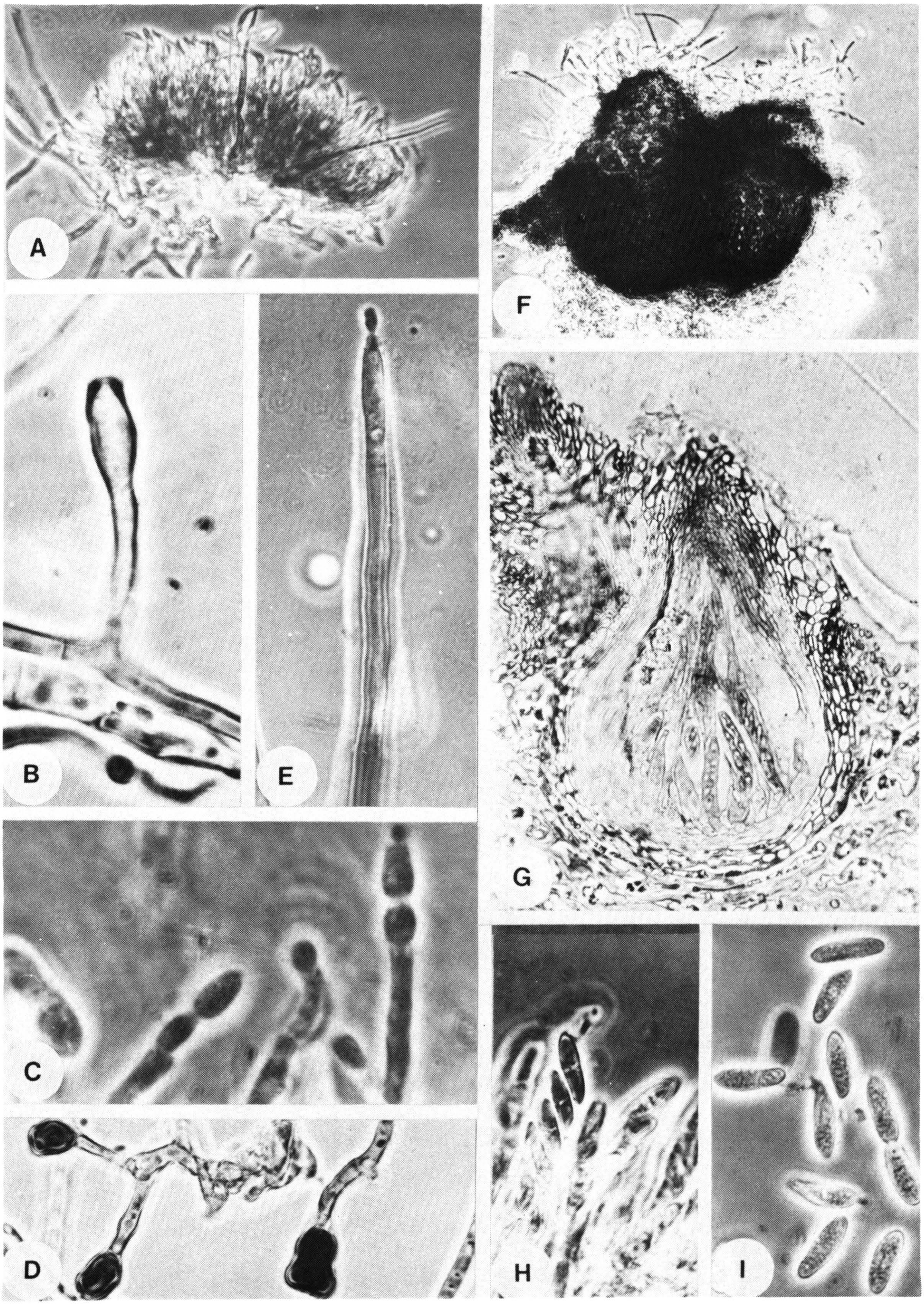

FIG. 18 **C. gloeosporioides,** *A, conidioma of PREM 45741 x 200; B, conidiogenous cell of PREM 45742 x 1 000; C, percurrently proliferating conidiogenous cells of PREM 45752 x 1 000; D, appressoria of PREM 45742 x 500; E, fertile seta of PREM 45775 x 500;* **Glomerella cingulata,** *F, perithecia of PREM 45840 x 100; G, longitudinal section of perithecium of PREM 45778 x 200; H, asci and ascospores of PREM 45840 x 400; I, ascospores of PREM 45844 x 400.*

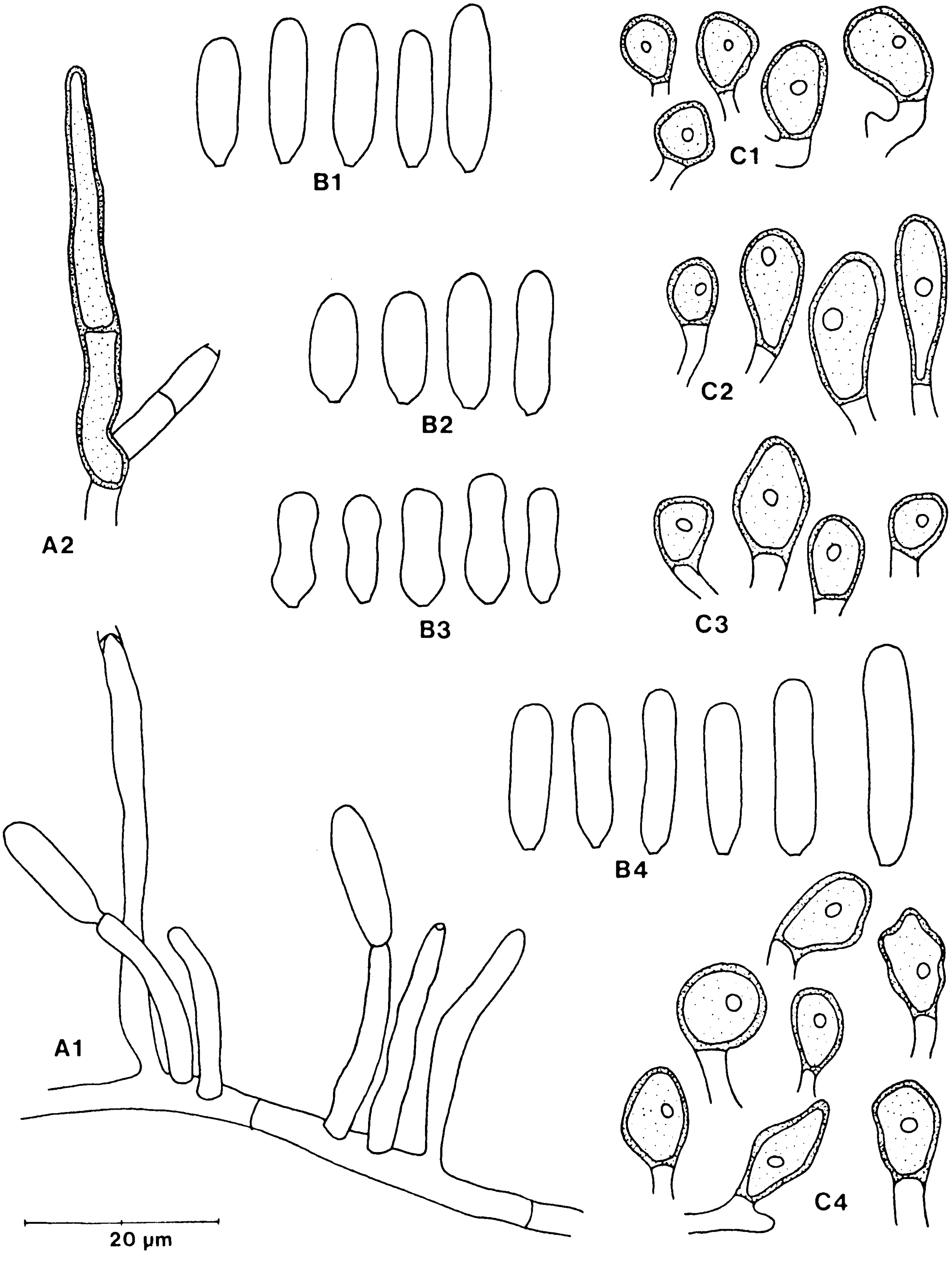

FIG. 19 C. gloeosporioides, *A1, conidiogenous cells, PREM 45854; A2, seta and conidiogenous cell, PREM 45847; B1, conidia and C1, appressoria, PREM 45847, 45848; B2, conidia and C2 appressoria, PREM 45850; B3, conidia and C3, appressoria PREM 45851; B4, conidia and C4, appressoria, PREM 45854.*

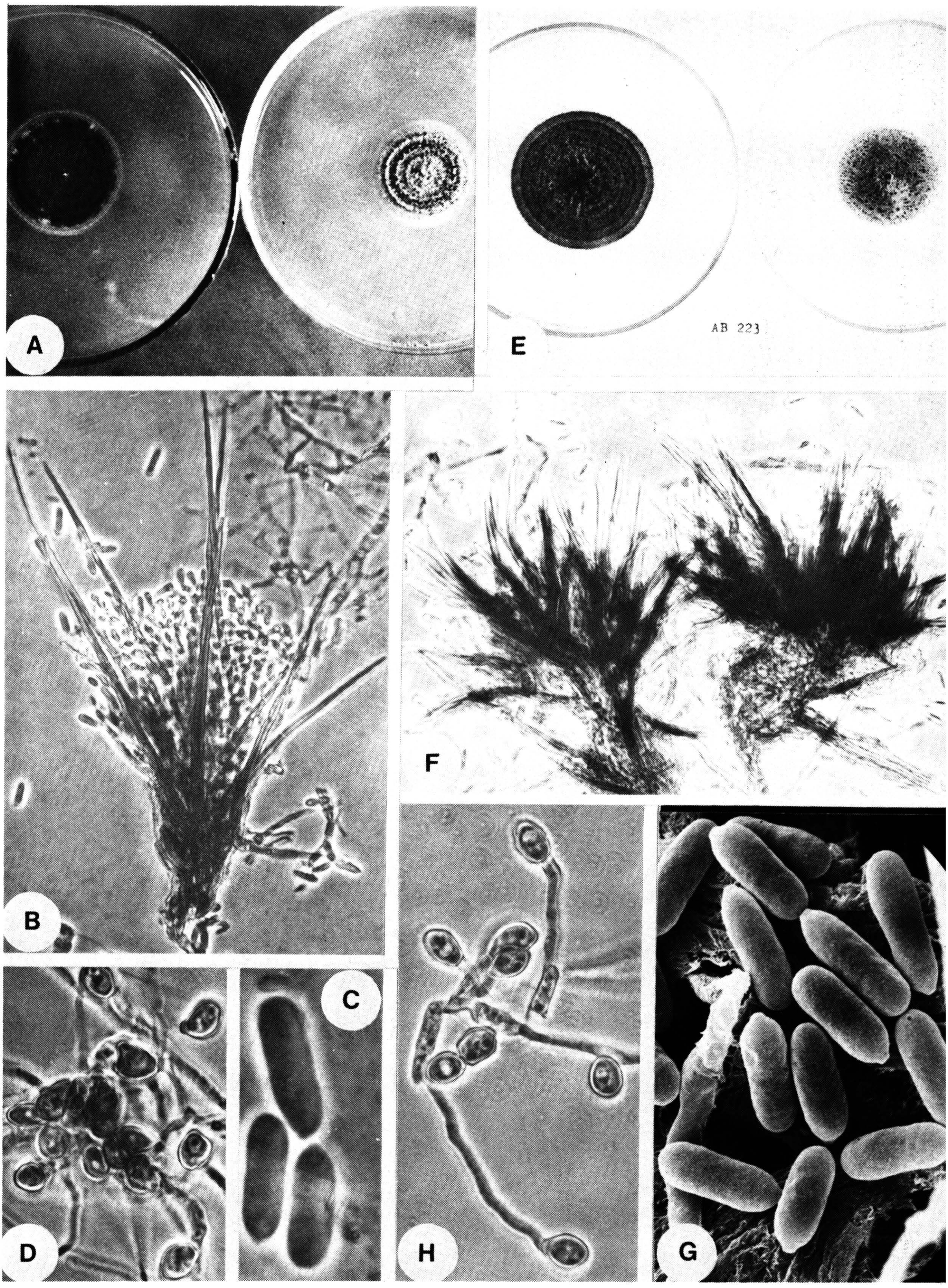

FIG. 20 **C. lindemuthianum** *PREM 45855, A, cultures on CDY (left) and MSA (right) at 10 days; B, conidioma x 200; C, conidia x 1 000; D, appressoria x 500;* **C. trifolii** *PREM 45859, E, cultures on CDY (left) and MSA (right) at 10 days; F, conidiomata x 200; G, conidia x 3 000; H, appressoria x 500.*

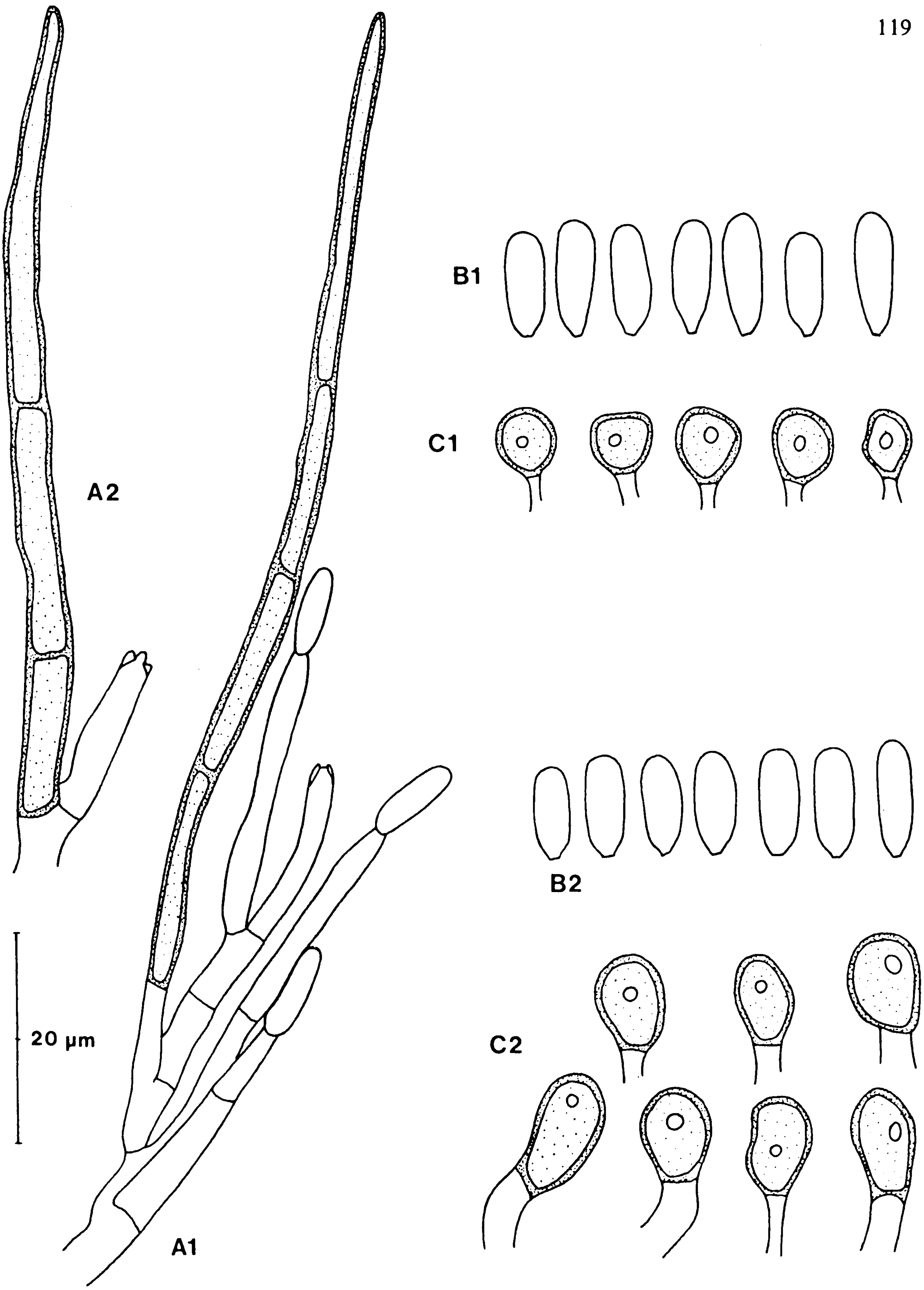

FIG. 21 *A1,* C. lindemuthianum, *PREM 45855, seta and conidiogenous cells; A2,* C. trifolii, *PREM 45857, seta and conidiogenous cells; B1,* C. lindemuthianum, *PREM 45855, conidia and C1 appressoria; B2,* C. trifolii, *PREM 45857, conidia and C2 appressoria.*

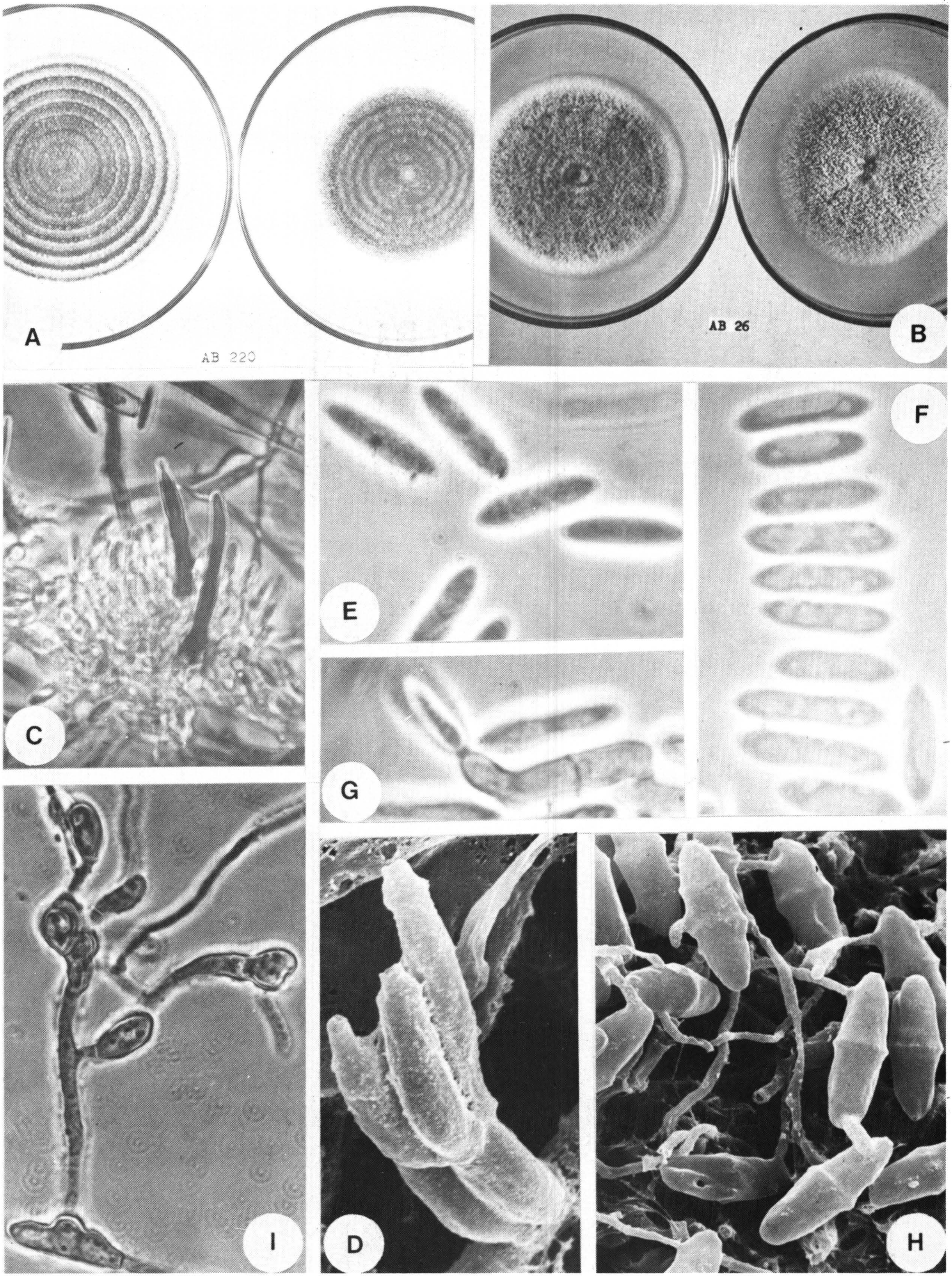

FIG. 22 A, C. **fructigenum** *PREM 45777 cultures on CDY (left) and MSA (right) at 10 days; B,* C. **fructigenum** *f. sp.* **chromogenum** *PREM 45379 cultures on CDY (left) and MSA (right) at 10 days; C, conidioma of chromogenic form PREM 45776 x 400; D, conidiogenous cells of chromogenic form PREM 45776 x 4 800; E, conidia of PREM 45776 x 1 000; F, conidia of PREM 45379 x 1 000; G, germinating conidia of chromogenic form 45379 x 1 000; H, germinating conidia of PREM 45776 x 3 000; I, appressoria of non-chromogenic form PREM 45777 x 500.*

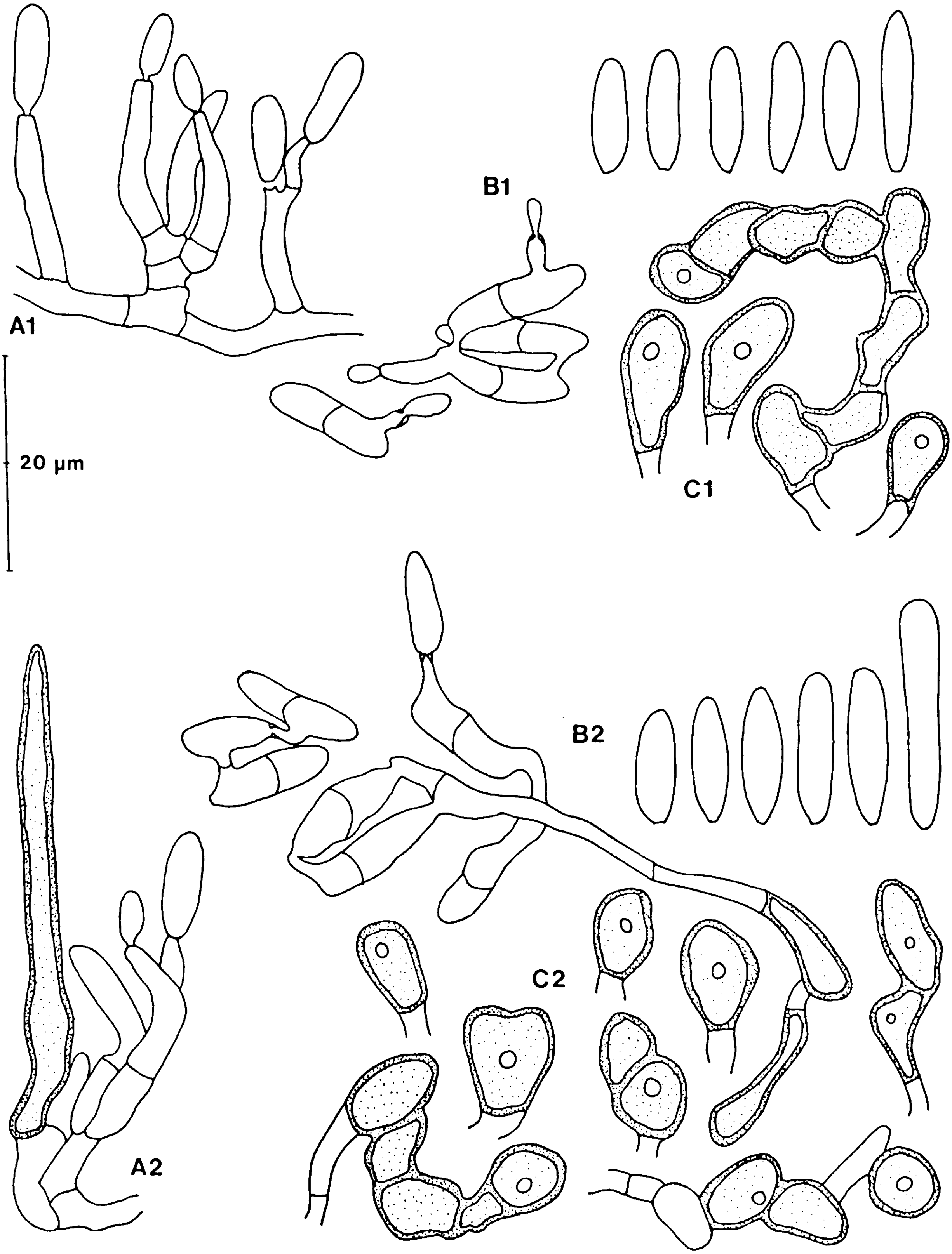

FIG. 23 C. fructigenum, *A1, conidiogenous cells, PREM 45777; A2, chromogenic form PREM 45776, seta and conidiogenous cells; B1,* C. fructigenum, *PREM 45777, conidia, germinating conidia with secondary conidia, and C1, appressoria; B2, chromogenic form PREM 45379, 45776, conidia, germinating conidia with secondary conidia, and C2, appressoria.*

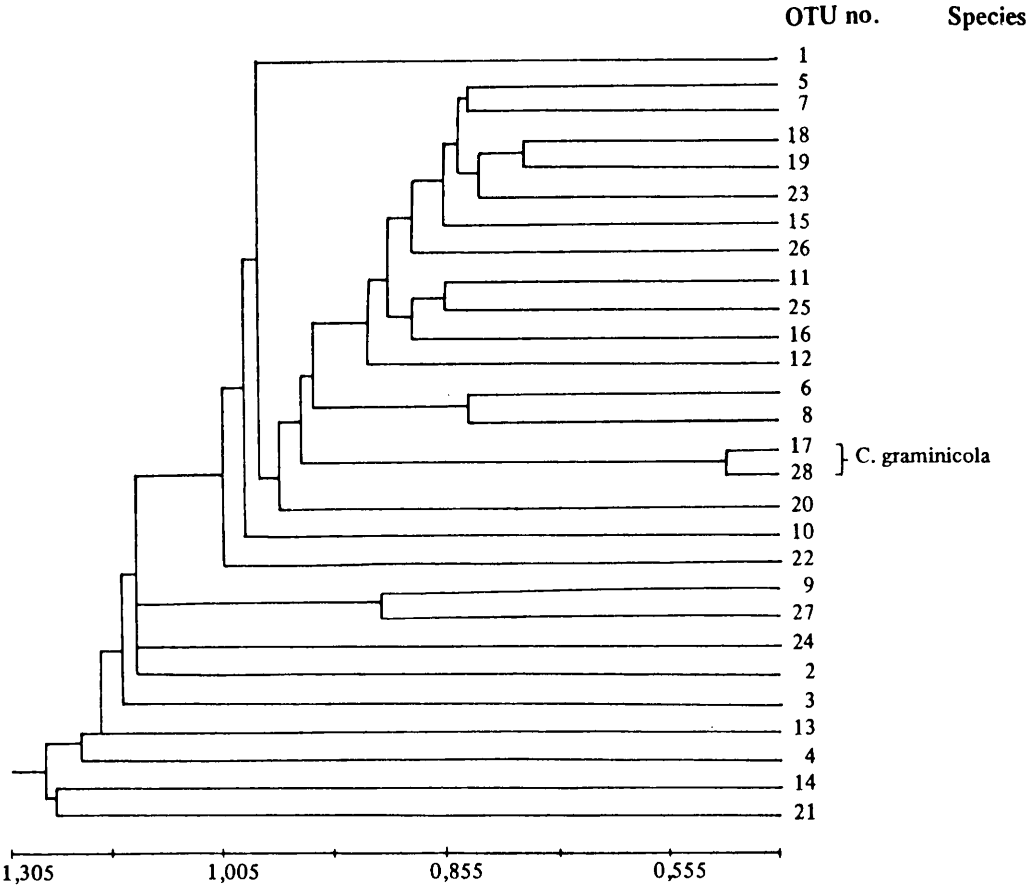

FIG. 24 Species of Colletotrichum. *Phenogram based on single linkage clustering. Correlation = 0,733.*

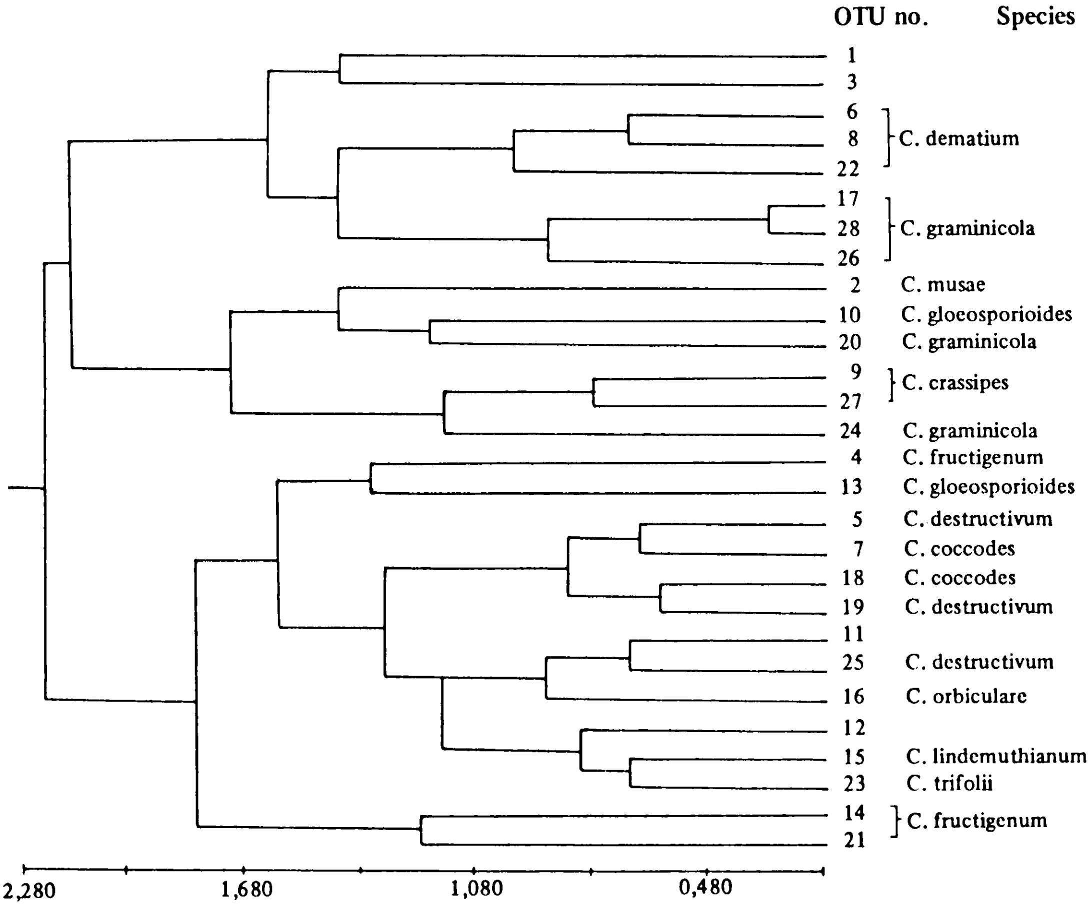

FIG. 25 Species of Colletotrichum. *Phenogram based on complete linkage clustering. Correlation = 0,558.*

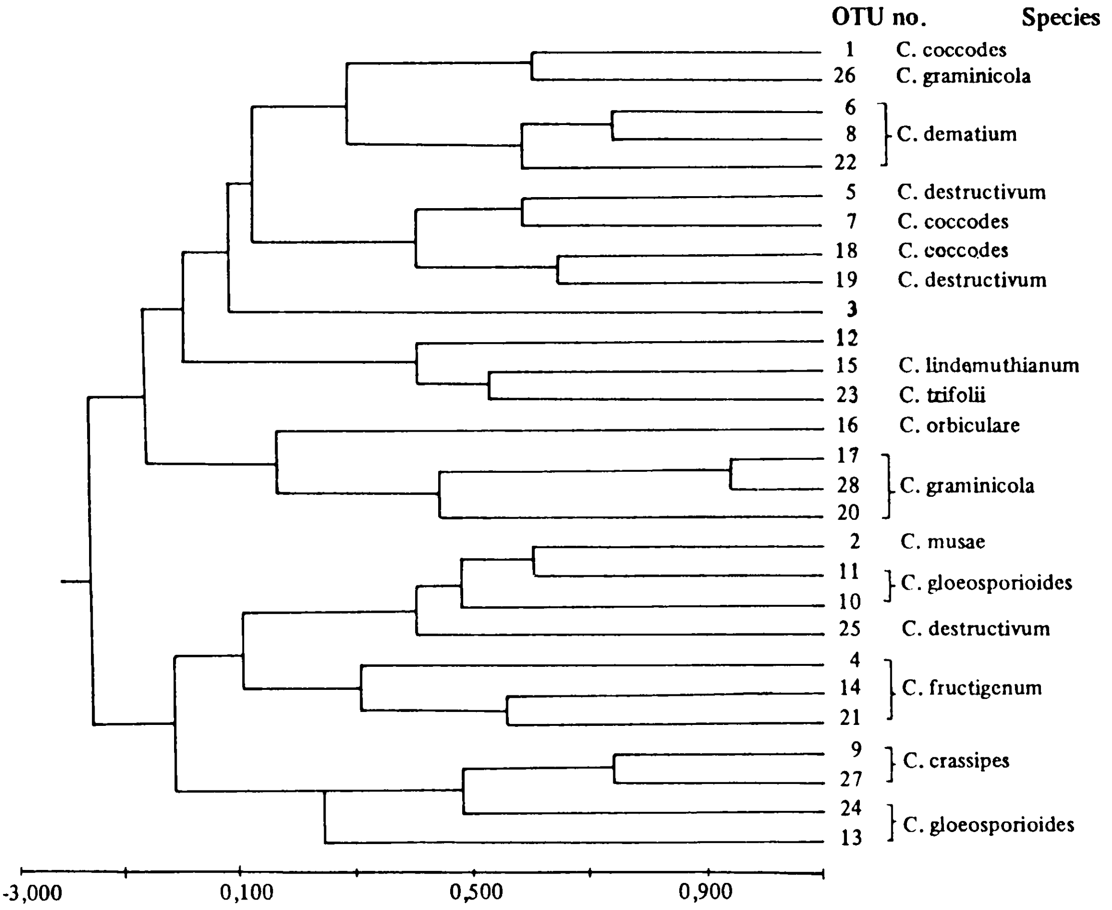

FIG. 26 Species of Colletotrichum. *Phenogram based on UPGMA, correlation between species. Correlation = 0,709*

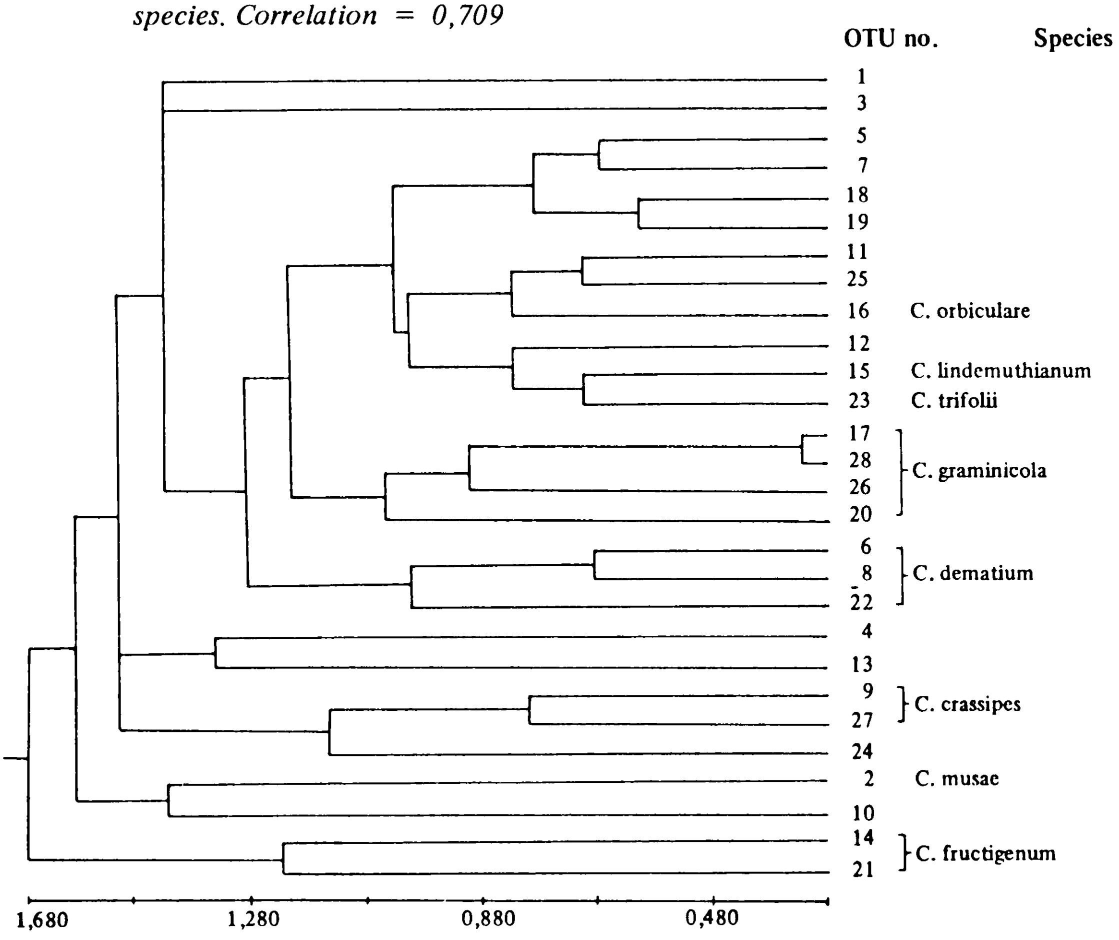

FIG. 27 Species of Colletotrichum. *Phenogram based on UPGMA taxonomic distances between species. Correlation = 0,781*

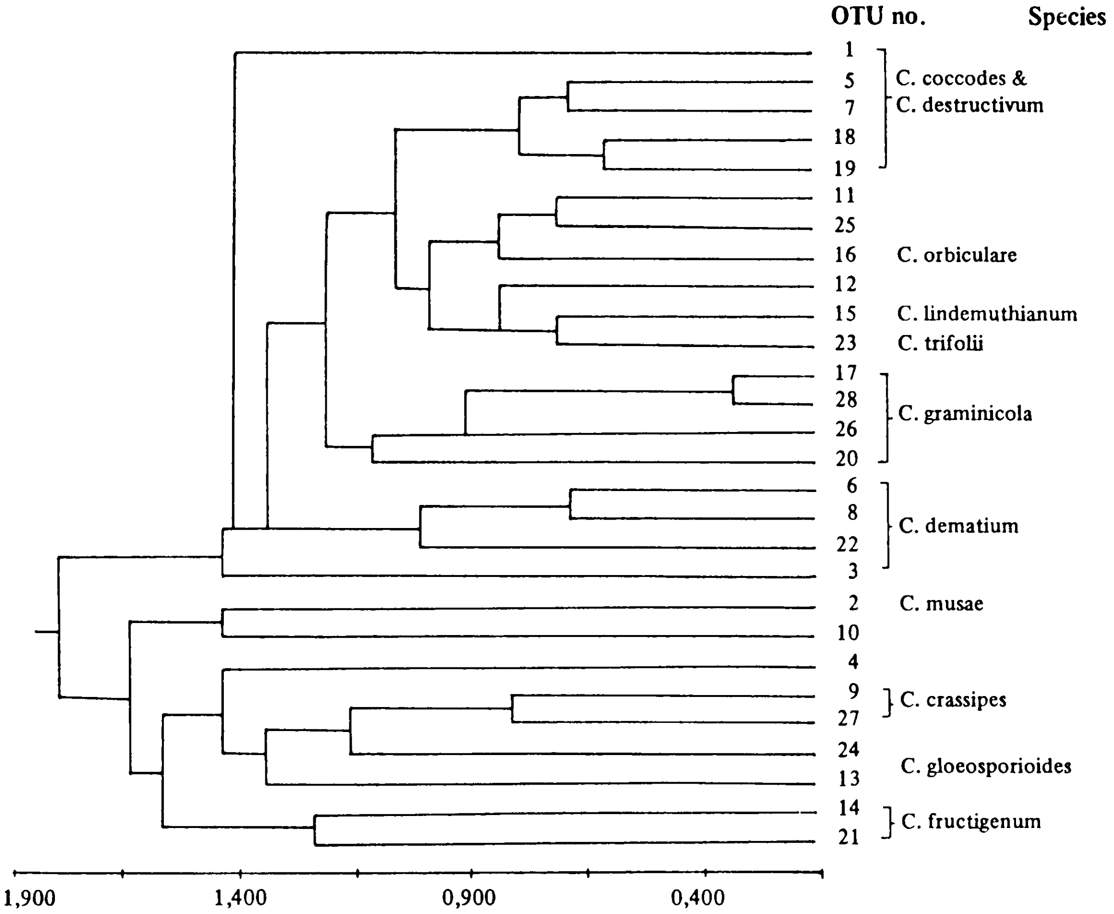

FIG. 28 Species of Colletotrichum. *Phenogram based on WPGMA. Correlation = 0,733*

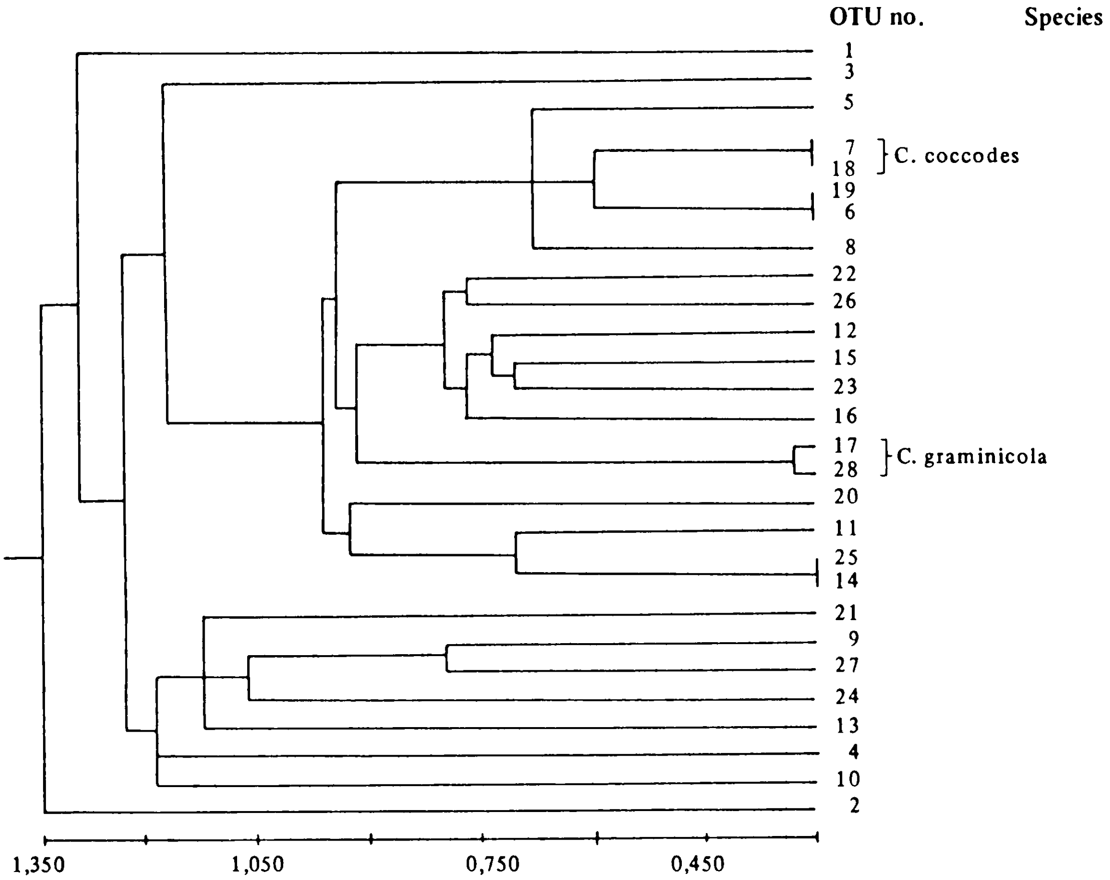

FIG. 29 Species of Colletotrichum. *Phenogram based on UPGMC. Correlation = 0,529*

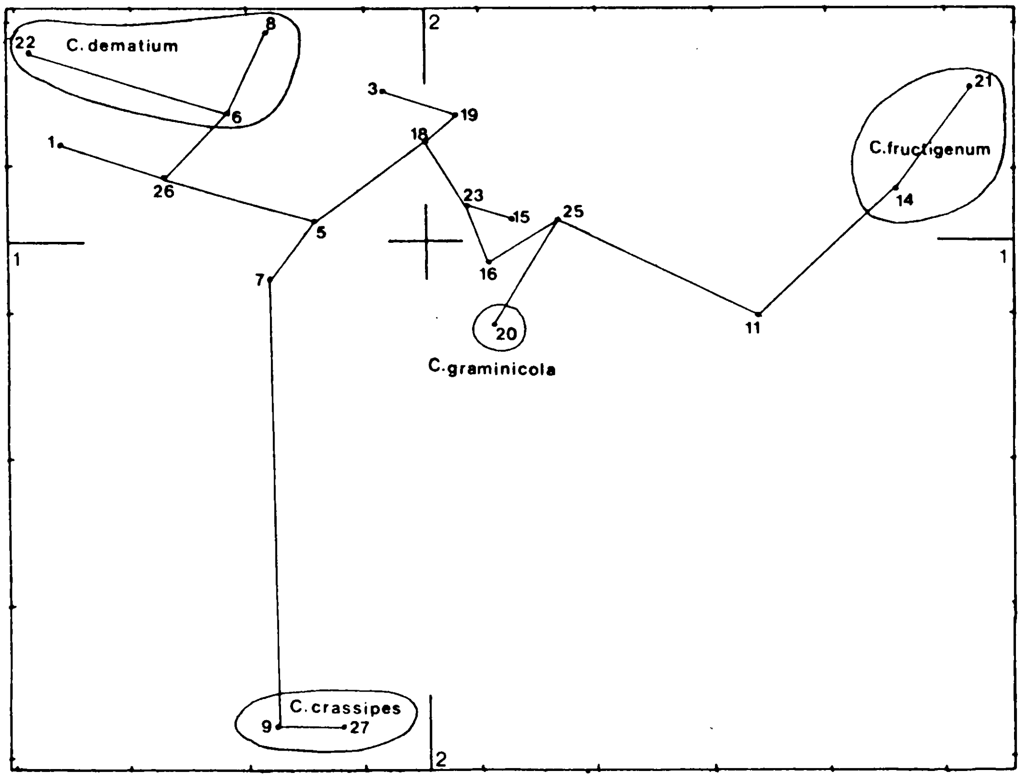

FIG. 30 Species of Colletotrichum, *20 OTU study. Ordination by Principal Component Analysis, component 1 vs. 2. MST and subsets superimposed.*

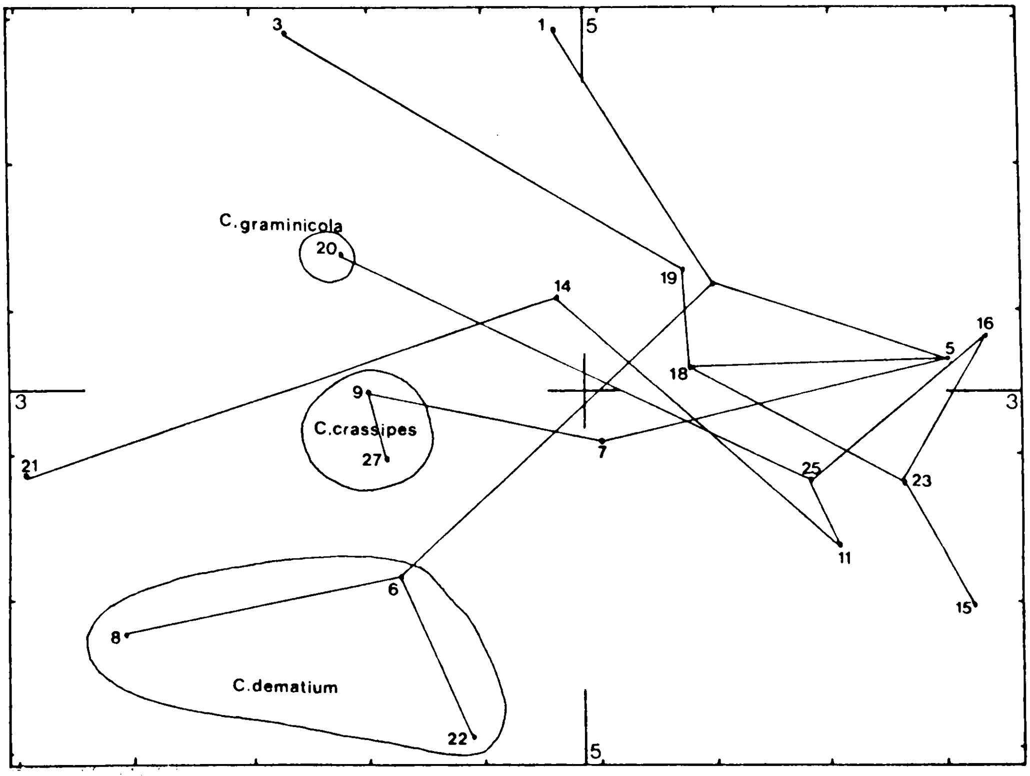

FIG. 31 Species of Colletotrichum, *20 OTU study. Ordination by Principal Component Analysis, component 3 vs. 5. MST and subsets superimposed.*

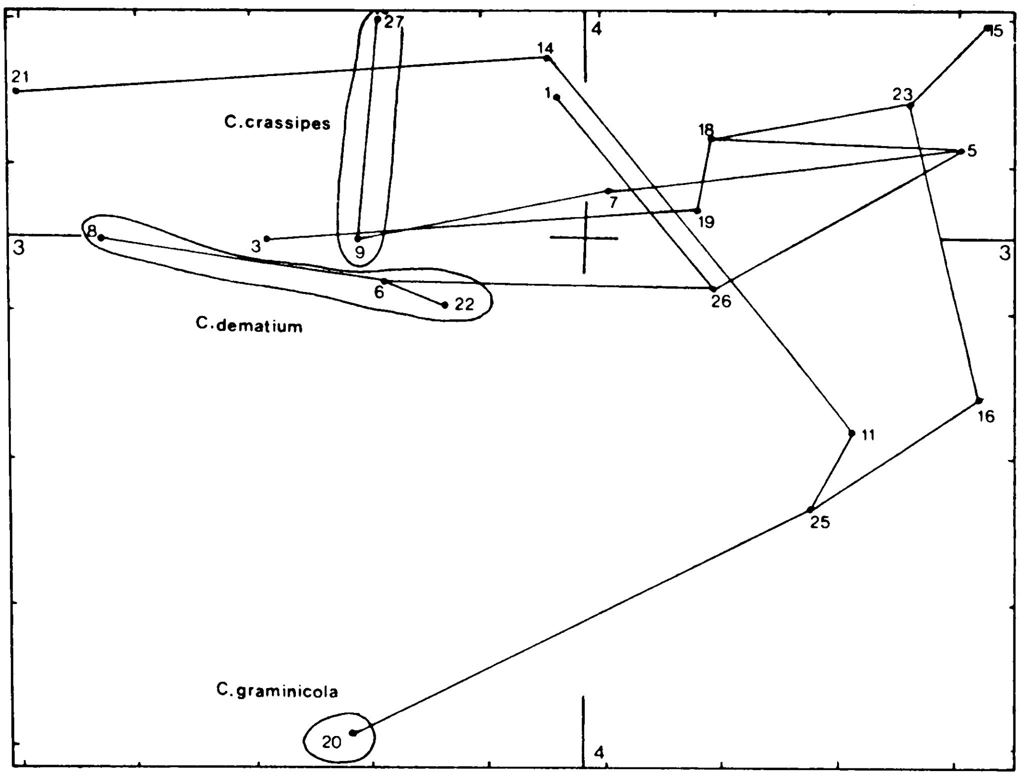

FIG. 32 Species of Colletotrichum*, 20 OTU study. Ordination by Principal Component Analysis, component 3 vs. 4. MST and subsets superimposed.*

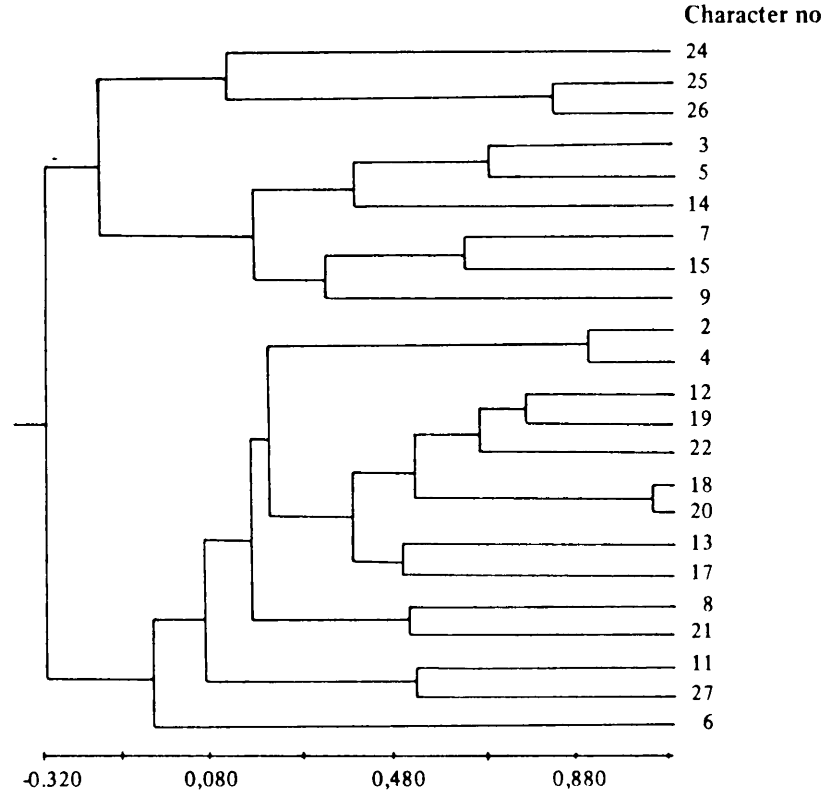

FIG. 33 Phenogram based on correlation between characters (Appendix 5) used in the identification of Colletotrichum *species.*

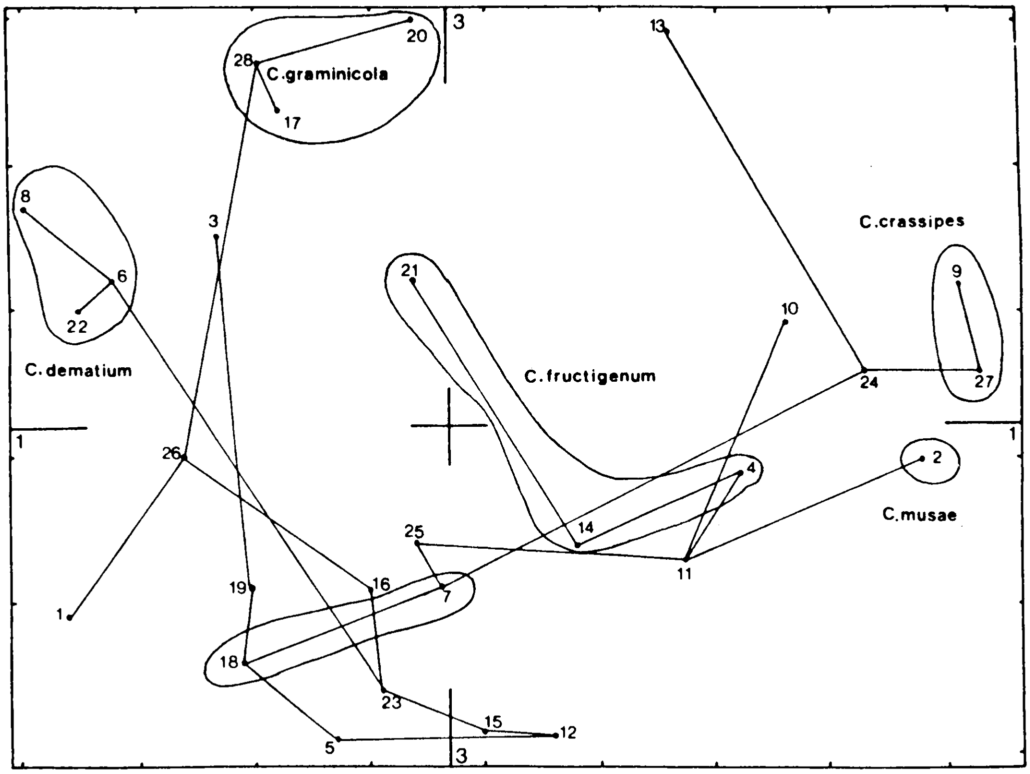

FIG. 34 Species of Colletotrichum, *28 OTU study. Ordination by Principal Component Analysis, component 1 vs. 3. MST and subsets superimposed.*

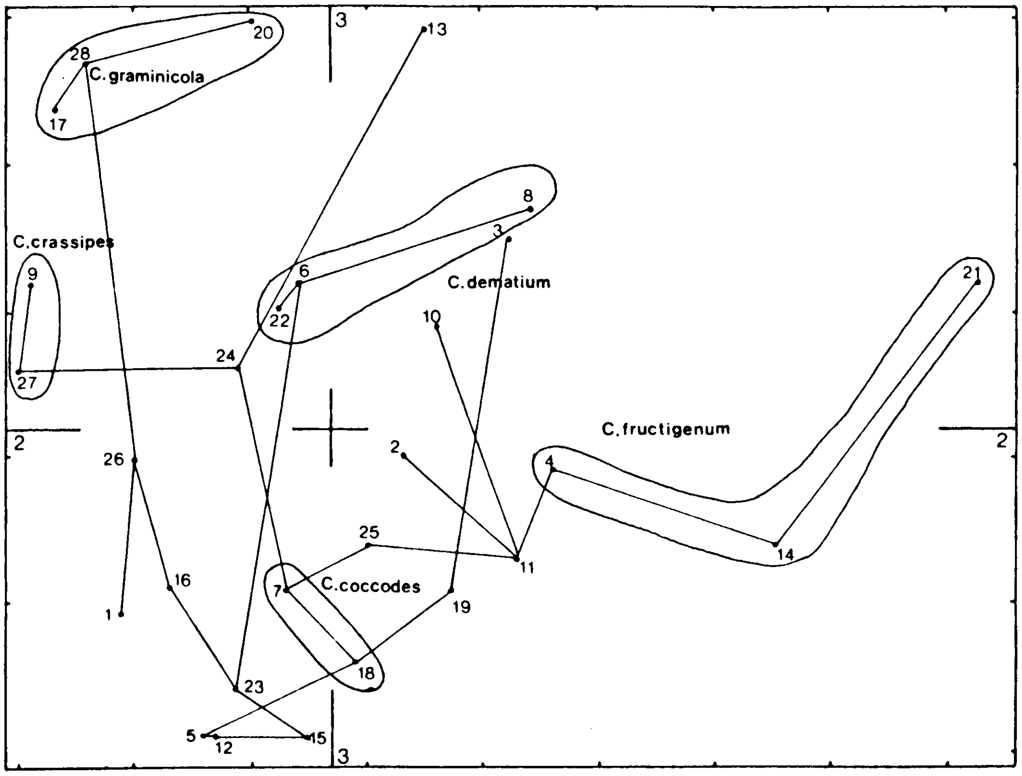

FIG. 35 Species of Colletotrichum, *28 OTU study. Ordination by Principal Component Analysis, component 2 vs. 3. MST and subsets superimposed.*

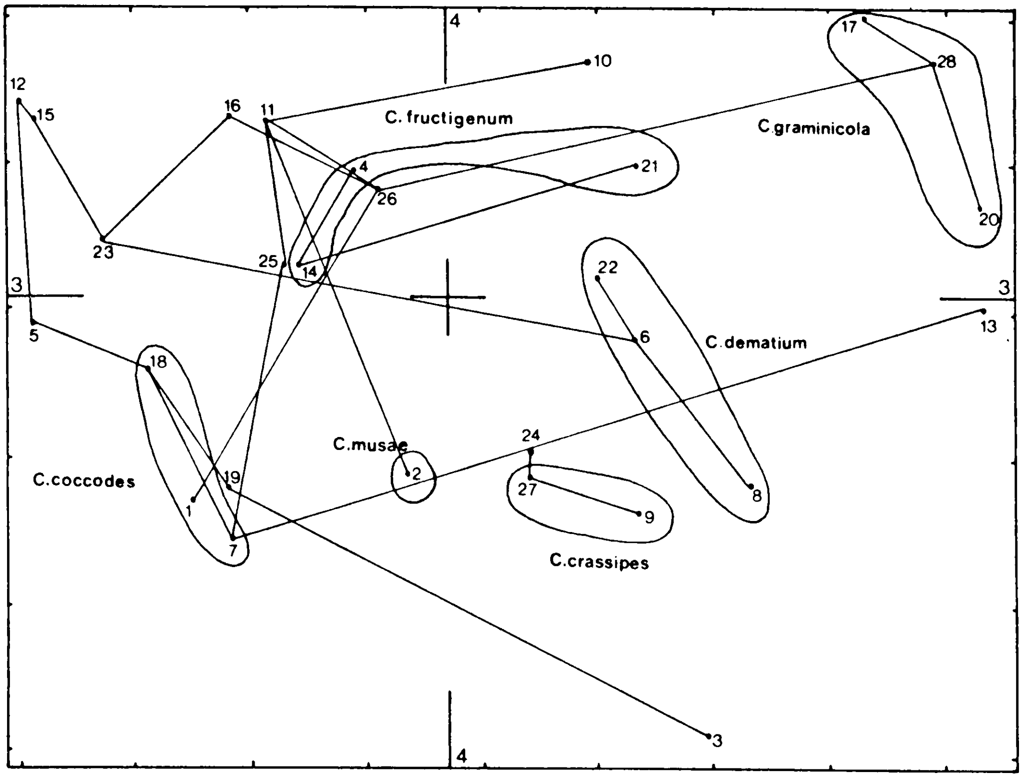

FIG. 36 Species of Colletotrichum, *28 OTU study. Ordination by Principal Component Analysis, component 3 vs. 4. MST and subsets superimposed.*

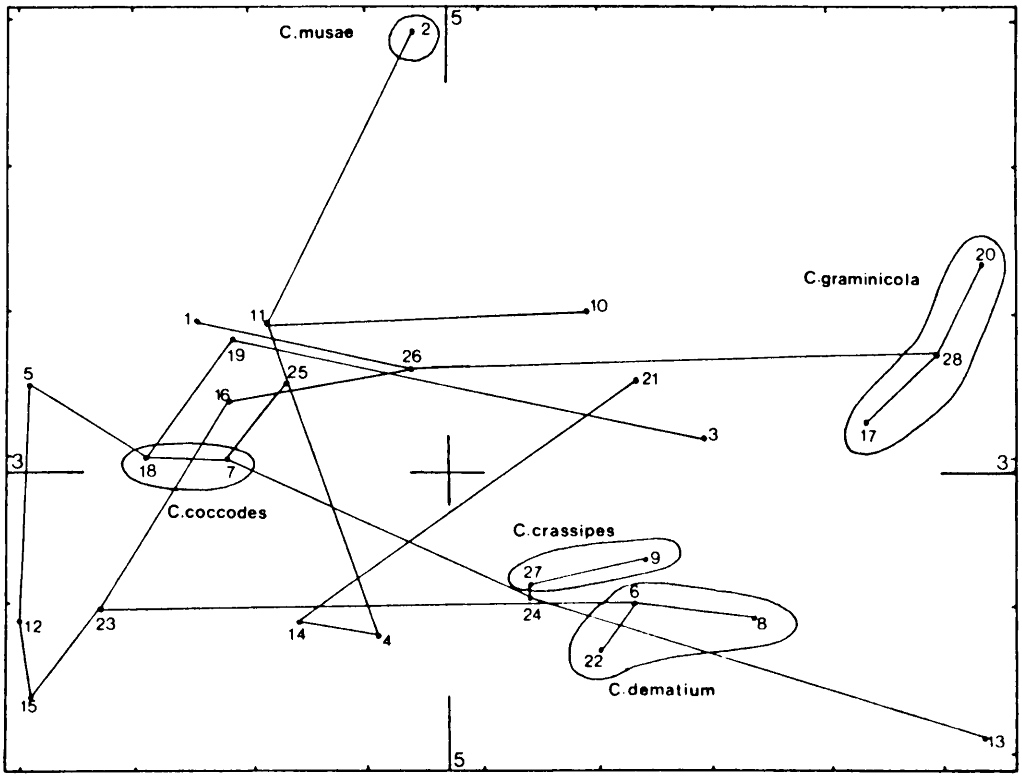

FIG. 37 Species of Colletotrichum, *28 OTU study. Ordination by Principal Component Analysis, component 3 vs. 5. MST and subsets superimposed.*

Table 1 *Colletotrichum* conidium dimensions on various substrates (given as minimum- (mean)- maximum, in µm).

Species	Substrate		
	MSA	CDY	HOST
C. dematium	18 – (23,4) – 32 x 2,5 – (2,9) – 4	16 – (23,1) – 34 x 2 – (2,9) – 4	16 – (25,4) – 35 x 2 – (2,9) – 4
C. graminicola	16 – (27,3) – 36 x 3 – (3,9) – 5	17 – (24,6) – 31,5 x 3 – (4,1) – 5	15 – (27,3) – 43 x 3 – (3,9) – 5,5
C. coccodes	16 – (19,2) – 22 x 2,5 – (3,6) – 4,5	14 – (18,6) – 24 x 2,5 – (3,6) – 4,5	15 – (17,8) – 22 x 3 – (3,6) – 5
C. destructivum	12 – (15,7) – 22,5 x 2,5 – (3,1) – 4,5	12,5 – (16,5) – 26,5 x 2,5 – (3,1) – 4,5	11 – (18,1) – 22,5 x 2,5 – (3,0) – 4
C. crassipes	14 – (20,8) – 28,5 x 5,5 – (6,8) – 7,5	17 – (25,0) – 33 x 5 – (6,3) – 7	15 – (21,0) – 30 x 5,5 – (6,4) – 7,5
C. gloeosporioides	10 – (15,9) – 23 x 3 – (4,4) – 5	9 – (14,8) – 24 x 2,5 – (4,2) – 7	9,5 – (14,8) – 20 x 3 – (5,0) – 6,5
C. musae	9 – (12,2) – 17 x 3 – (4,3) – 5	9 – (13,7) – 20 x 4 – (4,6) – 7	7 – (13,6) – 22 x 3 – (4,5) – 6
C. orbiculare	15 – (16,9) – 19 x 4 – (4,2) – 5	15 – (20,2) – 22 x 3,5 – (4,2) – 5	17 – (19,5) – 23 x 4 – (4,4) – 5,5
C. lindemuthianum	10 – (11,8) – 13 x 3 – (3,8) – 4	10 – (12,7) – 19 x 3 – (4,0) – 5	9 – (10,4) – 18 x 4 – (4,5) – 5
C. trifolii	9,5 – (10,9) – 12 x 4 – (4,1) – 4,5	10 – (12,1) – 14 x 3,5 – (4,0) – 4,5	11 – (14,6) – 18 x 4 – (5,2) – 6
C. fructigenum	10 – (12,9) – 15 x 3 – (3,2) – 3,5	9 – (11,4) – 13 x 3 – (3,5) – 4	10,5 – (12,5) – 14 x 3 – (3,3) – 4
C. fructigenum f. sp. chromogenum	8 – (12,8) – 15,5 x 3 – (3,6) – 4	9,0 – (12,7) – 15 x 3 – (3,3) – 4,5	13 – (14,5) – 17 x 3,5 – (3,9) – 4,5

Table 2 *Colletotrichum* seta dimensions and number of septa on various substrates (given as minimum- (mean). maximum, dimensions in µm).

Species	Substrate		
	MSA	CDY	HOST
C. dematium	72 – (165,4) – 640 x 3 – (5,3) – 8 1 – (3,9) – 18 septa	63 – (171,8) – 400 x 2,5 – (5,8) – 10,5 1 – (3,8) – 9 septa	45 – (109,0) – 280 x 3 – (5,8) – 13 2 – (3,1) – 5 septa
C. graminicola	50 – (116,5) – 305 x 3 – (5,6) – 7,5 2 – (3,9) – 8 septa	55 – (115,1) – 280 x 4 – (5,8) – 8,5 1 – (3,2) – 6 septa	45 – (128,7) – 305 x 3,5 – (6,5) – 11 1 – (3,7) – 7 septa
C. coccodes	52 – (131,1) – 255 x 3 – (4,8) – 8 1 – (3,6) – 11 septa	52 – (106,9) – 222 x 4 – (5,1) – 7 1 – (3,9) – 8 septa	50 – (85,1) – 265 x 4 – (5,5) – 10,5 1 – (2,3) – 5 septa
C. destructivum	45 – (103,9) – 192 x 3,5 – (5,2) – 11 2 – (3,2) – 7 septa	42 – (87,1) – 205 x 4 – (5,3) – 7 1 – (2,7) – 6 septa	45 – (98,2) – 160 x 3 – (6,6) – 15 1 – (2,6) – 5 septa
C. crassipes	85 – (121,6) – 167 x 5 – (6,6) – 8 1 – (2,7) – 4 septa	48 – (90,1) – 161,5 x 6 – (7,8) – 11 1 – (2,0) – 4 septa	80 – (110) – 155 x 4,5 – (6,0) – 10 1 – (3) – 4 septa
C. gloeosporiodes	35 – (78,7) – 159 x 3 – (4,6) – 7 1 – (2,9) – 6 septa	27 – (79,4) – 143 x 3,5 – (5,0) – 9 1 – (2,2) – 5 septa	30 – (71,4) – 135 x 2 – (5,2) – 11 1 – (2,1) – 6 septa
C. musae	No setae	No setae	No setae
C. orbiculare	80 – (116,9) – 148 x 4 – (5,0) – 6,5 1 – (2,2) – 4 septa	77 – (113,4) – 168 x 4,5 – (5,6) – 6,5 1 – (2,1) – 4 septa	65 – (115,0) – 195 x 4 – (5,7) – 7 1 – (2) – 4 septa
C. lindemuthianum	78 – (141,2) – 276 x 3,5 – (5,0) – 7 2 – (4,3) – 9 septa	74 – (122,4) – 234 x 3,5 – (4,9) – 7 2 – (3,2) – 7 septa	45 – (81,8) – 155 x 3 – (4,4) – 7 1 – (2,8) – 6 septa
C. trifolii	53,5 – (75,2) – 98,5 x 4 – (4,9) – 7 1 – (1,7) – 3 septa	54 – (67,9) – 89 x 4,5 – (5,4) – 8,5 1 – (1,4) – 2 septa	50 – (69,2) – 95 x 4 – (5,6) – 8 1 – (2,1) – 3 septa
C. fructigenum	42 – (53,0) – 73 x 3 – (3,9) – 5 0 – (0,4) – 2 septa	No setae	No setae
C. fructigenum f. sp. chromogenum	32 – (43,9) – 71 x 3,5 – (3,9) – 4,5 0 – (0,1) – 1 septa	23 – (35,9) – 43 x 3,5 – (4,1) – 4,5 0 – (0,1) – 1 septa	No setae

Table 3 *Colletotrichum* appressorium dimensions (given as minimum- (mean)-maximum, in µm).

Species	length x width on MSA
C. dematium	7,5 – (11,7) – 18 x 4 – (7,1) – 12,5
C. graminicola	7,0 – (10,3) – 25 x 6 – (7,5) – 14,5
C. coccodes	8,5 – (13,9) – 19,5 x 5 – (6,9) – 11,5
C. destructivum	6,0 – (9,7) – 15,0 x 4,5 – (6,1) – 10,0
C. crassipes	10 – (14,7) – 24 x 6 – (7,8) – 13
C. gloeosporioides	6 – (10,2) – 20 x 4,5 – (6,6) – 9
C. musae	8 – (10,9) – 15,5 x 6 – (7,4) – 10,5
C. orbiculare	6,5 – (9,3) – 16 x 5,5 – (6,8) – 10
C. lindemuthianum	5,5 – (6,2) – 7 x 5 – (5,2) – 6
C. trifolii	7 – (9,5) – 17 x 5,5 – (6,6) – 9,5
C. fructigenum	7,5 – (10,6) – 15 x 5 – (6,2) – 8
C. fructigenum f. sp. chromogenum	7,5 – (9,6) – 15 x 5 – (6,1) – 7,5

Table 4 Data recorded for the 27 characters listed in Appendix 5 for 28 *Colletotrichum* OTU's used in the statistical analyses.

OTU's	Characters and character states																									
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
1	6.1	11	0	11	0	9	0	0	1	1	1	1	1	0	0	0	2	165.2	5.3	5.2	3	19.6	3.1	1	18.2	11.9	2
2	14.0	3	4	3	4	9	1	0	1	3	1	0	0	0	1	0	0	–	–	–	8	12.1	4.4	5	10.9	11.5	1
3	7.1	11	4	8	4	1	1	1	2	1	1	0	0	0	0	0	2	152.0	4.9	3.5	13	20.1	3.6	3	12.4	9.5	2
4	6.5	8	7	10	7	7	1	0	0	3	1	0	0	1	1	0	0	–	–	–	7	12.7	3.6	1	10.4	6.3	0
5	9.2	8	0	8	2	9	1	0	1	3	1	1	1	0	0	0	2	132.7	5.2	3.8	2	15.0	3.2	3	10.0	5.9	2
6	4.5	8	4	8	2	9	0	3	1	3	1	1	1	0	0	0	2	148.9	5.0	2.5	12	21.5	2.7	2	12.5	7.1	1
7	6.5	8	5	8	5	9	1	0	1	3	1	1	1	0	0	0	2	155.3	5.3	4.5	3	19.4	3.1	5	11.0	6.8	2
8	3.1	8	8	8	2	8	0	3	2	1	1	1	1	0	0	0	2	185.9	6.0	3.4	12	20.7	2.8	2	11.1	6.3	1
9	8.0	4	4	8	4	8	1	0	1	4	1	1	1	0	0	1	1	121.7	6.7	3.0	1	23.7	7.1	5	16.5	9.0	0
10	11.6	1	9	4	4	8	1	0	1	4	0	–	–	–	0	0	1	75.7	4.2	3.0	1	13.6	4.2	1	8.4	6.4	0
11	7.6	4	4	3	4	9	1	0	1	3	1	0	0	0	1	0	1	88.0	4.5	2.9	2	13.2	4.0	1	8.3	6.5	0
12	5.7	9	1	9	2	9	3	0	0	4	1	0	0	0	0	0	0	–	–	–	2	12.8	4.2	1	12.6	6.6	1
13	7.7	9	4	8	4	5	1	3	1	3	0	–	–	–	0	1	0	–	–	–	9	12.7	4.0	2	10.4	6.9	0
14	6.1	8	4	10	4	4	6	0	2	3	1	0	0	0	1	0	1	44.0	3.9	0.1	7	12.9	3.6	2	9.6	6.1	0
15	4.6	9	2	8	2	6	3	0	0	4	1	0	1	0	0	0	1	125.7	5.2	3.7	2	11.8	3.8	1	6.2	5.2	1
16	8.1	5	0	7	0	9	1	0	1	3	1	0	0	0	0	0	2	117.0	5.0	2.2	2	16.9	4.2	1	9.3	6.8	0
17	7.6	9	0	9	2	9	0	0	0	3	0	–	–	–	0	0	2	114.5	5.9	3.6	13	27.7	4.1	1	8.6	6.6	0
18	6.3	9	4	9	2	9	3	0	2	3	1	0	1	0	0	0	2	103.8	5.2	2.8	3	19.2	3.1	2	9.4	6.2	2
19	8.4	8	4	8	4	9	1	0	2	1	1	0	1	0	0	0	2	110.0	4.7	4.0	5	14.5	3.0	2	9.3	6.5	2
20	7.9	3	4	6	4	9	1	0	1	3	0	0	0	0	0	0	2	91.8	5.4	2.2	13	26.4	3.8	2	14.0	9.3	0
21	5.2	8	8	5	2	8	6	1	3	1	0	0	1	1	1	0	1	53.0	3.9	0.4	7	12.9	3.2	1	10.6	6.2	0
22	4.1	9	2	8	2	9	0	3	1	3	1	1	1	0	0	0	2	320.8	6.4	8.1	12	22.3	2.8	2	10.8	5.5	1
23	5.1	8	2	9	2	9	1	1	1	4	1	0	1	0	0	0	2	75.2	4.9	1.7	2	10.9	4.1	2	9.5	6.6	1
24	8.1	8	5	8	5	9	1	0	1	3	1	0	0	0	0	1	0	–	–	–	1	20.7	4.1	5	11.3	6.4	0
25	6.8	4	4	4	4	9	1	0	1	3	1	0	0	0	0	0	2	118.3	4.9	3.1	5	16.2	3.1	2	9.6	5.9	1
26	8.9	9	0	9	0	9	1	0	1	3	1	1	1	0	0	0	2	183.4	5.5	5.1	12	21.3	3.6	1	13.1	7.3	1
27	7.8	8	4	8	4	8	1	0	0	4	1	1	1	1	0	1	1	121.5	6.5	2.4	1	18.0	6.6	5	12.9	9.4	0
28	8.8	9	0	9	2	9	0	0	1	3	0	–	–	–	0	0	2	111.6	5.9	3.3	13	30.0	4.2	1	8.2	6.5	0

Table 5 Factor matrix : 20 OTU Principal Component Analysis

Character	Factor Matrix				
	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5
1	0,039	– 0,458	0,347	– 0,253	0,545
2	– 0,337	0,466	– 0,127	0,724	0,214
3	0,422	0,047	– 0,700	– 0,018	– 0,302
4	– 0,502	0,101	– 0,001	0,603	0,345
5	0,309	– 0,370	– 0,208	– 0,172	– 0,045
6	– 0,261	– 0,093	0,243	– 0,264	– 0,355
7	0,811	0,052	– 0,181	0,339	0,082
8	– 0,313	0,455	– 0,493	– 0,019	– 0,530
9	0,429	0,524	– 0,480	0,073	0,216
10	– 0,041	– 0,604	0,466	– 0,018	– 0,389
11	– 0,442	– 0,028	0,482	0,349	– 0,081
12	– 0,752	– 0,210	– 0,268	0,189	– 0,169
13	– 0,480	0,001	– 0,134	0,601	– 0,301
14	0,343	– 0,343	– 0,465	0,334	– 0,129
15	0,806	0,064	– 0,172	0,097	– 0,059
16	– 0,147	– 0,906	– 0,254	0,191	– 0,056
17	– 0,570	0,536	0,141	– 0,331	0,205
18	– 0,812	0,238	– 0,123	– 0,080	– 0,288
19	– 0,758	– 0,492	– 0,176	– 0,053	– 0,254
20	– 0,800	0,196	0,104	– 0,126	– 0,113
21	– 0,184	0,512	– 0,555	– 0,383	0,015
22	– 0,620	– 0,152	– 0,473	– 0,484	0,139
23	0,022	– 0,943	– 0,057	0,100	0,039
24	– 0,271	– 0,654	– 0,247	0,158	– 0,009
25	– 0,494	– 0,321	– 0,498	– 0,089	0,481
26	– 0,332	– 0,369	– 0,341	– 0,061	0,678
27	– 0,495	0,495	0,201	0,272	0,291

Table 6 Factor matrix : 28 OTU Principal Component Analysis

Character	Factor Matrix				
	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5
1	0,508	– 0,181	0,094	0,003	0,699
3	0,330	0,658	0,242	– 0,203	– 0,067
4	– 0,353	– 0,303	– 0,100	– 0,131	– 0,544
5	0,627	0,298	0,164	– 0,253	– 0,085
6	– 0,076	– 0,419	– 0,185	0,304	0,326
7	0,201	0,694	– 0,198	0,153	– 0,076
8	– 0,386	0,214	0,415	– 0,171	– 0,479
9	– 0,333	0,652	0,116	– 0,332	0,206
10	0,541	– 0,452	– 0,169	0,429	– 0,243
11	– 0,031	– 0,108	– 0,688	– 0,484	– 0,185
15	0,359	0,682	– 0,085	0,144	0,224
16	0,616	0,282	0,307	– 0,311	– 0,398
17	– 0,780	– 0,245	0,006	– 0,078	0,207
21	– 0,516	0,110	0,684	0,018	0,066
22	– 0,350	– 0,528	0,601	– 0,058	0,099
23	0,735	– 0,432	0,160	– 0,404	– 0,059
24	0,500	– 0,224	0,043	– 0,705	0,023
26	0,181	– 0,263	0,171	– 0,514	0,463
27	– 0,539	– 0,069	– 0,499	– 0,538	0,145

APPENDIX 1

CULTURE MEDIA

1. CZAPEK-DOX (CD) (C.M.I., 1968)

Sodium nitrate ($NaNO_3$)	2,0 g
Potassium chloride (KCl)	0,5 g
Potassium phosphate (K_2HPO_4)	1,0 g
Magnesium sulphate ($MgSO_4$)	0,5 g
Ferrous sulphate ($FeSO_4$)	0,01 g
Dextrose (in place of sucrose)	20 g
Oxoid no. 3 agar	17 g
Distilled water	1 litre

2. CD + 0,1% YEAST EXTRACT (CDY)

As in (1), above plus Merck yeast extract 1 g

3. MALT EXTRACT AGAR (MEA)

Oxoid malt extract	15 g
Oxoid no. 3 agar	17 g
Distilled water	1 litre

4. MALT SALTS AGAR (MSA) (VAN DER WESTHUIZEN & HOLTZHAUSEN, 1980)

Ammonium nitrate (NH_4NO_3)	1,0 g
Magnesium chloride ($MgCl_2$)	1,0 g
Potassium phosphate (K_2HPO_4)	1,0 g
Oxoid malt extract	5,0 g
Oxoid no. 3 agar	17,0 g
Distilled water	1 litre

APPENDIX 1 (CONTINUED)

5. POTATO CARROT AGAR (PCA) (C.M.I., 1968)

Carrot	20 g
Potato	20 g
Oxoid no. 3 agar	17 g
Distilled water	1 litre

6. PCA + N

As in (5), above plus 100 mg/l sodium novobiocin

APPENDIX 2

TERMINOLOGY USED IN THE DESCRIPTION OF CULTURES AND THEIR GROWTH CHARACTERISTICS (+ FROM LONG & HARSCH, 1918; * FROM CAMPBELL, 1938; ** FROM AINSWORTH, 1971).

1. TEXTURE

SUBMERGED – growing beneath the surface of the agar.

CLOSELY APPRESSED+ – mycelium prostrate on the surface of the agar.

SODDEN APPRESSED+ – appressed mycelium having a watersoaked appearance.

COBWEBBY+ – long, weak, intertangled hairs which are not thick enough to be termed woolly or felty and are not short enough to be considered as downy.

COTTONY+ – erect, rather long (3 - 5 mm) mycelium spreading in all directions.

SUBFELTY to FELTY+ – thin layer of mycelium consisting of short intertwined hairs becoming matted, resembling felt.

DOWNY+ – short, fine hairs, loosely scattered over the surface of the mycelium, giving it a downy appearance.

FLOCCOSE* – thin, cottony pubescence, collected in very small tufts.

FARINACEOUS** – like meal.

WOOLLY+ – a dense mass of mycelium consisting of long, tortuous, matted hairs.

2. ZONATION

CENTRAL ZONE* – portion of colony about centre.

MARGINAL ZONE* – part of mat surrounding central zone.

MARGIN* – region of advancing growth.

SECTORING** – 'mutation' in plate cultures resulting in one or more sectors of the cultures having a changed form of growth.

CONCENTRIC ZONATION** – regular concentric variation of texture, pigmentation or sporulation frequently associated with fluctuations in light, temperature or other factors.

3. MARGIN

EVEN** – margin a smooth line.

SINUATE** – waved.

IRREGULAR – uneven.

APPENDIX 3

COLOUR NOMENCLATURE USED IN THE DESCRIPTION OF *COLLETOTRICHUM* CULTURES

Ridgway (1912) Colour Name	Rayner's (1970) Determination of the Equivalent ISCC-NBS (Kelly & Judd, 1963) Designation
Apricot Orange	strong orange (50)
Army Brown	betw. light reddish brown (42), moderate r. br. (43), l. grayish r. br. (45) & gr. r. br. (46)
Benzo Brown	gr. r. brown (46)
Blackish Mouse Gray	betw. dark gray (266) & black (267)
Brownish Drab	grayish red (19)
Buff-Pink	moderate yellowish pink (29)
Cartridge Buff	betw. pale yellow (89) & yellowish white (92)
Chaetura Black	betw. brownish gray (64) & dark gray (266)
Chaetura Drab	brownish gray (64)
Chestnut Brown	betw. mod. r. br. (43) & gr. r. brown (46)
Cinnamon-Buff	betw. mod. orange yellow (89) & yellowish white (92)
Cinnamon-Rufous	betw. gr. r. orange (39) & brownish orange (54)
Cream-Buff	betw. pale gr. yellow (89) & gr. yellow (90)
Dark Grayish Olive	olive gray (113)
Dark Mouse Gray	dark gray (266)
Dark Olive	moderate olive brown (95)
Dark Olive-Gray	olive gray (113)
Dark Quaker Drab	betw. dark gray (266) & dark purplish gray (234)
Dark Vinaceous-Gray	grayish purple (228)
Deep Brownish Vinaceous	grayish red (19)
Deep Grayish Olive	betw. gr. olive (110) & olive gray (113)
Deep Hellebore Red	grayish purplish red (262)
Deep Mouse Gray	betw. brownish gray (64) & dark gray (266)
Deep Olive-Buff	grayish olive (90)
Deep Quaker Drab	betw. purplish gray (233), dark purplish gray (234) & dark gray (266)
Drab	grayish yellowish brown (80)
Drab-Gray	yellowish gray (93)
Ecru -Drab	pinkish gray (10)

APPENDIX 3 (CONTINUED)

Ridgway (1912) Colour Name	Rayner's (1970) Determination of the Equivalent ISCC-NBS (Kelly & Judd, 1955) Designation
Flesh Ocher	moderate orange (53)
Flesh Pink	betw. light yellowish pink (28) & mod. y. pink (29)
Fuscous	brownish gray (64)
Grayish Olive	light grayish olive (109)
Hair Brown	betw. l. br. gray (63) & gr. yellowish brown (80)
Hydrangea Pink	moderate pink (5)
Hydrangea Red	grayish red (19)
Iron Gray	dark gray (266)
Light Buff	pale yellow (89)
Light Cinnamon-Drab	light gr. r. brown (45)
Light Drab	betw. l. gr. brown (60) &l. gr. yellowish br. (79)
Light Grayish Olive	betw. l. br. gray (63) & medium gray (265)
Light Grayish Vinaceous	moderate pink (5)
Light Mouse Gray	betw. l. br. gray (63) & medium gray (265)
Light Ochraceous-Salmon	betw. mod. y. pink (29), gr. y. pink (32) & brownish pink (33)
Light Olive-Gray	light olive gray (112)
Mouse Gray	betw. l. br. gray (63) & medium gray (265)
Neutral Red	dark red (16)
Ochraceous-Salmon	moderate orange (53)
Olivaceous Black (2)	betw. dark gr. olive green (128) & dark greenish gray (156)
Olive	grayish olive (110)
Olive-Brown	betw. mod. y. brown (77) & gr.y. brown (80)
Olive-Buff	betw. gr. yellow (90) & y. gray (93)
Olive-Gray	light olive gray (112)
Orange-Cinnamon	strong orange (50)
Pale Drab-Gray	betw. y. gray (93) & l. gray (264)
Pale Mouse Gray	light gray (264)
Pale Ochraceous-Salmon	pale orange yellow (73)
Pale Olive-Buff	yellowish gray (93)
Pale Olive-Gray	light gray (264)
Pale Pinkish Buff	yellowish gray (93)
Pale Pinkish Cinnamon	betw. pale y. pink (31) & br. pink (33)
Pallid Quaker Drab	light purplish gray (232)

APPENDIX 3 (CONTINUED)

Ridgway (1912) Colour Name	Rayner's (1970) Determination of the Equivalent ISCC-NBS (Kelly & Judd, 1955) Designation
Pinkish Buff	pale orange yellow (73)
Pinkish Vinaceous	moderate pink (5)
Pomegranate Purple	strong purplish red (255)
Quaker Drab	purplish gray (233)
Rhodonite Pink	betw. mod. purplish pink (250) & dark p. pink (251)
Russet	moderate brown (58)
Salmon-Buff	betw. l. y. pink (28) & mod. y. pink (29)
Salmon Color	moderate yellowish pink (29)
Seashell Pink	betw. l. y. pink (28) & pale y. pink (31)
Vinaceous-Buff	brownish pink (33)
Vinaceous-Cinnamon	mod. purplish pink (250)
Vinaceous-Fawn	light reddish brown (42)
Vinaceous-Pink	moderate y. pink (29)
Warm Buff	betw. pale orange yellow (73), l. yellow (56) & moderate yellow (87)
Wood Brown	betw. light brown (57) & l. gr. brown (60)

APPENDIX 4

COLLETOTRICHUM OTU PREM NUMBERS, HOSTS AND HOST LOCALITIES.

OTU no.	PREM no.	Host	Host locality	Date collected
1	45384	*Solanum tuberosum* tuber	Kouebokkeveld	1977 - 02 - 07
2	45380	*Musa* sp. fruit	Port St. Johns	1977 - 02 - 11
3	45738	*Beta vulgaris* leaf	Pretoria	1977 - 02 - 18
4	45379	*Olea europaea* fruit	Western C. Prov.	1941 - 06
5	45773	*Trifolium africanum* leaf	Cedara	1977 - 04 - 06
6	45751	*Allium cepa* leafbase	Weenen	1977 - 12 - 14
7	45739	*Capsicum frutescens* stem	Magaliesberg	1978 - 02 - 14
8	45740	*Tribulus terrestris* leaflet	Middelburg C.P..	1978 - 03 - 07
9	45774	*Psidium guajava* leaf	Nelspruit	1978 - 05 - 25
10	45741	*Persea americana* fruit	Nelspruit	1978 - 05 - 25
11	45752	*Persea americana* leaf	Nelspruit	1978 - 05 - 25
12	45775	*Adinia microcephala* var. *galpini* leaf	Nelspruit	1978 - 05 - 25
13	45742	*Bauhinia galpini* leaf	Nelspruit	1978 - 05 - 25
14	45776	*Grewia monticola* leaf	Nelspruit	1978 - 05 - 25
15	45855	*Phaseolus vulgaris* pod	Dendron	1978 - 07 - 11
16	45750	*Cucurbito pepo* fruit	Nylstroom	1978 - 08 - 10
17	45744	*Zea mays* leaf	Lions River, Natal	1978 - 07 - 18
18	45745	plant débris	Middelburg, C.P.	1978 - 08 - 16
19	45746	*Trifolium* sp.	Stellenbosch	1978 - 03 - 23
20	45747	*Sorghum caffrorum* stem	W. Tvl.	1978 - 04
21	45777	*Fragaria* sp. stolon	Cullinan	1979 - 03 - 07
22	45832	*Lycopersicum esculentum* fruit	Pretoria	1979 - 02
23	45857	*Medicago sativa* stem	Bethlehem, O.F.S.	1979 - 03 - 14
24	45778	*Malus* sp. fruit	Langkloof, C.P.	1979 - 03 - 30
25	45748	*Tribulus terrestris* leaflet	Middelburg, C.P.	1979 - 05 - 30
26	45779	*Lolium multiflorum* seed	Howick	1979 - 06 - 29
27	45833	*Bixa* sp. leaf	Burgers Hall, E. Tvl.	1978 - 05 - 23
28	45749	*Zea mays* fruit	Delmas	1979 - 06

APPENDIX 5

ORDERED CHARACTERS AND CHARACTER STATES OF *COLLETOTRICHUM* OTU'S USED IN STATISTICAL ANALYSES.

1. Linear growth rate: mm/24 hours
2. Colony colour: above, central zone
3. Colony colour: above, marginal zone
4. Colony colour: reverse, central zone
5. Colony colour: reverse, marginal zone

   Colour categories:
   hyaline (0) white (1) pale yellowish (2) moderate orange (3) yellowish pink (4) light grayish brown (5) moderate yellowish to reddish brown (6) purplish gray (7) brownish gray (9) grayish purplish red (10) black (11)
6. Colony texture: central zone
7. Colony texture: marginal zone

   Texture categories:
   submerged (0) closely appressed (1) sodden appressed (2) cobwebby (3) cottony (4) subfelty to felty (5) downy (6) floccose (7) woolly (8) farinaceous (9)
8. Nature of colony margin: even (0) sinuate (1) fimbriate to coarsely fimbriate (2) irregular (3)
9. Colour of conidial masses: categories:
   absent (0) white (1) pale yellow (2) moderate orange (3) moderate yellowish pink (4)
10. Zonation of colony: absent (0) concentric (1) sectoring (2)
11. Conidiomata: absent (0) present (1)
12. Nature of conidiomata: stromatic thickening absent (0) present (1)
13. Nature of conidiomata: pigmentation light (0) dark (1)
14. Nature of conidiomata: form pulvinate (0) cupulate (1)
15. Conidia formed predominantly from mycelial side branches: absent (0) present (1)
16. Perithecia formed in culture: absent (0) present (1)
17. Setae: absent (0) few, scattered (1) abundant (2)
18. Setae: length (mean)
19. Setae: width (mean)
20. Setae: number of septa (mean)

APPENDIX 5 (CONTINUED)

21. Conidium shape:
cylindrical, ends obtuse (0) cylindrical, apex obtuse base tapered, truncate (1) cylindrical, both ends slightly tapered (2) straight fusoid (3) cylindrical, ends unilaterally tapered (4) clavate (5) ellipsoidal (6) ovoid (7) hourglass-shaped (8) curved cylindrical, ends obtuse (9) curved, ends acutely tapering (10) fusoid, curved mainly at apex and truncate base (11) curved, tapering gradually towards apex, base truncate (12) curved, tapering gradually towards apex, base truncate, broadest point nearer apex (13) comma-shaped (14)
22. Conidium length (mean)
23. Conidium width (mean)
24. Appressorium shape:
globose to subglobose (0) obovoid (1) clavate to broadly clavate (2) cuneiform (3) lobed (4) irregular (5)
25. Appressorium length: (mean)
26. Appressorium width: (mean)
27. Sclerotia: absent (0) sparse (1) abundant (2)