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Cultural Characters and Carpophore Construction of Some Poroid Hymenomycetes*

by

G. C. A. van der Westhuizen†

ABSTRACT

The cultural characters and construction of the carpophores of 24 species of poroid Hymenomycetes were studied. The microstructures formed in culture and oxidase reactions of the cultures were compared with the microstructures present, the construction and type of decay of the carpophores from which they were made. The type of interfertility of seven species was determined.

Intercollection pairings of haploid mycelia derived from single basidiospores and the technique of dikaryotizing a large haploid mycelium growing in culture by pairing it with a small dikaryotic mycelium, were used to confirm the identity of different collections of eight different species.

The literature on the classification, structure and anatomy of the carpophores and pure culture studies of Hymenomycetes, was reviewed.

It was found that the 24 species were distributed among nine of the groups proposed by Nobles (1958) on the basis of their cultural characters. The structures formed in culture were also found to be present in the carpophores so that the carpophores could also be assigned to the some groups as their cultures. The carpophores did not indicate the same relationships as the cultures however. Differences in the micromorphological characters of hyphae and in the types of hyphae present in carpophores of species in the same group were found. Differences in construction of the carpophores were noticed in species with similar types of hyphae. Micromorphological characters of hyphae and the microstructures as well as the construction of the carpophores are constant for each species. Differences and similarity of micromorphological characters and construction of carpophores of different species are not adequately conveyed by the concept of hyphal systems.

All seven species tested displayed the tetrapolar type of interfertility. Six of these are associated with white rots. In the intercollection pairings, dikaryotization and clamp-formation of the haploid test mycelium could not be achieved with *Polyporus dichrous* and *Polyporus pubescens*.

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† Plant Protection Research Institute, Department of Agricultural Technical Services, Pretoria

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1. INTRODUCTION

The increasing use of timber and the afforestation of new regions of South Africa necessitates the detection and control of factors that cause losses of trees and timber. The recognition and identification of fungi which cause diseases of living trees and decay of timber, are important in this respect.

Identification of decay fungi, most of which are placed in the Hymenomycetes, poses many problems however. The fruit-bodies which are required for identification of a causal organism may be lacking or they may be abnormal or in a state in which they can not be identified with certainty. In many cases the wood-decaying fungus may be isolated in pure culture but this is no assurance that the fungus will be identified unless it is one of the relatively small number of species of which the characters in pure culture have been described. The characters of cultures of many wood-rotting Hymenomycetes can not be related to the existing descriptions of their carpophores. There is as yet no correlation between generic characters of fruit-bodies and cultural characters. Identification of these wood-rotting fungi from culture must go directly to the species. Studies relating cultural characters to characters of the carpophores from which cultures were made, thus need to be undertaken.

Most of the known species of Hymenomycetes in South Africa have been described by a number of older workers, listed by Doidge (1950), around the turn of the century. Later, Van der Bijl (1922 a, b, c; 1924; 1925; 1926) described a number of poroid Hymenomycetes but most of these descriptions are based on gross morphological characters. Not many of these descriptions include details of spore characters. Since morphological characters are known to be variable, it is often difficult to identify specimens with the aid of such descriptions. More precise descriptions are thus required.

The South African fungal flora includes a wide range of species, some of which are known from the cool temperate regions of the Northern Hemisphere, while others are truly subtropical or tropical species. The relationships between these taxa are, in most cases, unknown. Most of the generic type species have been described from the cool temperate regions where a number of systems of classification of the poroid Hymenomycetes were also developed. It is thus necessary to compare the taxa from the warmer regions with these generic types in order to determine their generic affinities as well as their relationships with other species in the same genera. Only in this way can a natural system of

classification of these fungi be developed. This need was also emphasized by Lowe (1963 a) recently.

Attempts to recognize relationships between species of poroid Hymenomycetes are of little value unless anatomical characters are taken into consideration. This view had been emphasized by the work of Corner (1932 a, b, 1947, 1948, 1950, 1953), Cunningham (1946, 1947, 1948 a-h, 1949 a, b, 1950 a, b, 1954, 1963), Pinto-Lopes (1952), Nobles (1956, 1958 b, 1965, 1967), Bondartzeva (1961, 1963) and Teixeira (1958, 1960, 1962 a,b). These workers have shown that the microscopic characters of the hymenial structures and hyphae that make up the carpophore, are more constant and reliable than the largely morphological criteria that have been used hitherto. Only Cunningham (1946, 1947, 1948 a-h, 1949 a,b, 1950 a, 1963) and Pinto-Lopes (1952) have proposed systems of classification of the Polyporaceae, based on their anatomical characters. These systems were however not generally accepted by students of this group. Nobles (1958 b) grouped cultures of 225 species of Polyporaceae on the basis of their biochemical activities, hyphal modifications and spore shape into 36 groups which she suggested to be natural taxa of generic or higher rank. This concept was favourably received by Bondartzeva (1961) and others as a new approach to the problem of polypore taxonomy, with great promise for the development of a natural system of classification of these fungi. Nobles' thesis however, is based on cultural characters where many hyphal modifications are known which have never been described from carpophores. It is thus necessary to undertake correlative studies of the cultures and carpophores in order to determine whether the structures found in culture are also present in the carpophores. Correlative studies which reveal the presence of identical vegetative structures in both carpophores and cultures should thus indicate relationships between carpophores similar to those indicated by cultural characters.

In some of Nobles' (1958 b) groups, however, species are included which differ widely in habit and morphology of their fruit-bodies although the cultures showed them to be similar in regard to hyphal morphology, spore shape and biochemical activity. Corner (1953) showed that certain species which may show superficial resemblances, may differ widely in the types of hyphae present as well as the arrangement of the hyphae or in the construction of the carpophores. It thus appears that together with hyphal morphology, the construction of the fruit-body must also be taken into account when considering relationships between different species of polypores. Although it has been known since the publication of Corner's (1932 a, b) classical papers that different types of hyphae are present in carpophores of poroid Hymenomycetes, relatively few serious attempts have been made to study these characters and apply these concepts to the solution of taxonomic problems. Studies in which cultural characters are correlated with the characters of hyphae and other microstructures and the construction of the carpophores of as many species of poroid Hymenomycetes as possible, should therefore provide the information which should make a natural system of classification of these fungi possible.

The present study was undertaken as a basis for future taxonomic work on the South African species of poroid Hymenomycetes. No taxonomic study had been undertaken on the South African polypores since the time of Van der Bijl (1922 a, b, c, 1924, 1925, 1926) and it has become necessary to apply modern techniques and concepts to the study of these fungi.

For this purpose a number of species were collected at random to obtain species with diverse characters and affinities. The cultural characters and carpophore characters of these species were studied to determine: (i) how Nobles'

(1958 b) concepts may be applied to them; (ii) whether the structures formed in their cultures are also present in their carpophores; (iii) whether the phylogenetic relationships indicated by their cultures also exist between the carpophores; (iv) to compare the cultural and carpophore characters of these species with these characters of other species, especially generic type species, in order to obtain possible indications of their phylogenetic affinities. In this way it was hoped to provide accurate descriptions of a number of common species to serve as a sound basis for future taxonomic studies of these fungi.

It has been shown by Davidson, Campbell & Blaisdell (1938), Overholts (1953), Nobles (1958 b) and Bondartzeva (1961) that the oxidase reaction of cultures of polypores, the type of decay caused by these fungi and their host preferences, are valuable characters for the identification of species and may also be of considerable taxonomic importance. The oxidase reactions of the fungi included in this study, were thus determined and their type of decay and host range recorded for these reasons.

Work by Vandendries (1922, 1923, 1924 and 1933), Mounce & Macrae (1936, 1937, 1938), Nobles (1943, 1967) and Boidin & des Pomeys (1961), among others, has shown that pairings between mycelia grown from single basidiospores may yield valuable information on the identity of morphologically similar fungi even when collected in different parts of the world. Nobles (1958 b) also advanced the thesis that species of the Polyporaceae causing brown rots, have the bipolar type of interfertility whilst species with simple clamp connections which cause white rots, have the tetrapolar type of interfertility. Where possible, single basidiospore cultures were thus prepared from the different South African species in order to determine whether this also applied to the South African species. It was also attempted to pair single basidiospore mycelia from South African collections with cultures of Canadian origin in order to confirm the identity of different collections whenever possible.

As this study was intended as an exploration of the usefulness of the modern techniques in the taxonomy of South African polypores, no attempt was made to determine the full synonymy of the different species. Instead, only generic synonyms are cited and the species are described under their basinyms or their more generally used binomials. No new combinations or genera were made or created and possible phylogenetic relationships are merely indicated in the descriptions.

2. REVIEW OF LITERATURE

Classification of the poroid Hymenomycetes

In his early classification of the pore fungi, Fries (1821) recognized five genera, viz. *Daedalea, Polyporus, Merulius, Boletus* and *Fistulina* of which the last three are not considered to be genera of the Polyporaceae by most workers today. The generic distinctions were based on hymenial configuration but this soon proved to be inadequate. In later works, Fries (1828, 1838, 1874) added new genera or accepted genera proposed by other workers until, in 1874, he recognized eight genera of Polyporaceae and seven others in which the hymenium is borne in tube-like structures. Hymenial configuration and gross morphological characters such as the nature of the surface of the carpophore, were the basis of these generic concepts. Other workers soon added more genera in recognition of the desirability of splitting up Fries' unwieldy and heterogeneous groups into smaller

more natural ones. Among the first workers in this respect were S. F. Gray (1821) who added nine genera and Quelet (1886) who listed the polypores of France under 15 genera, ten of which were new. Karsten (1880, 1881, 1889) split Fries' genera *Polyporus* and *Daedalea*, into 26 different genera most of which are considered to be acceptable genera today. Murrill (1907 b, 1908), recognized 74 genera of Polyporaceae, which he divided into 4 sub-families on the basis of habit and hymenial configuration of the carpophore. The basis for segregation of the genera, was partly gross morphological characters and to a lesser extent, anatomical characters, mainly spore characters. Lloyd (1898, 1905, 1909, 1913, 1916, 1920, 1922) in his Mycological Writings on the other hand recognized only 12 genera in the Polyporaceae. The basis for these was mainly gross morphological characters. Anatomical characters were considered to be of value at the species level only.

Van der Bijl (1922 a, b, c, 1924, 1925, 1926) published descriptions of the South African species of polypores during this period. Morphological characters were the basis for this work in which anatomical details are often lacking. The generic concepts in this work were those of Fries (1838, 1874) and Lloyd (1898-1925). Only 8 genera were recognized and distinguished on the basis of hymenial configuration and pore shape, method of attachment of the carpophore and consistency of the pileus. The resupinate forms included in the genus *Poria*, were omitted. More recent works on Polyporaceae by Overholts (1953), Lowe (1946, 1947, 1948, 1957, 1958, 1963 b, 1966), Lowe & Gilbertson (1961 a, b) and Gilbertson (1961) are still based on the generic concepts of Fries (1821, 1838, 1874) although many micromorphological characters are included in their descriptions of species.

The trend to delimit genera on the basis of micromorphological characters was initiated by Patouillard (1887) who recognized 39 genera delimited on the basis of microscopic and morphological characters (Patouillard, 1900). These concepts were later applied and extended by other workers, namely Carlton Rea (1922), Bourdot & Galzin (1928), Donk (1933), Pilát (1936), Imazeki (1943), Bondartzev & Singer (1941), and Bondartzev (1953) to the polypore floras of their respective countries. Among these workers a tendency towards recognizing an increasing number of genera in the polypores is clearly evident ranging from 10 genera in the British Isles (Rea, 1922) to 61 genera in the European part of the U.S.S.R. (Bondartzev, 1953).

Systems of classification of the Polyporaceae in which the micromorphology of the hyphae or the concept of hyphal systems as advanced by Corner (1932 a, b) were used to characterize genera, were proposed by Cunningham (1946, 1947, 1948 a-h, 1949 a, b, 1950 a) and Kotlaba & Pouzar (1957). Cunningham (1946, 1947, 1948 a-h, 1949 a, b, 1950 a) applied these concepts of hyphal systems to his studies of the Polyporaceae of New Zealand in which he recognized only 12 genera.

Pinto-Lopes (1952) regarded Corner's (1932 a, b) and Cunningham's (1947, 1948 a-h, 1949 a, b, 1950 a) concepts and application of hyphal systems to be of little value. He instead regarded the type of septation and thickening of the walls of hyphae as the only criteria of taxonomic value. On this basis he proposed a system of classification of the Polyporaceae in which he recognized 22 genera divided among seven sub-families.

Kotlaba & Pouzar (1957) proposed a system of classification of polypores of Czechoslovakia based on hyphal systems in which they recognized 48 genera, seven of which were new. Most of their concepts were based on the work of Cunningham (1946, 1947, 1948 a-h, 1949 a, b, 1950 a) and Teston (1953 a, b).

Bondartzeva (1961) critically reviewed the more recent systems of classification of the polypores. She rejected the systems of Cunningham (1947, 1948 a-h, 1949 a, b, 1950 a) and Pinto-Lopes (1953) as artificial and instead regarded that of Kotlaba & Pouzar (1957) as more natural but incomplete. In her opinion the system of Bondartsev & Singer (1941), which was later adopted with certain modifications by Bondartzev (1953), is the most natural one since it considers structure or texture in relation to anatomy and morphology of the fungi.

It is evident that the basis for classification of the poroid Hymenomycetes have undergone profound changes since Fries (1821) published his system. It is also evident that there is an almost total lack of agreement on generic concepts in these fungi. These different systems of classification and generic concepts had been reviewed by Cooke (1959) who listed about 300 genera which had been proposed for the Polyporaceae. He considered about 100 of these to be valid and usable.

Donk (1960, 1962) discussed the origin, usage and status of the generic names proposed for polypores and agreed with Cooke (1959) in many respects. Later, in his conspectus of the families of the Aphyllophorales, Donk (1964) recognized the impossibility of including in the family Polyporaceae, genera of which the characters had not been clearly defined. Consequently the Polyporaceae were not discussed in full in that work.

Despite this confusion two main trends are noticeable in a survey of these works, viz.: (i) a tendency toward the recognition of a larger number of genera of poroid Hymenomycetes and (ii) a change in the relative importance of the taxonomic criteria away from the macroscopic morphological characters of the older taxonomists towards the micromorphological and anatomical characters considered to be more important by the modern workers. This must mean that there is a growing conviction among mycologists that the micromorphological characters are more constant and reliable in taxonomic studies than the macroscopic characters and therefore more capable of indicating phylogentic relationships. This in turn would allow the grouping of species and consequently more precise generic deliminations.

It must be emphasized however that most of the systems of classification and generic concepts proposed so far, were based on species found in the cool temperate regions of the Northern Hemisphere. Very few tropical or sub-tropical species, of which many occur in South Africa, have been described or included in these classifications. This shortcoming was recognized by Lowe (1963 a) when he stated: "I have been and will for some time be preoccupied with species concepts. Until these are cleared up for a large proportion of the polypores particularly the tropical species, I cannot consider, without crippling misgivings, the larger aspects of generic separations." The accurate description of micromorphological characters of the hyphae and other microstructures in fruit-bodies is thus of the greatest importance in the taxonomy of these fungi.

Structure and Anatomy of the Carpophore in Taxonomy

The first important work on the taxonomic value of micro-structures and anatomy was published by Patouillard (1887) who included details of hyphal morphology, structure of the surface of the pileus and characters of basidia, spores and cystidia, in his generic descriptions. Later he used these characters to delimit genera of the Hymenomycetes (Patouillard, 1900).

Ames (1913) studied structure of the fruit-bodies in relation to generic concepts of 130 North American species. She considered anatomical features such as consistency and hyphal arrangement of the trama, modifications of the surface of the pileus, the relation of the hymenophore to the pileus and spore characters, to be of great taxonomic value. Characters of the cystidia were regarded as too variable to be of any value above the species level while spore colour was regarded as the most important spore character and preferable to context colour as a criterion for generic delimitation. Ames concluded that the character of the flesh or the consistency of the fruit-body indicate the broader relationships within the Polyporaceae most clearly but that in the recognition of genera a complex of characters rather than separate characters must be considered. On the basis of her studies, which did not include the resupinate species, she recognized 16 genera among the temperate North American species.

The great advance in the study of micromorphology of basidiomycete carpophores was made possible by the work of Corner (1932 a, b) who introduced the concept of hyphal systems. He demonstrated that the fruit-body of *Polyporus xanthopus* (Corner, 1932 a) is constructed of three types of hyphae which differ morphologically in respect of type of septation, wall-thickness, morphology, ontogeny and function. The generative hyphae are hyaline, thin-walled and nodose-septate and are the basic hyphae from which all other hyphae as well as the basidia are produced. The skeletal hyphae are thick-walled, unbranched and aseptate and form the main structural elements of the pileus. They arise from lateral branches of the generative hyphae. The binding hyphae are thick-walled and aseptate and also arise from generative hyphae but are of limited growth and have many short, tortuous branches which bind the other hyphae into the tough, leathery tissues of the pileus. These three types of hyphae thus constitute a fruit-body with a trimitic hyphal system. The fruit-body of *Fomes laevigatus* (Corner, 1932 b) on the other hand consists only of thin-walled, simple-septate generative hyphae and thick-walled, aseptate, unbranched, skeletal hyphae. Because the binding system is lacking, the fruit-body of *Fomes laevigatus* has a dimitic hyphal system. The term "monomitic hyphal system" was proposed to describe the construction of fruit-bodies in which only generative hyphae are present. Later, Corner (1953) showed that certain species have fruit-bodies with dimitic hyphal systems which consist of generative and binding hyphae. *Asterodon* spp. and *Asterostromella* spp. (Corner, 1948) were shown to have other specialised structures in their dimitic fruit-bodies, which are similar to structures found in the fruit-bodies of *Aleurodiscus* spp., *Hymenochaete* spp. and *Fomes spp.* But Corner regarded the elaborate fruit-body of *Polystictus xanthopus*, with trimitic hyphal system, as more highly evolved than the dimitic or monomitic types (1932 b). He showed that differences in colour and texture of fruit-bodies are determined by the characters of the crust and hyphal systems while the microscopic structure of the upper surface determines whether it will be smooth, mat, velutinate, tomentose, laccate and so forth (Corner, 1932 a, b; 1953).

Corner (1950) used the concepts of hyphal systems as well as other microscopic characters to delimit genera in a monographic treatment of the clavarioid fungi and later of the cantharelloid fungi (Corner, 1966).

Corner thus showed that thin-walled, septate hyphae are present together with other hyphae, modified in various ways, in the tissue of fruit-bodies of Hymenomycetes. He further demonstrated the interrelationships of these different kinds of hyphae and showed that the consistency of the tissues and the nature of the upper surface depend on the nature of the hyphae present in the fruit-body. He also indicated the phylogenetic significance of the different kinds of hyphae and their possible use in the classification of these fungi.

Humphrey & Leus (1931) made anatomical studies of the upper surfaces of the pilei of *Ganoderma* spp. They found that there were anatomical differences in the surfaces of these species and that these anatomical characters were constant for each species.

K. Lohwag (1940) made anatomical and morphological studies of the upper surfaces of a number of European fungi. Many of these were type species of genera which had been proposed by various European workers at different times. Lohwag distinguished five main types of covering of the pilei, viz.:

1. The derm which consist of hyphae which run more or less perpendicular to the surface. Of this, there are three kinds, (a) the *hymeniderm* in which the elements are tightly packed, resembling a hymenium; (b) the *trichoderm* consisting of hair-like elements, either separate or bundled together, and closely joined and, (c) the *palisadoderm* similar to the hymeniderm but consisting of slender, loose elements.
2. The hymenophoral cover, which consists of a sterile hymenophore.
3. The cutis, which consists of elements arranged parallel to the surface giving the smooth glabrous appearance.
4. The cortex which consists of a denser matting of more or less modified hyphae of the context.
5. The crust, which consists of a hard and sharply distinguished layer on the surface without regard to its structural origin.

Later, H. Lohwag (1941) adopted K. Lohwag's terminology in his studies on the anatomy of the Asco- and Basidiomycetes and introduced the term paraderm to describe the surface covering which consists of a pseudo-parenchymatic structure built up of isodiametric cells.

Furtado (1965 a), in his studies of the relation of the microstructures to the taxonomy of the Ganodermoideae, reformulated the older concepts of the types of structure of the pilear cover in more exact terms. He also introduced the terms "lacca-like substance" and "laccate appearance" to replace "lacca" and "laccate", as previously used by many authors, because the chemical nature of this substance is unknown. He regarded the "cortex" and "derm" as the two major categories of structures found in the Ganodermoideae. The term "cortex" he applied to "a structure lacking any distinctive layer" but characterized by a "continuous and progressive condensation of the context hyphae towards the periphery." The "derm" was defined as "all types of structures in which the hyphae are anti-clineal to the pilear surface." Five types of derm, viz., the Hymeniderm, Palisadoderm, Trichoderm, Paraderm and Indeterminate derm, were recognized. The first four terms agreed with those of K. Lohwag (1940) and H. Lohwag (1941) while the fifth was proposed for "the type of derm found in a structure formed of incrusted and intermingled hyphae in which the original arrangement cannot be traced precisely." These studies clearly demonstrated the varied nature of the upper surface and the morphological differences that exist between the hyphae that comprise the various types of covering of the pileus. The proposed terms, however, do not indicate which type of hyphae, if more than one type of hypha is present in the pileus, undergo the modifications to produce a specific kind of upper surface.

After publication of Corner's concepts of hyphal systems (1932 a, b) and Lohwag's (1940) work on the nature of the upper surface of fruit-bodies several workers realized the potential usefulness of these concepts in Hymenomycete taxonomy and called for urgent application of Corner's methods to studies of

Hymenomycetes. Corner (1954) a) stated that only by a study of hyphal characters could a natural system of classification of the Hymenomycetes be worked out. Both Corner (1954) a) and Wakefield (1948) mentioned the existence of series of Hymenomycetes related by structure but differing in hymenial configuration and characters. They stressed the importance of separating species and genera by considering the sum of all the characters present in the carpophore. Kotlaba (1964) restated the views that the microstructures of carpophores and spore characters are the only constant and reliable characters in Hymenomycete taxonomy. He stated: "The importance of these characters lie in their particular combinations. Furthermore, the same character may have different taxonomic value in different groups and cannot be generalized." He thought that genera of higher fungi should be delimited on the basis of a complex of characters while species may be delimited on single characters only.

Cunningham (1946, 1947, 1948 a, b, c, d, e, f, g, h, 1949 b, 1950 a, 1954) was the first worker to apply Corner's concept of hyphal systems to the classification of polypores. In his studies of the Polyporaceae of New Zealand, in which he recognized 17 genera, he regarded the types of hyphal systems present in the fruit-bodies, together with the absence or presence of clamps on the generative hyphae, the colour of the hyphae and the type of basidia produced, as important at the generic level. These criteria, however, were not used consistently. While some genera were characterized by the absence of clamp connections, e.g. *Fomes* Kickx, *Fomitopsis* Karsten, *Coltricia* Mich. ex S. F. Gray and *Inonotus* Karst., species both with and without clamp connections were left in *Poria* and *Merulius* Hall. ex Fr. Similarly, he included in some genera, e.g. *Lenzites* Fr., *Trametes* Fr., *Coriolus Quél.* and *Daedalea* Fr., only species with trimitic hyphal systems while species with monomitic, dimitic, and trimitic hyphal systems were included in *Poria*. This inconsistency is perhaps not surprising since a study of Cunningham's (1946, 1954) definitions of the different types of hyphae, do not reveal distinct and constant differences between skeletal and binding hyphae. It appears that Cunningham himself was not too clear about differences between these types of hyphae.

Pinto-Lopes (1952) also proposed a system of classification of the Polyporaceae based mostly on the characters of the hyphae which comprise the fruit-body. In a bio-taxonomic study of polypores, he concluded that the characters of the hyphae were fixed and genetically constant under many different conditions of growth in the carpophores as well as in culture on artificial media. He distinguished between three types of hyphae, viz. primary, secondary and tertiary. Hyphae produced by germinating basidiospores are primary hyphae but they become secondary hyphae, which may form clamp connections, after fusion with other genetically compatible primary hyphae. Differentiated hyphae, which are characterized by thickening of the wall, are the tertiary hyphae. According to him the carpophores of all species consist of secondary and tertiary hyphae of which the micromorphological characters are constant. In order to prove the constant characters of the tramal hyphae, he also investigated those characters in artificial culture and found that: (1) secondary and tertiary mycelium were always present in cultures although it was difficult to distinguish the tertiary mycelium in some cases; (2) species with clamp connections on the secondary hyphae of the carpophore also have them on the secondary hyphae in culture; (3) with some exceptions, the colour of the mycelium in culture was the same as that of the hyphae of the carpophore and was produced in the same way. He concluded that the same types of hyphae are present in both carpophores and cultures. Pinto-Lopes concluded that each species has a plan of anatomical organization which is always constant in all carpophores and that carpophores of the same species always have

the same structure in spite of differences in the appearance of the upper surface of the carpophores. Hyphal characters have great taxonomic value while characters such as surface of the carpophore and consistency of the context are of lesser value. Macroscopic characters such as carpophore shape, pore shape, tube length and microscopic characters such as spore shape and spore colour he regarded as having no taxonomic value. He agreed with Ames (1913) that certain microscopic structures such as cystidia are useful aids for the recognition of species but are too variable to be of taxonomic importance above this level. Pinto-Lopes regarded the characters of the secondary hyphae as of prime value and the characters of tertiary hyphae of secondary value but the characters of the secondary and tertiary hyphae taken together are of prime value and permit the division of the family into sub-families On this basis he distinguished eight main groups in the Polyporaceae with the following hyphal characters:—

A. Secondary hyphae with clamp connections:
   (1) tertiary hyphae hyaline, with clamp connections and walls not thickened or slightly thickened;
   (2) tertiary hyphae hyaline, with clamp connections, walls thickened;
   (3) tertiary hyphae hyaline without clamp connections, walls more or less thickened, and
   (4) tertiary hyphae yellow or brown, without clamp connections and walls more or less thickened.

B. Secondary hyphae without clamp connections:
   (1) tertiary hyphae hyaline, septate and walls slightly thickened;
   (2) tertiary hyphae yellow, septate, and walls slightly thickened;
   (3) tertiary hyphae hyaline, aseptate, walls much thickened, and
   (4) tertiary hyphae yellow or brown, aseptate and walls much thickened.

These distinctions formed the basis for his system of classification of the Polyporaceae consisting of 22 genera distributed among 7 sub-families.

The work was severely criticized by Corner (1954 b) for the author's views on hyphal modifications and his disregard for characters other than those of the hyphae. His lack of close adherence to the International Code of Botanical Nomenclature also drew criticism (Cooke, 1959; Teixiera, 1962 b) and the work did not meet with acceptance among mycologists. Nevertheless, Pinto-Lopes' work is of considerable value because of the accurate and reliable observations on the hyphal characters of the species described and his confirmation of the existence of different types of hyphae in the fruit-bodies of a large number of species of Polyporaceae. Despite its shortcomings, it cannot be disregarded by any student of micromorphology and taxonomy in the Polyporaceae.

Both Corner and Pinto-Lopes thus focussed the attention of taxonomists sharply on the varied nature of the microscopic characters of the hyphae in the carpophores and have indicated their value in the taxonomy of this group. Both workers have indicated the important differences between the undifferentiated and differentiated hyphae in fruit-bodies of Hymenomycetes.

The use of hyphal characters and Corner's (1932 a, b) concepts of hyphal systems have been applied to taxonomic studies of polypores by a number of different workers. Teston (1953 a) stated that Corner's (1932 a) and Cunningham's (1946) definitions of hyphal systems do not distinguish clearly between skeletal and binding hyphae. In her study of the hyphal systems of 100 species of Polyporaceae from the Bourdot herbarium in the Museum of Natural History

in Paris, Teston (1953 a, b) often found it difficult to place particular hyphae in one of the three systems and to decide whether a particular species was monomitic, dimitic or trimitic. She reported that thickened walls and lack of septa distinguish the skeletal systems from the generative system but that intermediate stages, i.e. hyphae with thickened walls and clamp connections can also be present. In less complex species, such intermediate hyphae, (mediate hyphal system, Corner, 1932 a) would be numerous and function as a pseudo-skeletal system. If species of each genus were arranged in order of decreasing importance of the pseudo-skeletal system, an almost continuous series is obtained in which it is difficult to separate clearly the monomitic species from the dimitic. In species where clamp connections are lacking on the generative hyphae, the distinction is even more difficult and can be based only on wall thickness which varies progressively. With regard to the binding hyphae, Teston (1953 a,b) believes that they cannot be defined absolutely, but only by comparison with the skeletal hyphae. Although distinctions exist in form and diameter and staining reactions, the binding and skeletal systems are related through a system of intermediates. Teston agreed with Cunningham (1946) and Pinto-Lopes (1952) that absence or presence of clamp connections is of great importance in relation to structure. Species which do not possess clamp connections on the generative hyphae do not attain the same complexity of structure which is found in species with clamp connections on their generative hyphae. She concluded that species can be arranged in order of increasing complexity, from monomitic species through all intermediates to trimitic species, within each genus. But the characters of differentiated hyphae cannot serve as a basis for taxonomy because it will lead to the fragmentation of genera. It is a badly defined character which may vary with size and age of the fruit-body. Only rarely does it permit the recognition and definition of natural groups. It can be used to advantage to arrange species in such groups.

Teston's (1953 a, b) observations thus indicate that the hyphal modifications are not as clearcut and fixed as Corner (1932 a, b, 1954), Cunningham (1946) and Pinto-Lopes (1952) believed. Teston's conclusions differ from these author's views that hyphal characters are of primary importance in the taxonomy of the Polyporaceae although she does admit that they may permit the recognition and definition of natural groups.

Hansen (1958) in her study of the anatomy of the Danish species of *Ganoderma,* confirmed some of Teston's (1953 a, b) observations and conclusions. Hansen found that the skeletal hyphae differed from Corner's (1932 a, b, 1953) definition in that they often have one or more branches near their distal ends. Their main stems are thick-walled and aseptate and arise at clamp-connections on thin-walled, generative hyphae. The lateral branches act as ties although the main stems are arranged longitudinally. In the dissepiments, these lateral branches of the skeletal hyphae take over the binding function completely. Binding hyphae are present in the context only and are of the bovista type. Hansen concluded that the differences in the skeletal systems of the species examined are of a qualitative as well as quantitative nature and not constant enough for use in the delimitation of species.

The American workers, Lowe and Overholts, on the other hand, largely ignored the concepts of hyphal systems in their work on American polypores. Overholts (1953) in his account of the Polyporaceae of the North-eastern United States and Canada, included details of spores, basidia, cystidia and other microstructures and hyphae in his descriptions of species. He often used the term "hyphal complexes" in descriptions of species which possess binding hyphae in Corner's (1932 a) terminology. No attempt was made to use these characters for generic delimitation or classification of the species described. Similar work was

published by Lowe (1946, 1947, 1948, 1956, 1957, 1958, 1961, 1963 b, 1966) who included details of characters of the spores, hyphae and other microstructures of the large number of species described by him. These characters were used for diagnostic purposes at the species level only while the generic concepts were Friesian.

Banerjee & Debi (1956) attempted to relate micromorphological and structural differences with morphological differences in the fruit-bodies of different collections of *Polystictus xanthopus*. They could distinguish three morphologically different types of fruit-body, viz.:

1. thin fruit-bodies with long, narrow, excentric stipes and minute, regular pores;
2. small, thick, fruit-bodies with thick, excentric stipes and regular but larger pore mouths, and
3. thin, sessile fruit-bodies with hydnoid to irpicoid pores.

Forms intermediate between all three types, were found. The basidia and spores of fruit-bodies of the first two types were similar in size and shape. The basidia of the third type of fruit-body were larger than those of the other two types and so were the spores, which also differed in shape. Fruit-bodies of the first two types consisted of generative hyphae with clamp connections and mediate hyphae, skeletal hyphae and binding hyphae. In fruit-bodies of the third type, no binding hyphae were present but only much branched generative hyphae which resembled binding hyphae. The authors described binding hyphae as much-branched, thick-walled, and without clamp connections. They concluded that two varieties of *Polystictus xanthopus* exist since "the separation into three types by macroscopic characters alone cannot be substantiated in all cases by microscopic characters and in other details." The larger pore, basidium and spore dimensions as well as the absence of binding hyphae, distinguish the third type of fruit-body from the other two. These workers thus did not regard these differences to be sufficiently important and constant to justify recognition of separate species.

Teixeira (1956, 1958, 1960, 1962 a, b) on the other hand firmly believes that the microstructures and hyphal morphology of the carpophores of polypores are the only characters of taxonomic value. Teixeira & Rogers (1955) noticed that *Aporpium caryae*, which has a poroid hymenial surface, also has cruciate-septate basidia. They transferred this species to the Tremellales which are characterized by such basidia. Teixeira (1956) published details of his methods of studying the construction of the carpophore. Essentially, these consist of carefully teasing apart thick sections, from different parts of the carpophore, cut parallel to the direction of growth of the hyphae and dissecting out individual hyphae with the aid of fine needles under 50x magnification of the dissecting microscope. The morphology of the hyphae and other microscopic structures and their inter-relationships, are then studied under the oil immersion lens. This method is essentially similar to that described by Corner (1932 a, b, 1953). Recently Fidalgo (1967), published a sophisticated method of obtaining intact hyphae for microscopic examination from carpophores by means of ultrasonic vibrations.

Teixeira (1958) applied his method to study the microstructure of *Laricifomes officinalis*. He showed that this fungus, which is the type species of the genus *Laricifomes* Kotlaba & Pouzar, differs in a number of structural details from *Fomes fomentarius* the type species of *Fomes* Kickx, (Donk, 1960). He also demonstrated (Teixeira, 1960) that the generative hyphae of a number of common North American species have clamp connections at the septa although this fact is not mentioned in a number of important reference works in this field. Clamp connections were absent from the generative hyphae of two of these species.

Teixeira (1926a) afterwards applied his method to the study of the microstructure of the basidiocarps of species of the genus *Fomes* Kickx. In this work he amended the generic description to include species of which the surface is covered by a definite crust over a chestnut-coloured context consisting of thin-walled, hyaline generative hyphae with clamp connections at the septa and thick-walled, differentiated hyphae without clamp connections, the skeletal and binding hyphae. The ends of the skeletal hyphae at the upper suface are agglutinated into the tough, hard crust. Hairs over the crust are produced by terminal proliferation of these skeletal hyphae. Although the skeletal hyphae are aseptate, generative hyphae with septa and clamp connections often produce branched structures which resemble the binding hyphae. Together with the type species *Fomes fomentarius*, two other species were recognized. Species were distinguished on the characters of the crust and the size of the pores. On the basis of this work, Teixeira concluded that the microstructures of the fruit-bodies, such as basidia, spores and other hymenial structures, as well as the nature of the generative hyphae and the specialised branches which they produce, are genetically constant in character and therefore more reliable in taxonomy than the morphological features which are still used to delimit genera in the Polyporaceae. These conclusions were restated and supported by numerous examples from earlier literature in a review of the taxonomy of the Polyporaceae published later (Teixeira, 1962 b).

O. Fidalgo & M. E. P. K. Fidalgo also used Teixeira's (1956) methods to study the hyphal systems and taxonomy of a number of genera and species of polypores. By these methods, M. E. P. K. Fidalgo (1958) demonstrated that *Lenzites cinnamomea* Fr. differs from *Gloeophyllum sepiarium* (Wulf. ex Fr.) Karst. in the characters of the skeletal and binding hyphae. She later proposed the genus *Phaeodaedalea* (M. E. P. K. Fidalgo, 1961) similar to *Gloeophyllum* Karst. and *Hexagona* Fr. in its trimitic hyphal system, but differing from these genera in having brown, globose spores. She also showed that *Trametes odoratus* Fr. is characterized by a dimitic hyphal system (M. E. P. K. Fidalgo 1962). The genus *Osmoporus* Sing., of which *Trametes odoratus* is the type is thus distinct from *Gloeophyllum* Karst. of which the type species, *Gloeophyllum sepiarium* (Wulf. ex Fr.) Karst., has a trimitic hyphal system.

O. Fidalgo (1958) concluded that *Ptychogaster rubescens* is the chlamydosporous form of *Polyporus guttulatus* Peck because of similarities between hyphae from cultures of *Polyporus guttulatus* and those from the fruit-bodies of *Ptychogaster rubescens*. Later, (O. Fidalgo 1962 a, b) he showed that *Bornetina corium* Mangin & Viala is the imperfect state of *Diacanthodes novoguinsensis* (P. Henn.) O. Fid. and that both are characterized by a monomitic hyphal system with clamp connections on the hyphae and a tendency to be dimitic.

In collaborative studies, Fidalgo & Fidalgo (1962) described the hyphal systems, the morphology and construction of the sporocarp of five species of polypores. They also proposed the new genus, *Pseudofistulina*, (Fidalgo & Fidalgo, 1963) for which extensive descriptions of the micromorphology of the hyphae and other structures, as well as descriptions of the construction of various parts of the fruit-body, were presented. This genus differs from *Fistulina* Bull. ex. Fr., as typified by *Fistulina hepatica* Huds. ex Fr., by the absence of clamp connections on the hyphae, the presence of a derm composed of acanthophyses and hyaline, thin-walled spores instead of yellow, thick-walled spores. Both genera have monomitic hyphal systems.

The presence or absence of clamp-connections on the hyphae of Hymenomycetes and their importance in taxonomy has been the subject of much discussion by various workers. Not much attention was given to these structures by Bourdot

& Galzin (1928), Donk (1933), Overholts (1953), and Lowe (1948, 1956, 1957, 1958, 1963 b) who often reported them to be absent from hyphae of species where they are now known to be present (Pinto-Lopes & Farinha, 1950). For taxonomic purposes, the presence or absence of clamp connections are regarded to be of value at the species level only by some workers such as Hesler & Smith (1963) and Smith (1966) while others, notably Pinto-Lopes (1952) Singer (1962) and Teixeira (1962 a, b) believe them to be of value at a higher level. The former view is supported by Smith's (1966) observations that clamp connections regularly occur only in a small number of species of some genera in the *Gasteromycetes*. Pantidou (1961), and Pantidou & Groves (1966) found that clamp connections were present in mycelium of species of Boletaceae grown in cultures but which do not have clamps on the hyphae of their fruit-bodies while in other species, clamp connections and simple septa were present in the same mycelium. Smith (1966) suggested that since the numbers of species with clamps vary in different groups, a quantitative study of the proportion of clamped septa in both clamped and clampless species is needed as well as mating compatibility studies between single spores of clamped and clampless species. Until such studies had been undertaken he regards the absence or presence of clamp connections on the hyphae of the basidiocarp as of significance at the specific level only. On the other hand the views of Pinto-Lopes (1952), Singer (1962) and Teixeira (1962 b) are supported by the work of Cunningham (1946, 1947, 1948 a-h, 1949 a, b, 1950 b), Teixeira (1958, 1960, 1962 a, b), O. Fidalgo (1958, 1963), M. E. P. K. Fidalgo (1961, 1962), Fidalgo & Fidalgo ((1962, 1963, 1966, 1967) and Furtado (1964, 1965 a, b, 1966, 1967) who found clamp connections to be constantly absent or present on the generative hyphae of different species of Polyporaceae, and who characterized genera on this basis. The position was well summarized by Singer (1962) who stated: "If the presence or absence of clamp connections is used as a character in taxonomy it is essential to make sure that the specimen studied is not merely a parthenogenetic form of a normally bipolar or tetrapolar species. If this possibility is excluded we have further to deal only with species with normal sexuality that have lost their ability to form clamp connections and homothallic forms, species or genera that find themselves in the same condition. Under these circumstances the presence or absence of clamp connections must be accepted as a valuable character." In Donk's (1964) recent treatment of the Aphyllophorales, it is evident that some groups contain species with clamp connections only while others contain species with simple septa only. Donk is of the opinion that "the value of clamps as a taxonomic feature differs from group to group and may even appear erratic within rather small taxa of lower rank such as species." Furtado (1966) pointed out that "in the clamped species studied experimentally, clamp connections are formed only in one specific heterokaryon, the dikaryon." He proposed that since clamp formation is controlled genetically, it is necessary to study the cytogenetic condition of the hyphae whenever the pattern of septation is decisive for definition of any taxa or the proposal of any hypothesis.

The concept of hyphal systems and the use of hyphal characters in taxonomic studies have also been applied to non-poroid Hymenomycetes. Ragab (1953) reported that most species of the Hydnaceae have monomitic hyphal systems while some are dimitic. In some genera monomitic as well as dimitic species are found. He included a key to 14 genera in the Hydnaceae, based on hyphal characters as well as morphology.

Cunningham (1963) applied his concepts of hyphal systems in studies of the Thelephoraceae of New Zealand. The hyphal systems were however used as a taxonomic character only at the generic or even sub-generic level. Cunningham (1963) attached greater importance to the microscopic structures of the hymenial

layer and differences in habit and hymenial configuration. Cunningham stated: "There is not the marked differentiation in hyphal systems in the Thelephoraceae that is so noticeable a feature of the Polyporaceae; far the greater number of genera possess species with both monomitic and dimitic systems, hyaline and brown hyphae and are with or without clamp connections. A few genera however do show some differentiation."

Talbot (1951, 1954 b, 1958 a, b) used micromorphological characters to delimit genera and species in his studies of the South African resupinate Hymenomycetes. In his descriptions, full details of hyphal characters and microscopic structures were included but the concept of hyphal systems is not always evident. He regarded the nature and absence or presence of microscopic structures in the hymenium as of greater taxonomic importance. In this respect he agreed with Cunningham (1963) and other workers.

Reid (1959, 1962, 1963, 1965) also placed much emphasis on micromorphological characters of hyphae and microscopic structures in his taxonomic studies which include mainly the lower Hymenomycetes.

Welden (1960), who revised the American species of *Cymatoderma* Jungh. on the basis of anatomical studies, could distinguish four main types of hyphae in the context of these fungi, viz.:

(1) long sub-solid to solid hyphae rarely branched or clamped, arising gradually or abruptly from thin-walled hyphae,

(2) similar but narrower and more tortuous hyphae,

(3) solid to sub-solid, narrow, short or long branching hyphae, and

(4) thin-walled, relatively wide branching and clamped hyphae.

Intermediates between these may also be found. Welden (1960) found that he could not apply Corner's (1932 a, b) terminology to the hyphae and hyphal structure despite the fact that Reid (1959) had divided the genus into dimitic and trimitic sections. Welden considered some of the branching hyphae to perform skeletal as well as binding functions while some of the thick-walled hyphae with clamp-connections served generative as well as skeletal functions. He concluded: "I do not wish to negate the useful terms 'dimitic' and 'trimitic,' but a strict interpretation of Corner's terms does not appear applicable to the American species of *Cymatoderma* unless all the species are considered trimitic". He used macroscopic morphological characters as well as microscopic characters of the hyphae and hymenial and sub-hymenial structures to delimit species.

Lentz (1960) made extensive use of micromorphological and hyphal characters to characterize type species of *Stereum* Pers. ex. S. F. Gray and allied genera after he realized that his earlier descriptions (Lentz, 1955) of the genus *Stereum* in the upper Mississippi Valley was based largely on macroscopic and gross microscopic characteristics.

Slysh (1960) used characters of the microscopic structures and hyphae of the fruit-bodies of *Peniophora* Cooke to describe the species found in New York State and surrounding regions. He reported that only one species, *Peniophora greschikii* is composed of two distinct types of hyphae, i.e. dimitic. All the others are monomitic but there are differences in the arrangement of the hyphae in different species. He further reported that some species have simple-septate hyphae, while they may be nodose-septate in others. Hyphal septation was used to distinguish between species of two out of the total of eight sections into which he divided this genus.

Maas Geesteranus (1962, 1964) found hyphal characters and anatomical structure to be of fundamental importance for the delimitation of genera in the Hydnaceae, and described differences in the morphology and arrangement of hyphae of a number of species whose carpophores consist of generative hyphae only. He stated: "The necessity and importance of the anatomical structure for the correct understanding of a genus becomes at once apparent when one considers *Steccherinum* as it was conceived by Banker and extended by subsequent authors . . . . . Also the apparent difficulty experienced by some authors sharply to delimit *Hydnellum* and *Sarcodon* disappears as soon as the hyphal system in both genera is taken into account." On the basis of this study of the generic types he concluded: "It is more than likely that, with the spines as the sole character in common, the connection of many of the hydnaceous genera, will have to be sought not within the 'Hydnaceae' but, irrespective of hymenial configuration, with groups now widely separted."

Bondartzeva (1963) discussed the use of the anatomical criteria for the taxonomy of the Aphyllophorales. She accepted Corner's (1932 a, b) concepts but concluded that the type of hyphal system is mainly of generic value in the taxonomy of this group. In cases, however, where adaptation to conditions of an external medium could have produced changes in the hyphal system, while other features make it evident that the species belong to the same genus, the type of the hyphal system may be either of supra-generic or infra-generic importance. She further regarded the type of hyphal system as an element of adaptive evolution. This view is supported by: (i) the relationship between the consistency of the context of the sporocarps and consequently their anatomical structure and the way of life of the species, and (ii) the limited number of types of hyphal systems and the occurrence of identical systems in species which differ widely in respect of other characters but are similar in ecological relationships. The anatomical structure, in her opinion, is an important indication of the life forms but not of the basic line of evolution. The anatomical structure is thus an element of partial and not general evolution and hyphal systems of the fruit-bodies cannot be considered as one of the basic features in the development of a phylogenetic system. In this respect, Bondartzeva believes that the problem of convergence, which occurs widely in the Hymenomycetes, requires elucidation since it offers the key to the understanding of the complex phylogeny of this group of fungi.

Smith (1966) in his discussion of the hyphal structure of the basidiocarp stated that the mitic system (Corner's hyphal systems, 1932 a, b) is not very suitable for application to the Agaricales and thought it "ineffectual to set up special terms for generalized situations when they can be properly evaluated only by careful attention to detail." He thought the the terms such as "generative hyphae" fail to express adequately what is actually seen under the microscope in individual species. He considered descriptions of hyphal modifications, cell shape and microstructures, especially cystidia, to be important in taxonomic studies and agreed with Bondartzeva (1963) by stating that most hyphal modifications in the basidiocarps appear to be adjustments to meet the problem of moisture loss. The diversity in form and content of end cells of hyphae is due to the different ways which different species have evolved to meet this problem.

Donk (1964) used the concept of hyphal systems together with macro- and micromorphological characters to characterize the families of the Aphyllophorales. He regarded these hyphal systems and micromorphological characters as of great importance in taxonomy. His descriptions of families were preceded by concise reviews of the anatomical features.

The morphology of microscopic structures and hyphal modification was reviewed by Talbot (1954 a) and Lentz (1954). Both authors discussed in detail the morphology of the structures found in the fruit-bodies and hymenia of the Hymenomycetes, their origin and probable functions. Many examples were cited and misconceptions in the terminology corrected.

The application of hyphal characters and characters of microstructures by different workers to the taxonomic problems of the Hymenomycetes, has thus met with varying degrees of success. The concept of hyphal systems has been rejected by some and enthusiastically adopted by others, but all the workers mentioned here show in some way that hyphal morphology and modifications cannot be ignored in Hymenomycete taxonomy.

Pure Culture Studies

Hyphal morphology and modifications have also been shown to be of basic importance in the recognition of Hymenomycetes in pure cultures. Numerous workers who studied decay of timber have demonstrated that pure culture studies are important diagnostic tools in such work. Certain workers (e.g. Boidin, 1964) also regard pure culture studies to be of great value in taxonomic studies of Hymenomycetes.

Among the pioneers in this field were Long & Harsch (1918) who studied a large number of species in culture and introduced the terms still used to describe the texture of the mat. Fritz (1923) described 18 species, destructive to balsam fir, in detail and indicated the characteristics which should be used in the identification of decay fungi in pure culture. She indicated the importance of microscopic characters. Baxter (1924-1945) made extensive use of cultural characters in his taxonomic studies of resupinate polypores but described micro-morphological characters of the cultures only on rare occasions. Baxter used 2 per cent malt agar at temperatures of 25°C, 30°C and 35°C. Humphrey & Siggers (1933) studied the temperature relations of decay fungi and found that they could be grouped into three groups on the basis of their growth rates at different temperatures.

Bavendamm (1928) observed that fungi which cause white rot, were capable of darkening the colour of media containg gallic acid or tannic acid or other related compounds by oxidation. Species which cause brown rot did not cause darkening of the medium. This observation was later confirmed by Davidson, Campbell & Blaisdell (1938) who referred to this phenomenon as the "oxidase reaction". In a study involving 210 species of decay fungi, these authors found that these fungi could be divided into eight groups on the basis of their reactions when grown on malt agar media containing gallic acid or tannic acid. Of the fungi tested, 166 produced diffusion zones and 36 did not produce diffusion zones on either medium while seven fungi gave inconsistent results. Of the 36 fungi that were negative for extra-cellular oxidase, 30 were associated with brown rots while 151 species out of the 166 that were positive, were associated with white rots. These reactions proved to be useful diagnostic characters in the identification of cultures of decay fungi and were later incorporated by Davidson, Campbell & Vaughn (1942) in their descriptions of cultures of fungi causing decay of living oak in the Eastern United States. In this work, extensive use was made of microscopic characters of the hyphae and other specialized structures in the mat as well as macroscopic appearance of the cultures. These workers also introduced a key in which various characters of the different cultures were expressed by alphabetical symbols. This allowed the incorporation of new species into the key with a minimum of disruption.

Refshauge & Proctor (1936), studied Australian wood-decaying fungi in culture. They found that most of the fungi associated with white rot of timber were also capable of decolourizing certain dyes which had been added to the media. This was also found to be due to oxidation.

Jorgensen & Vejlby (1953) described a method for the preparation of an extract from red cabbage leaves to determine the presence of polyphenol oxidase enzymes in cultures of wood-rotting fungi. Etheridge (1957) suggested the use of meal of white spruce as an indicator medium for the presence of oxidase enzymes in white-rot fungi. More extensive studies of the occurrence and function of oxidase enzymes in wood-rotting fungi were carried out by Lyr (1955, 1963) and Luthardt & Lyr (1965).

The oxidation of phenolic compounds by wood-rotting fungi was reviewed by Käärik (1965) in her extensive study of the oxidation of 20 different phenolic compounds by a large number of decay fungi in pure culture. By applying drops of alcoholic solutions of the phenolic compounds to growing cultures of the fungi she found that four main types of reactions occurred, viz.: (i) production of tyrosinase only; (ii) production of laccase only; (iii) production of both laccase and tyrosinase, and (iv) production of neither laccase nor tyrosinase. On the basis of their reactions the mycelia could be divided into four groups which in turn could be sub-divided according to the intensity of the reactions and specific reactions to specific compounds.

Campbell (1938), in a study of 32 species of *Fomes* in culture, included extensive microscopic details of hyphae and structures formed in culture. The presence or absence of brown diffusion zones around mycelia grown on media containing gallic acid and tannic acid, was used as a diagnostic character in this work also.

Cartwright (1929, 1931), studied decay fungi in pure culture in England. In collaboration with Findlay he later described the cultural characters of many fungi causing decay of soft wood and hard wood trees and timber (Cartwright & Findlay, 1946). Their descriptions, which were devised primarily for the recognition of fungi from decayed timber, include details of microscopic structures, hyphae, physiological data and details of the decay.

A number of workers described wood-rotting fungi in culture from specialized habitats or a single host. Snell (1922) described fungi causing decay of building timber and in cotton mills. Walek-Czernecka (1933) described cultures of fungi from decayed railway sleepers in Poland. Davidson, Lombard & Hirt (1947) described fungi causing decay in wooden boats, while large-brown-spored house-rot fungi in the United States were described by Davidson & Lombard (1953). Earlier, Davidson & Campbell (1943) reported on nine species of decay fungi from black cherry. Robak (1942) described six species of decay fungi from pine in Norway.

A lack of similarity of methods adopted was apparent among these workers. This made it very difficult if not impossible to compare results reported by different authors. An attempt to overcome these difficulties was made by Nobles (1948) with the publication of descriptions of the cultural characters of 126 species of wood-rotting fungi from Canada. For this purpose the topography and colour changes of the mat as well as other macroscopic characters, the reactions on gallic acid and tannic acid media and micromorphological details of hyphae and other structures were combined in the descriptions of the various species. These characters were also reflected in a key for the identification of species, in which a number of characters, both macroscopic and microscopic, were represented by different numerals arranged in 11 vertical columns. This key, like that devised

by Davidson *et al.* (1942), is capable of continued expansion by the incorporation of new species. Later Nobles (1958 a) devised a rapid test for the presence of extra-cellular oxidase enzymes in cultures of decay fungi. By the application of a drop of an alcoholic solution of gum guaiac directly to a culture, the presence of extra-cellular oxidase enzymes is indicated by rapid blueing of the gum guaiac solution. No colour change occurs when the solution is applied to cultures of species that cause brown rots. Parallel tests on 33 species with the gum guaiac solution and the standard Bavendamm (1928) method, in which cultures are grown on malt agar containing gallic acid and tannic acid, gave identical results for nearly 90 per cent of the species. Inconsistent reactions were obtained by both methods from 19 species.

Nobles' methods were adopted by Van der Westhuizen (1958, 1959) for descriptions of South African wood-rotting fungi in culture. Very similar methods were used by Da Costa, Matters & Tamblyn (1952) for their descriptions of Australian wood-rotting basidiomycetes in culture.

Studies of pure cultures have been used by various workers to distinguish between species with morphologically similar carpophores. In many cases inter-collection pairing of mycelia each derived from a single basidiospore, a technique pioneered by Bensaude (1918), Vandendries (1922, 1923) and Kniep (1928), has been employed to enhance and confirm the results obtained from pure culture studies. The formation of hyphae with clamp connections when clampless mycelia each derived from a single basidiospore, are grown together in pairs, is regarded as positive proof of conspecificity of the mycelia and consequently of the spores and carpophores from which they were obtained. By using this method Mounce & Macrae (1936) showed that *Lenzites sepiaria, Lenzites trabea* and *Trametes americana,* which have very similar carpophores, are indeed three distinct species, while *Lenzites thermophila* is conspecific with *Lenzites trabea* because mycelia from single basidiospores from carpophores assigned to these two species, were interfertile. Later Mounce & Macrae (1937) found that no clamp connections formed when monosporous mycelia of *Fomes roseus* and *Fomes subroseus* were paired thus confirming the validity of the two species, which differ further in respect of spore shape and other minor characters of the carpophores. Nobles (1943) showed by this method that different cultures isolated from decay in pines were identical to those derived from a carpophore of *Poria microspora* and distinct from those of *Trametes serialis* which had been considered to be the cause of the decay. More recently, studies of cultural characters, including in most cases tests for interfertility, were used by various workers to solve taxonomic problems in Hymenomycetes. Among these were Bose (1952) and McKay (1959) with studies of *Polyporus cinnabarinus* and *Polyporus sanguineus*; McKeen (1952) with studies of three species of *Peniophora*; Nobles, Macrae & Tomlin (1957), various species of polypores; Harmsen, Bakshi & Chowdhury (1958) with two species of *Merulius*; Sarkar (1959) with six species of *Coriolellus*; Davidson, Lentz & McKay (1960) with *Stereum* spp. causing pecky cypress; Denyer (1960) with two species of *Flammula;* Harmsen (1960) with *Merulius* spp.; Weresub & Gibson (1960) with *Stereum pini;* Aoshima, Lentz & McKay (1961) with *Stereum taxodii;* Boidin & Des Pomeys (1961) with various resupinate homobasidiomycetes; Lombard, Davidson & Lowe (1961) with *Fomes ulmarius* and *Poria ambigua;* Nobles & Frew (1962) with *Pycnoporus*; McKay (1962) with *Polyporus palustris* and other brown rot species: Lombard & Gilbertson (1965, 1966) with various *Poria* spp.; Macrae & Aoshima (1966) and Macrae (1967) with *Hirschioporus* spp.; Sen & Sehgal (1967) with twelve Indian polypores and McKay (1967) with *Polyporus meliae* and two similar species.

In some of these studies use was made of the "Buller phenomenon" to determine the identity of many of the cultures studied. Buller (1931) showed that a large monokaryotic mycelium of *Coprinus lagopus* was dikaryotized rapidly by a small inoculum of dikaryotic mycelium of the same species placed at its periphery. Kawamura (1941) showed that a haploid mycelium of *Polystictus sanguineus* could be dikaryotized by mating with a theoretically incompatible dikaryotic mycelium, produced by mating two haploid mycelia, neither of which was compatible with the test haploid mycelium. Terra (1953) summarized the literature on the "Buller phenomenon" and reported similar dikaryotization of a large haploid mycelium by small dikaryotic mycelia with *Schizophyllum commune*, *Leucoporus brumalis*, *Cytidia flocculenta*, and *Panus stipticus*. In these cases the haploid and dikaryotic mycelia were obtained from carpophores of the same species but collected in different regions. Boidin & Des Pomeys (1961) used this method in a study of certain species of resupinate Homobasidiomycetes. Nobles & Frew (1962) though that the "Buller phenomenon" could be a valuable tool for the confirmation of identification of cultures if it could be repeated with most species of the Hymenomycetes. In their study of the genus *Pycnoporus* Karst. these authors examined 103 cultures from many parts of the world. The identity of 57 isolates was confirmed by means of mating tests between single spore cultures while 46 isolates were identified by means of the "Buller phenomenon". Three types of reactions were observed, viz.: (i) a positive reaction in which the haploid test colony, originally composed of hyphae with simple septa, was converted to the dikaryotic condition, as shown by the presence of hyphae with clamp connections around the periphery; (ii) a negative reaction in which the haploid test fungus continued to grow in the haploid condition whilst the dikaryotic inoculum grew to produce a sector distinguishable by difference in colour or texture or growth rate, and (iii) a negative reaction in which the dikaryotic inoculum failed to grow; the test fungus grew around it, without dikaryotization taking place. By means of these tests, the isolates of *Pycnoporus* Karst. were divided into three groups of interfertile isolates. These three groups also exhibited similarities in cultural characters and carpophore morphology and anatomy within each group. The authors were thus able to distinguish between the three species of orange-red polypores which had originally been described under the specific epithets of *Polyporus cinnabarinus* Jacq. ex Fr., *Polyporus coccineus* Fr. and *Polyporus sanguineus* L. ex Fr. Van der Westhuizen (1963) used the "Buller phenomenon" to confirm the conspecificity of eight collections of *Cerrena unicolor* (Bull. ex Fr.) Murr., a white rot fungus which has the bipolar type of interfertility. Studies with pure cultures are thus valuable tools in taxonomic studies of the Hymenomycetes.

After extensive studies with pure cultures, Nobles (1958 b) presented a guide to the taxonomy and phylogeny of the Polyporaceae on the basis of their micromorphological characters and oxidase reactions in culture. In a study of 212 species, evidence was provided that the family is composed of two main groups: a primitive group consisting of species that produce no extra-cellular oxidase and, if heterothallic, show the bipolar type of infertility; and a more advanced group made up of species that produce extracellular oxidase and if heterothallic, show the tetrapolar type of infertility in those species whose hyphae are regularly nodose-septate and a third, intermediate and minor group of species in which the advancing hyphae are simple-septate but the older hyphae become nodose-septate, and which also display the bipolar type of infertility. Within each group, species were arranged in smaller groups on the basis of their hyphal characters in culture and basidiospore characters. In this way a total of 36 groups of species resulted. Some of these groups appear to represent natural taxa while others appear to require further sub-divisions suggesting supra-generic grouping, but whether homogenous or not, the groups can be arranged in the order of increasing complexity

of their hyphal structures to form a sequence suggesting their phylogenetic development. Nobles warned however that these groups can be accepted as representing natural taxa only if the cultural characters used in the segregation and arrangement of the species have recognizable counterparts in the carpohores of these species. The evaluation of the taxonomic significance of the groups thus requires correlated studies of the micromorphological characters of carpophores and cultures of the species in each group Later Nobles (1965) again presented these views in a diagnostic key with brief descriptions of 149 species of wood inhabiting Hymenomycetes devised primarily for their recognition in culture.

Some important facts are evident from Nobles' work viz.: (1) there is little correlation between cultural characters and morphology, on the one hand and morphology and hymenial configuration of the carpophores, the traditional bases for generic delimitation, on the other; (2) hyphal characters such as septation and modification, in combination with spore characters, are regarded as of supra-generic or generic importance; (3) despite statements to the contrary by Whitehouse (1949) and Raper (1953, 1954) strong evidence is presented in favour of the view that the type of infertility is constant for each genus of the Polyporaceae; (4) the absence or presence of extra-cellular oxidase in culture is of prime phylogenetic importance; and (5) divisions between groups are based on a complex of characters. In a critical review of the most recent systems of classification of the Polyporaceae, Bondartzeva (1961) commented favourably on Nobles' views which she regarded as a sound approach to the development of a phylogenetic system of classification. Lowe (1963 a) did not agree with Nobles' views. He believed that the Hymenomycetes with short-lived fructifications composed of thin-walled, nodose-septate hyphae, are the more advanced species. He saw a parallel in the flowering plants, where fast-growing herbaceous annuals with resistant seeds are regarded as more advanced than woody perennials.

Studies in which structures found in culture were correlated with those of the carpophores as suggested by Nobles (1958 b), have since been undertaken by various workers. Sarkar (1959) studied six species of the genus *Coriolellus* Murr. which were all found to be similar in cultural characters and carpophore morphology. These six species which cause brown rots, do not produce extra-cellular oxidase enzymes in culture. Five of them were shown to have the bipolar type of infertility while one, *Coriolellus malicola,* was found to be homothallic. Sarkar showed tha ttaxonomically important characters found in cultures were also present in the corresponding carpophores from which the cultures were made.

Nobles & Frew (1962) in an exhaustive study of the orange-red polypore genus, *Pycnoporus* Karst., presented cultural, morphological and genetical evidence in support of the recognition of three species in this genus. All three species cause white rots of both hardwood and coniferous trees. The authors showed that hyphae, similar to those found in culture, are also present in the carpophores. Basidia and basidiospores too, were alike in both the cultures and carpophores but iodia which were present in most cultures were not found in the carpophores.

Van der Westhuizen (1963) showed that the thick-walled as well as thin-walled hyphae of *Cerrena unicolor* (Bull. ex Fr.) Murr. have clamp connections at the septa in both the cultures and fruit-bodies. This fungus differed in this respect from the type species of the different genera to which it had been referred.

Farinha (1964) described the characters of the hyphae from carpophores and cultures of 30 species of polypores according to the methods of Pinto-Lopes (1952). She concluded that the microscopal characters of the secondary hyphae of the carpophores and those from cultures of the same species are identical. This

also applied to some kinds of tertiary hyphae, but other forms of growth were apparently lacking in culture. She thought that a large number of species should be studied in detail before a general terminology for the different types of hyphae could be devised. Such a terminology should take the different forms of growth of the hyphae, throughout the life cycle, into consideration and should be applicable to hyphae from the carpophores as well as from cultures on artificial media.

Lombard & Gilbertson (1965) described the cultural characters and carpophores of 14 species of *Poria* with negative or weak oxidase reactions. These species displayed different hyphal characters but in most species the hyphae present in the cultures were also present in the carpophores. Only in those species in which nodose-septate hyphae with irregularly thickened walls were present in the cultures, were those hyphae not found in the carpophores as well.

It thus appears that most of the structures formed in cultures, may also be found in the carpophores. A statement to this effect had been made by Pinto-Lopes (1952) but was not supported by any evidence at that time. It must however be determined whether this is true for all species of Hymenomycetes and whether some of the hyphal modifications described in cultures, such as cuticular cells and hyphae with interlocking projections, are also present in the carpophores of the relevant species and, finally, whether the relationships indicated by cultural characters can also be demonstrated to exist between the fruit-bodies.

3. MATERIALS AND MEHODS

Materials

Culture media:

1.25 per cent Difco malt agar;
1.25 per cent Difco malt agar + 0.5 per cent tannic acid;
1.25 per cent Difco malt agar + 0.5 per cent gallic acid.

Extra-cellular oxidase enzyme test solution:

0.5 gm gum guaiac in 30 cc of 96 per cent alcohol, (Nobles, 1958 a).

Mounting media for microscope preparations:

5 per cent aqueous KOH solution (Talbot, 1951);
1 per cent aqueous phloxine solution (Talbot, 1951);
Lactophenol (Smith, 1960).

Specimens for study:

Dried fruit-bodies from the following herbaria were examined: National Herbarium, Mycological Collection, Pretoria (PRE); P. A. van der Bijl Herbarium, University of Stellenbosch (STE); Canada Department of Agriculture, Mycological Herbarium, Ottawa, Ont. (DAOM); New York Botanical Gardens, New York, (NY); Royal Botanic Gardens, Kew, England, (K); Farlow Herbarium of Cryptogamic Botany, Cambridge, Mass., U.S.A. (FH).

Abbreviations of these herbaria are according to Lanjouw & Stafleu (1964).

Fresh, living fruit-bodies were collected at random in different localities, as indicated in the descriptions of different species, in Canada and South Africa.

Cultures were available for study from the collections in the Mycology Section, Department of Agricultural Technical Services, Pretoria and the Mycology Section, Plant Research Institute, Canada Department of Agriculture, Ottawa.

Methods

Cultural characters were studied by growing the different fungi on 1.25 per cent Difco malt agar plates. Agar was poured to a depth of about 4 mm into 90 mm petri dishes for this purpose and the plates were inoculated at the side. Four to six plates were made of each isolate. The cultures were incubated at room temperature, 72° — 76°F, in the dark for six weeks. Cultures were examined macroscopically and microscopically at weekly intervals and details of texture, colour and topography were recorded. Details of micromorphological characters of structures from different parts of the mycelial mat, mounted in a mixture of equal parts of KOH solution and phloxine solution (Talbot, 1951) or lactophenol and examined with the aid of the high dry and oil immersion lenses, were recorded and illustrated by means of camera lucida drawings and photomigrographs according to methods described by Nobles (1948) and Van der Westhuizen (1958).

The production of extra-cellular oxidase enzymes by the growing mycelia were detected either by the application of a drop of alcoholic gum guiacum solution to the growing mycelium, (Nobles, 1958 a) or by growing the fungi on plates of malt agar containing 0.5 per cent gallic acid and 0.5 per cent tannic acid for seven days (Davidson, Campbell & Blaisdell, 1938). The appearance within a few minutes of a blue colour in the gum guaiacum solution and dark coloured zones in the malt-gallic acid and malt-tannic acid media, presented positive proof of the production of extra-cellular oxidase enzymes by the fungus under test.

Cultures of single basidiospores were obtained by suspending freshly collected fruit-bodies in damp chambers. Under these conditions basidiospores were shed on sterile glass slides placed under them. The spores were then suspended in sterile water. Small quantities of this suspension, (about 1 ml) were poured over malt agar plates which were incubated for about 24 hours. Afterwards, single germinating spores were picked off under a dissecting microscope by means of a sterile inoculating needle and transferred to malt agar slants. The absence of clamp connections on the mycelia which developed from these spores, was regarded as an indication that they originated from single spores.

The type of interfertility of individual species was determined by mating pairs of inocula from single basidiospore cultures on malt agar slants. For this purpose 16 cultures, each grown from a single basidiospore obtained from one carpophore, were used. Inocula from these single spore cultures were placed in pairs, about 15 mm apart on malt agar slants and incubated until the mycelia developing from them met and mingled on the slant. Inocula from each set of 16 single basidiospore cultures were mated in this way in all possible combinations. After incubation the resultant mycelia on these slants were examined microscopically for the presence of clamp connections which would indicate compatible mating types in the parent single basidiospore mycelia. The results were plotted in a pairing table, as illustrated by Macrae (1967) among others, but are presented here in the abbreviated form used by Yen (1950), Nobles, Macrae & Tomlin (1957) and Nobles & Frew (1962).

Pairings between different isolates of species for which single basidiospore cultures were available, were made by mating three or four single spore mycelia from each collection in all possible combinations in the way described above. The formation of clamp connections on the resultant mycelia was regarded as positive proof of the conspecificity of the collections from which the single spore cultures were obtained.

When single spore cultures were not available for all collections examined for each species, attempts were made to determine conspecificity of the collections by

dikaryotizing a large monokaryotic mycelium with a small dikaryotic mycelium placed at the periphery of the growing monokaryotic colony, according to the "Buller phenomenon" as described by Buller (1931), Terra (1953), Boidin & Des Pomeys (1961) and Nobles & Frew (1962). The appearance of clamp connections on the peripheral hyphae of the monokaryotic mycelium within four to seven days after contact between the growing mycelia, was regarded as positive proof of genetic compatibility of the two mycelia and hence conspecificity of the two collections involved.

To study the anatomy and hyphal morphology of the carpophores, thick radial-longitudinal sections were cut from them and examined as described by Teixeira (1956). Small portions about 5 x 2 x 1 mm were removed from different parts of these sections at the margin, the upper surface, upper and lower context, tubes and stipes when present, and soaked in a mixture of equal parts of KOH and phloxine. With the aid of sharpened sewing needles, these portions were then gently teased out and dissected by transmitted light under 25 x magnification of a dissecting microscope to obtain undamaged hyphae and other micro-structures for examination. Excess material was removed from the slide and the dissected parts were covered with a coverslip and examined in the KOH-phloxine mixture with the aid of the oil immersion lens. Both fresh and dried fruit-bodies were examined in this way.

Radial-longitudinal sections of fruit-bodies were also cut with the aid of a freezing microtome at a thickness of 15μ and mounted in lactophenol or the KOH-phloxine mixture in order to study the relationships and orientation of hyphae in the carpophores.

The hyphal characters of both cultures and carpophores were described in accordance with Nobles' (1948, 1958 b, 1965) terminology, but terms proposed by Corner (1932 a), Teixeira (1962 b) and Donk (1964) were also used.

All colours in quotation marks are according to Ridgway (1912).

The description of each species given below, was compiled from examination of all the specimens cited for that species. Collections of which the cultures were also examined, are indicated by an asterisk (*) placed before the herbarium number. All the sets of drawings were similarly compiled from drawings of structures from the different collections.

4. KEY TO GROUPS OF SPECIES STUDIED

In the following descriptions of species studied, the species are placed in groups based mainly on their cultural characters, as proposed and numbered by Nobles (1958 b). A key to these groups is given below:

1. Extra-cellular oxidase reaction in culture negative 2
1. Extra-cellular oxidase reaction in culture positive 5
2. Only thin-walled, nodose-septate hyphae formed in culture 3
2. Thin-walled, nodose-septate hyphae and fibre hyphae formed in culture 4
2. Thin-walled, nodose-septate hyphae, fibre hyphae and nodose-septate hyphae with irregularly thickened walls formed in cultures ..... Group 25
3. Basidiospores subglobose to ovoid ..... Group 7
3. Basidiospores allantoid ..... Group 9
4. Mycelial mat in culture white ..... Group 18
4. Mycelial mat in culture brownish ..... Group 13

5. Mycelial mat consisting of thin-walled, nodose-septate hyphae only Group 32
5. Mycelial mat consisting of thin-walled, nodose-septate hyphae and fibre hyphae Group 45
5. Other special structures present in the mat besides thin-walled, nodose-septate hyphae and fibre hyphae 6
6. Cuticular cells also present Group 51
6. Hyphae with irregular or interlocking projections present as well Group 53

5. DESCRIPTIONS OF SPECIES

5.1 Group 7

Cultures of species in this group form white mycelial mats which do not produce extra-cellular oxidase enzymes; their thin-walled hyphae have simple clamps at the septa, do not form thick-walled, aseptate fibre hyphae and rarely form chlamydospores. Their basidiospores are globose, ovoid or ellipsoidal. Their interfertility is of the bipolar type with multiple allelomorphs for heterothallism at one locus only.

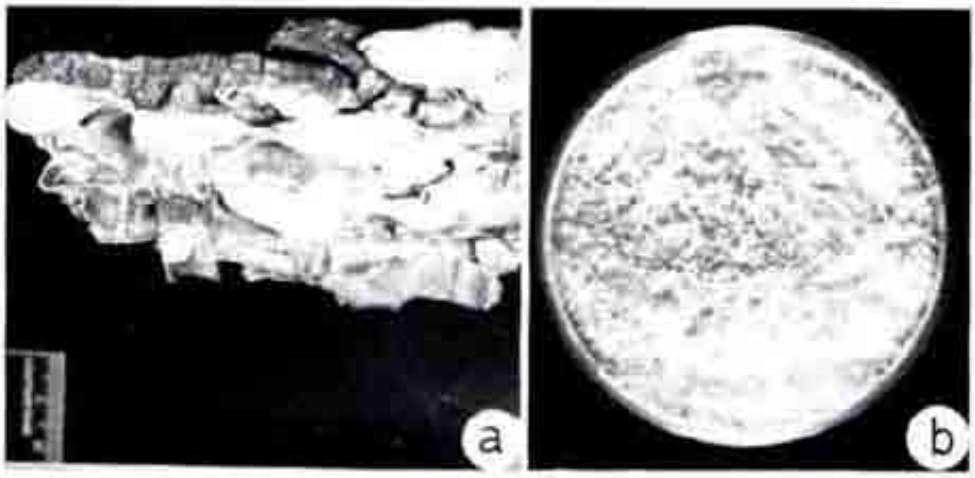

Fig. 1 **Polyporus adustus.** (a) Carpophores of DOAM 53500; (b) culture of PRE 42039 at six weeks.

Polyporus adustus *Willd. ex. Fr.*, Syst. Myc. 1, 363, 1821;

Boletus adustus Willd., Fl. Berol., p. 392, 1787;

Bjerkandera adusta (Willd. ex Fr.) Karst., Medd. Soc. Fauna Fl. Fenn. 5, 38, 1879;

Leptoporus adustus (Willd. ex Fr.) Quel., Ench. Fung., p. 177, 1886;

Gloeoporus adustus (Willd. ex Fr.) Pil., Atl. Champ. Eur., III, (I), 157, 1936.

Cultural characters

Growth is fairly rapid, the plates being covered in two to three weeks. The advancing zone is even, with hyphae raised and extending to the limit of growth. Mat at first white, loose, thick, cottony to woolly over large areas but soon forming a zone of pale "cream-buff" colour about half-way across the plate where the mycelium appears more compact and tends to agglutinate in strands forming a vague network over the surface of the agar. Mat remains white, raised, but after four weeks collapsing in the pockets of the network and becoming more appressed felty, assuming a dirty white colour. The network of agglutinated hyphae increases slowly in extent and darkens in colour to "pale ochraceous buff," while irregular, rounded, lumps of compact, felty mycelium ranging in colour from "tilleul buff" to "avellaneous" or "Dresden brown" may form along the sides of the dish, becoming poroid later. At six weeks the mat may be appressed, thin, felty, pellicular for some distance around the inoculum, raised in the darker areas, but collapsed elsewhere with small patches of thin, white, felty, mycelium similar to that around the inoculum, appearing on the agar surface. Odour faint to fairly strong, unpleasant mushroomy. Reverse is bleached. Oxidase reaction with gum guaiac is variable being either negative or weakly positive to strongly positive in one case. On gallic acid and tannic acid media, no growth or a trace of growth may take place but no diffusion zones are produced. Reactions observed from different isolates are tabulated in TABLE I.

Advancing mycelium: hyphae hyaline, thin-walled, branching at or near the septa, nodose-septate with deeply staining contents and often with short, repeatedly branched lateral branches submerged in the agar, 2.5 — 4.0μ in diameter, (Fig. 2a).

Aerial mycelium: (a) hyphae hyaline, thin-walled, nodose-septate, branching at the septa as in the advancing zone, 2.0 — 4.5 μ (Fig. 2 a); (b) nodose-septate hyphae as in (a) but with walls somewhat thickened and tending to be refractive or occasionally solid, 3.0 — 5.2μ in diameter. In coloured areas similar hyphae are numerous but with the contents dark-coloured, often with simple septa present as well or, in parts, without contents (Fig. 2b); (c) narrow, hyaline hyphae, repeatedly branched and tapering to slender tips 0.4 — 0.6μ in diameter arise from thin- or thick-walled nodose-septate hyphae and become tightly interwoven to form the tough, pellicular patches on the agar in some isolates (Fig. 2c); (d) oidia hyaline, elongate, ovoid, cylindrical or irregular, thin-walled 3.0 — 9.0μ x 2.0 — 3.0μ very numerous in some isolates (Fig. 2d); (e) chlamydospores intercalary and terminal, ellipsoid, ovoid, thick-walled, with staining contents 7.0 — 13.0 x 4.5 — 9.0μ wide, found in two isolates (Fig. 2e).

Fructifications: composed of nodose-septate hyphae with slightly thickened walls as in (b), tightly interwoven and with dark coloured contents, 2.5 — 3.5μ in diameter; basidia arising on these hyphae, small hyaline, ovoid to narrowly clavate, with 4 slender, straight sterigmata, 11.0 — 15.0 x 4.0 — 5.5μ, sterigmata 2.0 — 2.5μ; spores hyaline, smooth ovoid or ellipsoid, thin-walled, with a small apiculus 3.0 — 3.6 x 2.4 — 3μ (Fig. 2f).

Submerged mycelium: hyphae hyaline, nodose-septate, walls slightly thickened, often with a number of small lateral branches arising close together (Fig. 2g).

Carpophore characters.

Carpophore annual, lignicolous, grouped or occasionally compound, sessile, effused-reflexed to almost entirely resupinate, occasionally dimidiate; pileus applanate, flabellate or spathulate often imbricate and laterally connate, soft, somewhat spongy when fresh drying to hard, rigid, 1.5 x 3 — 10 x 0.1 — 0.8 cm; surface

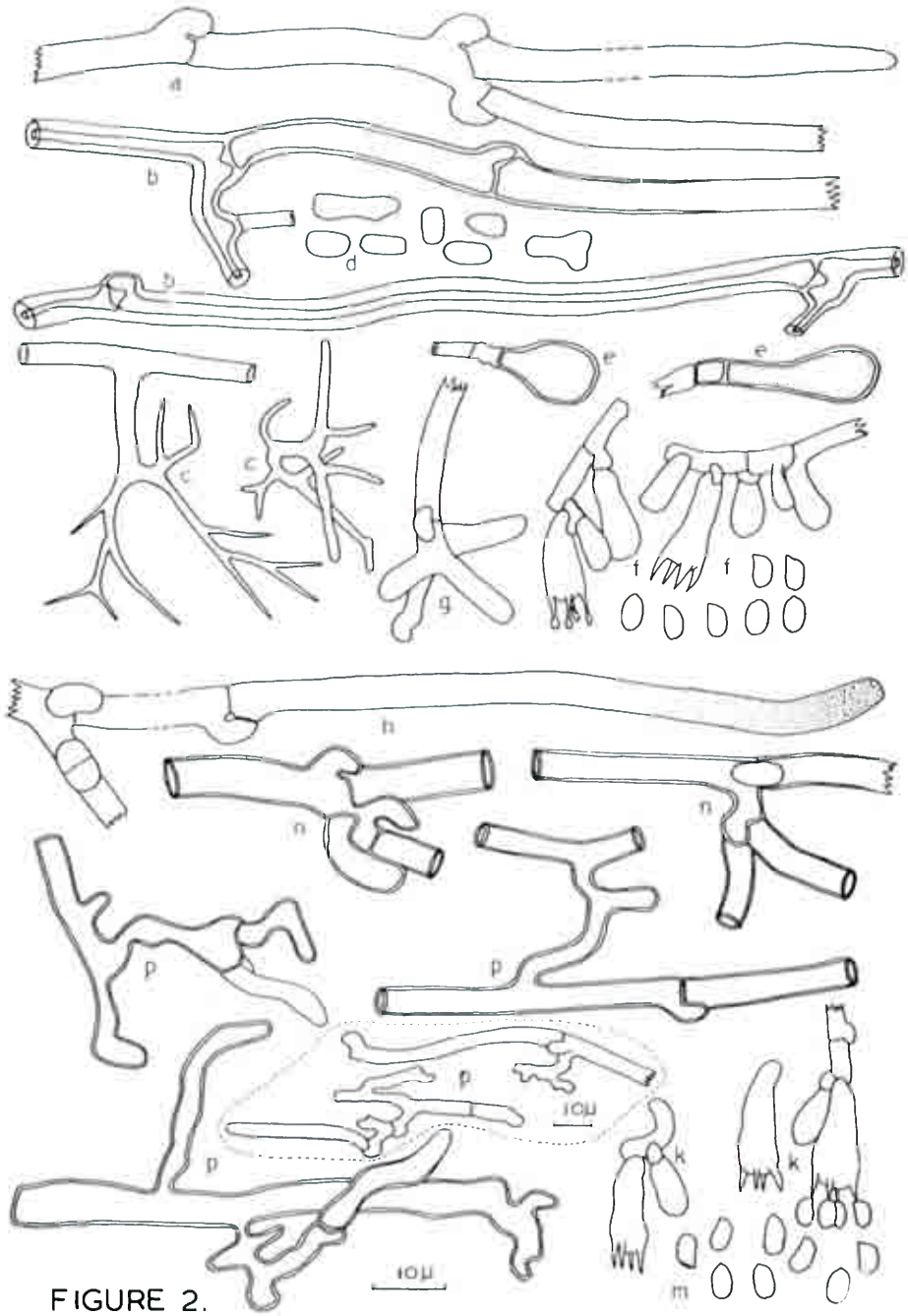

FIGURE 2.

Fig. 2.— **Polyporus adustus.** a - f. Hyphae and structures from cultures: (a) thin-walled, nodose-septate hyphae from advancing zone; (b) thick-walled, nodose-septate hyphae; (c) narrow, branching hyphae; (d) oidia; (e) chlamydospores; (f) basidia and spores; (g) submerged hypha with lateral branches.
h - p. Hyphae and structures from carpophores: (h) thin-walled, nodose-septate hypha with dark-coloured contents; (k) basidia; (m) basidiospores; (n) thick-walled, nodose-septate hyphae from context; (p) nodose-septate context hyphae with lateral, branched, binding processes.

velutinate to somewhat villose, occasionally glabrescent, smooth or concentrically sulcate, pale creamy white when fresh often with a faint blueish tint, drying to smoky grey, cinereous or pale tan; margin acute, thin, entire, occasionally lobate, concolorous or slightly darker and drying to black, sterile below for 1 — 2 mm; pore surface grey to greyish black or darker where bruised, drying to dark brownish grey; pores angular, minute 4 — 7 per mm; dissepiments even or somewhat irpicoid, tubes concolorous, in one layer, up to 2 mm deep; context white or nearly so, often ochraceous 1 — 6 mm thick, azonate or occasionally with a dark zone and with a brown or blackish line above the tubes and extending into the dissepiments.

Hyphal characters: hyphae nodose-septate, more or less straight or flexuous to tortuous, branching at or near the septa, the branches more or less straight or flexuous to very tortuous, walls hyaline or faintly coloured, thin, or variously thickened with contents hyaline or dark brown, 1.8 — 5.0μ diameter (Fig. 2h).

Hymenium: basidia short, broad clavate to narrow ovoid 11.0 — 15.0 x 4.0 — 5.5μ with 4 slender, straight sterigmata 2.0 — 2.5μ long and borne in clusters on the short, thin-walled, terminal and sub-terminal cells of the tortuous hyphae of the dissepiments (Fig. 2k); basidiospores ellipsoidal to ovoid, hyaline, smooth, thin-walled, with a small apiculus, 3.0 — 3.6 x 2.4 — 3.0μ (Fig. 2m).

Construction. At the margin, the pileus consists of branching, thin-walled, nodose-septate hyphae intertwined and extending to the extreme edge. Contents of some hyphae are dark-brown imparting the dark edge to some pilei (Fig. 2h). The upper context consists of hyaline, nodose-septate hyphae with walls only slightly thicker than in the margin or with walls much thickened, clamp connections conspicuous, branching at or near the septa 2.8 — 4.75μ in diameter (Fig. 2n). These adhere together in strands running parallel to or inclined upward from the direction of growth of the pileus. Individual hyphae bend away from these strands to join others so that an open lattice-like structure is formed. Hyphae from the context project upward to a common level forming the upper surface, where they are agglutinated by a faintly brownish, laquer-like substance into small tufts or, the ends free, hyaline, with dark contents or empty, thin-walled, 2.0 — 4.7μ in diameter. The lower context consists of nodose-septate hyphae, as in upper context, with slightly thicker, occasionally almost solid, hyaline walls and dark brown contents, turning downward toward the trama and dissepiments, intertwined and tortuous and narrowing to 1.8 — 3.0μ and walls somewhat thinner. From these, lateral branches arise with numerous septa and conspicuous clamp connections, very tortuous, profusely branched, narrow 1.5 — 3.0μ, tightly binding other hyphae and branches into a smooth, dense tissue (Fig. 2p). The edges of the dissepiments consist of slightly interwoven parallel, hyaline, nodose-septate hyphae 1.8 — 3.0μ in diameter.

Decay and hosts

Polyporus adustus causes a white rot of various species of hard woods (Cartwright & Findlay, 1946; Nobles, 1948).

Specimens examined

* Indicates culture studied as well.

Herb. DAOM: 9209, on *Fagus grandifolia,* Chelsea, Que., Oct. 1937; 10157, on *Thuja occidentalis,* Oakville, Ont., Jan. 1941; *17571, on *Populus tremuloides,* Brule, Alta., Oct. 1947; *17575, on *Ostrya virginiana* stump, Chelsea, Que., Oct. 1947; 17889, on *Populus*

tremuloides, Candle Lake, Sask., Oct. 1959; *22576, on *Populus* sp., Sheep Island, Lake Opinicon, Ont., Sept. 1950; *53500, on hardwood, Pack Forest, Warrensburg, N.Y. Oct. 1959. *Herb.* PRE: 15607, on *Podocarpus elongatus*, Harold Forest, Natal, Sept. 1915; 24859, Kirstenbosch, C.P., June 1929; 30383, on *Fagus sp.*, U.S.D.A., Washington, F. P. 52045; 31420, Stellenbosch, C.P., July 1919; 31462, Stellenbosch, C.P., May 1921; 35949, Oxshott, England, Oct. 1946; *42039, on *Populus* sp. log, Stellenbosch, Aug. 1959; *42328, on hardwood log, Dorset, Ont., Sept. 1962 (DAOM 94016); *42329, on hardwood log, Dorset, Ont., Sept. 1962 (DAOM 94010); *42332, on hardwood log, Dorset, Ont., Sept. 1962 (DAOM 73987); *42350, on dead deciduous tree, Dorset, Ont., Sept. 1962 (DAOM 94014); *42365 on *Acer* sp. log, Packenham, Ont., Aug. 1962 (DAOM 94007).

Interfertility studies

When tested for the production of extra-cellular oxidase in culture, the isolate from South Africa showed a strong positive reaction while some of the cultures of Canadian origin showed no reaction. Nobles (1958 a) reported a similar variable reaction for *Polyporous fumosus* which Overholts (1953) described as closely similar to and at times indistinguishable from *Polyporus adustus*. Nobles (1958 b) further reported *Polyporus fumosus* as having the tetrapolar type of interfertility while *Polyporus adustus* has the bipolar type of interfertility. It was therefore necessary to determine whether the South African isolate was interfertile with other isolates and therefore conspecific with Canadian collections of *Polyporus adustus*. For this purpose four cultures obtained from single spores from the South African isolate PRE 42039, were paired with similar cultures isolated from Canadian collections of *Polyporus adustus*. These single spore cultures were paired in all possible combinations on malt agar slopes. The results are presented in TABLE 2 according to the method of Nobles, Macrae & Tomlin (1957), Macrae (1967) and others.

From the results, it is clear that all the Canadian isolates of *Polyporus adustus* used, were interfertile. The South African isolate only had a low degree of interfertility with the Canadian isolates of *Polyporus adustus*. In three out of a total of 48 pairings numerous clamps were formed. This South African collection differed from the Canadian collection only in respect of the more intense reaction of its culture when tested for extra-cellular oxidase, but was closely similar in all other respects. It can thus be concluded that this South African isolate is conspecific with the Canadian isolates of *Polyporus adustus* but belongs to a different geographical race. The existence of geographical races had been reported by Mounce & Macrae (1938) for *Fomes pinicola*, a species with bipolar interfertility.

Discussion

All hyphae formed in cultures of *P. adustus* are nodose-septate with hyaline walls. Hyphae from various parts of the culture differ only in the thickness of the wall, overall diameter and manner of branching while differentiated hyphae are lacking. Differences in cultural characters between different isolates exist only in the absence or presence of accessory spores and the intensity of the reaction for extra-cellular oxidase when tested with gum guaiac solution.

The narrow, repeatedly branched hyphae in the pellicular patches of the mat of some of the isolates have not been reported before. Chlamydospores were reported from cultures by Cartwright (1931) and oidia by Nobles (1948). Chlamydospores were present in some of the cultures only but oidia were present in all cultures although their numbers varied considerably in the different isolates.

This description of the cultural characters agrees fairly closely with that of Nobles (1948) and earlier descriptions by Bose (1930), Cartwright (1931), Cartwright & Findlay (1946) and Davidson, Campbell & Blaisdell (1938).

Irregularities in the reaction of this fungus when tested for extra-cellular oxidase in culture, have been reported by Davidson *et al.* (1938) and Nobles (1958 a) who found that the reaction may vary from negative to weakly-positive on gallic acid and tannic acid media. Davidson *et al.* (1938) stated that "these fungi may require from 7 to 14 days to form brown diffusion zones but the reactions are always positive." Nobles (1958 a) recorded a strong positive reaction with her gum guaiac test. The results given in Table 1, however, show that no positive reactions were obtained on gallic and tannic acid media even after 14 days and that results with the gum guaiac test also varied from negative to positive. Yet all workers reported that *Polyporus adustus* causes a white rot. Lyr (1955) reported that *Polyporus adustus* were among the 13 species out of 103 wood-rotting fungi tested by him which formed peroxidase in small amounts. Most of those species which formed peroxidase were also able to utilize lignin by oxidation and cause white rots. He thought that the peroxidase could act like laccase, the extra-cellular oxidase enzyme present in most white-rot, lignin-destroying Hymenomycetes, in this respect. It thus seems probable that the weak and erratic reactions observed when *Polyporus adustus* was tested for extra-cellular oxidase may be due to small and varying amounts of peroxidase enzyme formed by different isolates of this species. Differences in the intensity of the reaction when different isolates of 173 species of wood-rotting Hymenomycetes were tested for oxidase enzymes by the application of drops of various compounds, were reported by Käärik (1965).

The above description of the fruit-body of *Polyporus adustus* agrees with that of Overholts (1953) who described the hyphae in the carpophore as "hyaline, considerably branched with cross-walls and clamps, 3 — 6μ in diameter." Teston (1953 b) and Cunningham (1948 b) reported that the carpophores are monomitic and consist of thin-walled, generative hyphae with numerous clamp connections. Pinto-Lopes (1952) and Farinha (1964) stated that the secondary hyphae are hyaline and nodose-septate, while the tertiary hyphae are nodose-septate and with walls never much thickened. Donk (1933), reported that fruit-bodies of this fungus consist of thin-walled, nodose-septate hyphae, more or less parallel in arrangement and forming a loose tissue in the upper part of the trama but closely packed and parallel in the lower part from where hyphae turn downward into the trama of the tubes. Bourdot & Galzin (1928) similarly reported thin-walled nodose-septate hyphae loosely interwoven in the upper context and very compact and closely packed and parallel in arrangement in the lower context. Ames (1913) also reported a difference in the consistency between the upper and lower layers of the context of this fungus but did not describe the morphology of the hyphae. All these descriptions thus agree that the fruit-bodies consist of nodose-septate hyhpae only and have a monomitic hyphal system while most reports by earlier workers agree that the hyphae are arranged more or less in parallel. These descriptions thus imply that the hyphae are all similar in appearance and that the fruit-bodies are simple in construction. From the description furnished above, and illustrations of hyphae, (Fig. 2h, n, p) it is evident that marked morphological differences exist between hyphae from the upper and lower context. Hyphae from the upper context are straight and sparingly branched with the septa far apart while hyphae from the lower context are tortuous, frequently branched and have septa fairly close together, and often lie across the direction of growth. Hyphae similar to those of the upper context are also present in the trama. By their tortuous branching in the lower context, all hyphae are tightly bound into the dense, tough tissue so characteristic of the lower context and trama of *Polyporus adustus*. Differences in the morphology of these hyphae are thus related to differences in the consistency and texture between the upper and lower parts of the carpophore on the one hand and function of the hyphae on the other hand.

Many of the lateral branches of hyphae binding the tissues in the lower context, resemble the binding hyphae described by Corner (1953) in the tissues of *Polyporus sulphureus*, in that they are lateral processes which differ from the parent hyphae solely in the method and extent of branching and in function. They do not resemble the binding hyphae described by Cunningham (1946) which are differentiated, branching, thick-walled, aseptate structures. It is thus clear that there is a diversification of function among the thin-walled, nodose-septate hyphae that make up the fruit-body of *Polyporus adustus*. The fruit-bodies are thus more complex in construction than was evident from previous descriptions. This complex construction may prove to be valuable in taxonomic considerations of this and other monomitic species.

A comparison of the structures formed in culture with those found in the carpophore, shows that in both, all hyphae are nodose-septate, although differences in the thickness of the walls are evident. The thick-walled hyphae found in the carpophore are however of the same type as those of the culture. The narrow, branching hyphae found in the felty, pellicular patches of the mat in culture appear to be homologous to the much branched, tortuous hyphae found in the lower context and trama of the carpophore. Basidia and basidiospores formed in culture are similar in all respects to those of the carpophores. With the exception of chlamydospores and oidia, structures formed in cultures of *Polyporus adustus* are thus present in the carpophores as well.

Polyporus adustus is the type species of the genus *Bjerkandera* Karst. (Cooke, 1959; Donk, 1960), but has also been referred to other genera by various workers. It differs from *Polyporus squamosus* Huds. ex Fr. and *Polyporus tuberaster* Jacq. ex Fr. the lectotypes of the genus *Polyporus* Mich. ex Fr. according to Murrill (1907 a) and Donk (1960), respectively. Carpophores of *Polyporus adustus* do not possess the characteristic thick-walled hyphae with tapering ends which are present in the fruit-bodies of these two species (Corner, 1953; Overholts 1953). Cultures of *Polyporus adustus* lack the dark, skin-like areas consisting of thick-walled hyphae with interlocking projections which characterize cultures of *Polyporus squamosus* and *Polyporus tuberaster* (Nobles 1948, 1958 b). Quélet (1886) placed *Polyporus adustus* in his genus *Leptoporus* and was followed in this by Bourdot & Galzin (1928) but there is uncertainty about the type species of this genus. *Polyporus mollis* Pers. ex Fr. the lectotype selected by Donk (1960), differs from *Polyporus adustus* by having the carpophore composed of "thick-walled, hyaline, sparingly branched hyphae with a few inconspicuous cross walls but no clamp connections" (Overholts, 1953). The identity of *Polyporus epileucus* Fr., the type species selected by Murrill (1903), is confused with that of *Polyporus spumeus* Fr. (Bourdot & Galzin, 1928). Murrill (1903), regarded the genus *Leptoporus* (Quél.), as synonymous with *Bjerkandera* Karst. and was followed in this by Donk (1933), Bondartzev & Singer (1941), and Bondartzev (1953), but a study of descriptions of hyphae by Overholts (1953), Teston (1953 b), and Pinto-Lopes (1952), of species placed in the genus *Leptoporus* by Bourdot & Galzin (1928), revealed many differences in hyphal characters between these species. It thus seems advisable to retain *Polyporus adustus* in the genus *Bjerkandera* Karst. of which it is the type species. The problems concerning its relationship with species of the genus *Leptoporus* Quél. can be solved only after the uncertainty about the type species of that genus had been clarified and its hyphal characters had been carefully studied.

Polyporus adustus cannot be regarded as congeneric with *Polyporus conchoides* Mont., the type of the genus *Gloeoporus* Mont. because it lacks the hymenium which is continuous over the edges of the pores, a characteristic of the genus *Gloeoporus* (Overholts, 1953; Hansen, 1956; Donk, 1960)

5.2 Group 9

The mycelial mats of cultures of species in this group remain white and do not produce extra-cellular oxidase enzymes; their thin-walled hyphae have simple clamps at the septa, do not form thick-walled, aseptate fibre hyphae and rarely form chlamydospores. Their basidiospores are cylindrical or allantoid. Their interfertility is of the bipolar type.

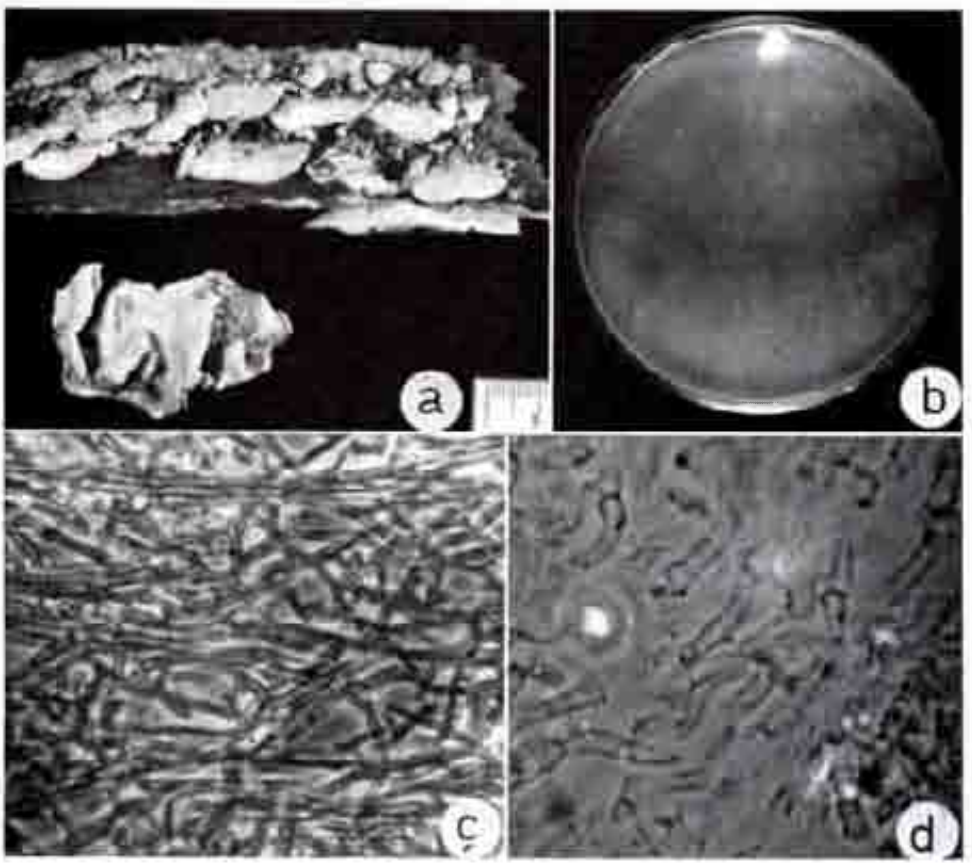

Fig. 3.— **Polyporus dichrous.** (a) Carpophores of PRE 42093 (top) and PRE 42384 (bottom); (b) culture of PRE 42384 at 6 weeks; (c) radial-longitudinal section through carpophore showing nodose-septate hyphae and hyphal strands of context. × 500 phase contrast; (d) delicate, thin-walled, nodose-septate hyphae of tramal layer. × 1000 phase contrast.

Polyporus dichrous *Fr.*, Syst. Myc 1, 364, 1821;
Leptoporus dichrous (Fr.) Quel., Fl. Myc., p388, 188;
Gloeoporus dichrous (Fr.) Bres., Ann. Mycol. 14, 230, 1916.

Cultural characters

The mycelium grows fast to moderately fast covering the plate in two to three weeks. Advancing zone even or slightly bayed, appressed or submerged and difficult to see. Mat hyaline to whitish, mostly submerged, with small, scattered areas of

finely farinaceous to short floccose mycelium developing after four weeks. Reverse remaining unchanged or developing a characteristic greenish-yellow colour after two to four weeks. Odour strong, unpleasant after two or three weeks then diminishing somewhat.

No diffusion zones formed on gallic acid and tannic acid media but trace of growth on the latter after seven days. Oxidase reaction with gum guaiac solution, negative.

Advancing mycelium: hyphae hyaline, branching, nodose-septate, thin-walled, 2.0 — 4.5μ in diameter (Fig. 4a).

Aerial and submerged mycelium: (a) hyphae as in the advancing zone; (b) narrow, hyaline, unbranched, thin-walled hyphae with conspicuous clamp connections and 1.5μ in diameter (Fig. 4b); (c) nodose-septate hyphae occasionally with irregular swellings up to 7.0μ in diameter, between the septa (Fig. 4c).

Carpophore characters

Carpophore annual, lignicolous, sessile, effused-reflexed or often imbricate; pileus 1.5 — 7.0 x 3.0 — 10.0 x 0.1 — 0.5 cm mostly pure white to faintly yellowish and coriaceous when fresh, drying creamy to ochraceous, rigid and brittle; surface velvety-villose to glabrous, azonate, mat when dry; margin entire, acute, concolorous, white, sterile below; pore surface waxy, flesh-coloured to reddish-purple, poroid; pores rounded, or somewhat angular, entire, thin-walled, 5-8/mm; tubes shallow less than 1 mm and hymenial surface separable from pileus as a thin elastic layer; context white, soft fibrous, thin, 1-4 mm.

Hyphal characters: hyphae branching, hyaline, nodose-septate, thin-walled or thick-walled 1.5—8.0μ in diameter (Fig. 4d, e).

Hymenium: basidia cylindrical to narrowly clavate 12.0 — 15.0 x 2.0 — 4.0μ with four short, straight sterigmata 1.5 — 2.0μ, the basidia packed into a tight palisade continuous over the dissepiments (Fig. 4f); basidiospores allantoid, hyaline, smooth, thin-walled 3.0 — 4.0 x 0.7 — 1.0μ (Fig. 4 g).

Construction. At the margin of the fruit-body the hyphae are narrow, 2.2 — 5.0μ in diameter, thin-walled and slightly interwoven parallel to the direction of growth of the pileus. Behind the margin in the upper context the hyphae become thick-walled (sclerified generative hyphae; Donk, 1964), and the branches more divergent and up to 8.0μ in diameter. Here the hyphae tend to form intertwined strands from which individual branches diverge to join adjacent strands thus forming a loose, lattice-like structure (Fig. 3c). Towards the upper surface the strands disappear and the hyphae are divergent, loosely interwoven, their ends thin-walled, free or agglutinated into irregular tufts which form the upper surface. Below this tissue, the loosely arranged, thick-walled hyphae pass rather abruptly into a dense layer, 40 — 80μ thick, of branching, thin-walled, tortuous, nodose-septate hyphae tightly interwoven into a pseudo-parenchymatous tissue. From this layer narrow hyphae 1.5 — 3.0μ in diameter with very thin, delicate walls turn downwards, branch occasionally and run parallel to or lightly intertwined with one another towards the hymenium where they branch profusely to form a narrow, sub-hymenial layer on which the basidia are borne. On the hyphal walls masses of amorphous granules of gelatinous material are deposited so forming the characteristic gelatinous tramal layer 50 — 300μ thick in fruit-bodies of this species (Fig. 3 d).

The small cylindrical basidia are borne on the pseudo-parenchymatous sub-hymenial layer 5.0 — 15.0μ thick formed by the numerous terminal branches of the thin-walled hyphae of the tramal layer. The hymenium is continuous over the edges of the pores.

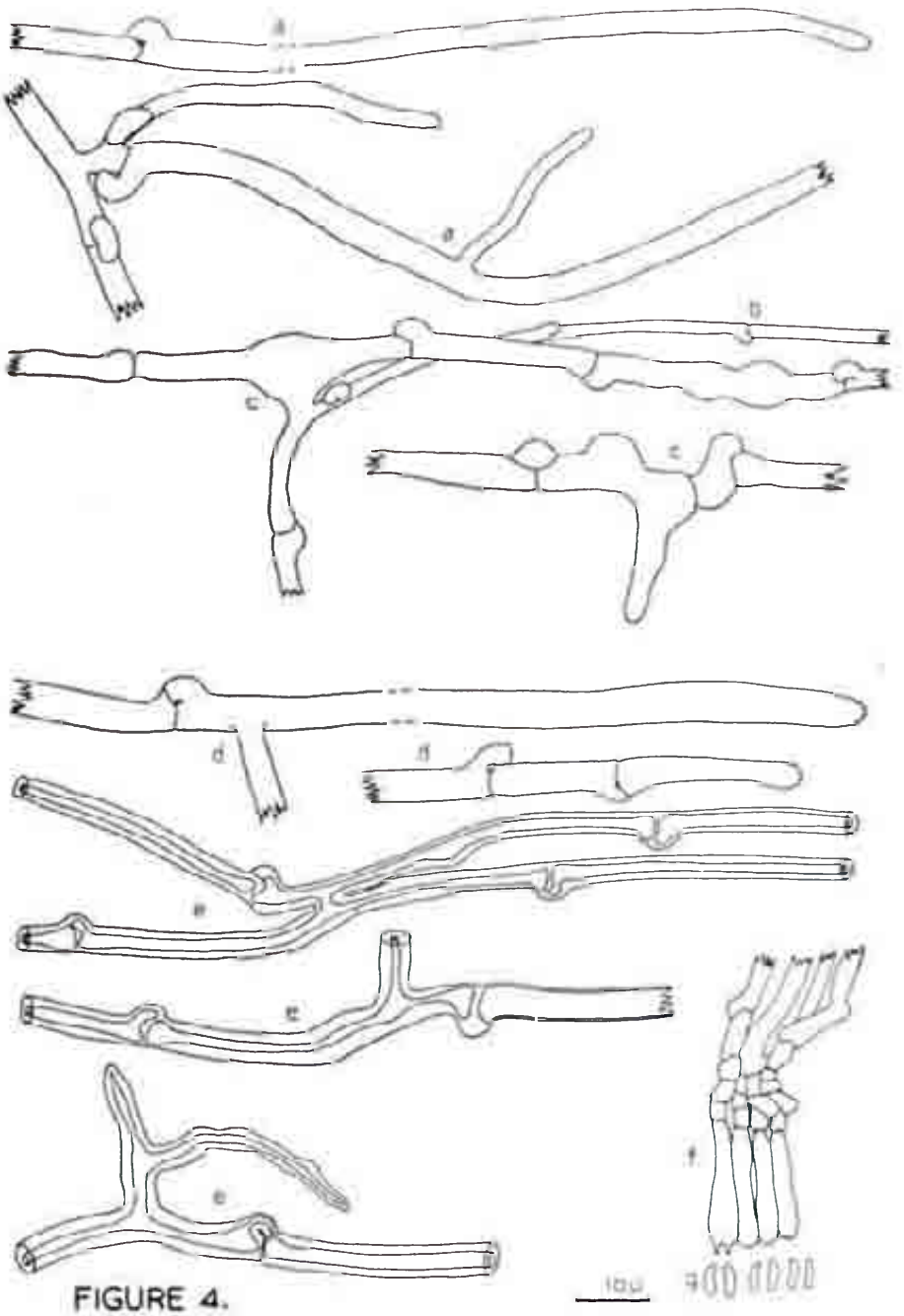

FIG. 4. — **Polyporus dichrous.** a - c. Hyphae from cultures: (a) hypha from advancing zone; (b) narrow, hyaline, unbranched, thin-walled hypha with conspicuous clamp connections; (c) hypha with irregular swellings.
d - g. Hyphae and structures from carpophores: (d) thin-walled, nodose-septate hyphae; (e) thick-walled nodose-septate hyphae; (f) basidia; (g) basidiospores.

Decay and hosts

Polyporus dichrous causes a white rot of angiosperm wood.

Specimens examined

Herb. DAOM: *8118, on *P. contorta* var. *latifolia*, Lumby B.C.; *11609; *22281.
Herb. PRE: 15617, Gingindhlovu, Natal, June 1915; 22285, Mycotheca Boreali Africana No. 349, R. Maire; 23479, Mont-aux-Sources, Natal, July 1928; 27739, on dead wood, Donnybrook, Natal, Jan. 1935; 28924, dead wood, Donnybrook, Natal, Febr. 1935; 30511, on dead wood, Potchefstroom, Transvaal, March 1939; 31602, on dry wood of *Rhus viminalis*, Aug. 1915; 31814, on dead wood, Nottingham Road, Natal Aug. 1917; 40205, Town Bush, Pietermaritzburg, June 1948; 41486, Ex Herb. Wm Bridge Cooke No. 30137; 42093, on dead log, Potgietersrust Dist., March 1960; *42384, on decaying log, Gatineau Park, Que., Sept. 1961; *42436, on decaying log, Barberton, Tvl., May 1960.

Interfertility studies.

Eighteen cultures, each grown from a single basidiospore obtained from a fresh carpophore of PRE 42384, were paired in all possible combinations on malt agar tubes to determine the type of interfertility. It was found that *Polyporus dichrous* has the tetrapolar type of interfertility with allelomorphs for heterothallism at two loci. The results, showing the distribution of mating types among the single spore mycelia, are presented in TABLE 3.

To test the conspecificity of collections of which cultures were available, by means of the "Buller Phenomenon," two mycelia from single spores of opposite mating types of PRE 42384-8 and PRE 42384-10 were used. The method described by Nobles & Frew (1962) in their studies of species of the genus *Pycnoporus* Karst., was used. Seven days after placing the dikaryotic mycelium on plates on which the haploid mycelia were growing, the latter were examined for the presence of clamp connections at the periphery. Results were negative. After five days more, the plates were again examined. No clamp connections had formed on any of the haploid mycelia, which had been inoculated with small dikaryotic mycelia from all the cultures studied of *Polyporus dichrous*.

It thus appears that the "Buller phenomenon" cannot be effectively used for confirming the identity of cultures of *Polyporus dichrous*.

Discussion

This description of the cultural characters of *Polyporus dichrous* agrees closely with those of Davidson *et al.* (1938) and Nobles (1948, 1965). The featureless mycelial mat, the greenish-yellow colour imparted to the agar, the usual lack of extra-cellular oxidase and the thin-walled, nodose-septate hyphae serve to distinguish this species in culture.

Cultures of *Polyporus dichrous* do not give positive reactions when tested for extra-cellular oxidase on gallic and tannic acid media but may give a weak positive reaction with gum guaiac solution (Nobles, 1965). Davidson *et al* (1938), and Nobles (1948) reported that this species causes a white rot. Overholts (1953) stated that the decay associated with it is "usually white, but careful dissection often shows a small amount of definitely brown rot in the vicinity of the sporophores". He thought that the fungus probably causes a brown, carbonizing rot, because of the negative reaction for extra-cellular oxidase. Petersen (1961), reported that this fungus causes a brown rot of deciduous fruit trees in the U.S.A. Käärik (1965) found no reaction when two isolates of *Polyporus dichrous* were tested for oxidative ability of 20 different phenolic compounds. Kirk & Kelman

(1965), found that although cultures of *Polyporus dichrous* gave negative reactions on 9 different phenolic compounds, the fungus caused a white rot of sweet gum test blocks. Extracts made of these blocks contained a phenol-oxidase active against catechol and guaiacol but not 1-napthol. Extracts of cultures of this fungus contained a weak catechol oxidizing agent inactive against guaiacol or 1-napthol. These authors concluded that "inability of certain wood decay fungi to oxidize phenols in agar cannot be assumed to indicate inability to utilize lignin". These observations could explain the erratic results of tests for extra-cellular oxidase by *Polyporus dichrous* and may indicate the presence of oxidation enzymes different from those of many other species of polypores which cause white rot.

The hyphae formed in the cultures were always thin-walled and nodose-septate and resembled those in the margin and gelatinous tramal layer of the fruit-body. Thick-walled, nodose-septate hyphae like those in the context of the fruit-bodies, were seen once in an old culture. These thick-walled, nodose-septate hyphae of the carpophores, are "sclerified generative hyphae" (Donk, 1964) and are formed by internal thickening of the walls of thin-walled, nodose-septate hyphae. The hyphae formed in cultures of *Polyporus dichrous* are thus present in the fruit-bodies as well.

The gelatinous nature of the trama of the pores of *Polyporus dichrous* had been mentioned by many earlier workers (Van der Bijl, 1922 a; Bourdot & Galzin, 1928; Overholts, 1953). The construction of this layer was first described by Hansen (1956) as consisting of hyphae with strongly gelatinized walls. From the present writer's observations it is clear that the gelatinous tramal layer consists of narrow, branched, nodose-septate hyphae with very thin walls which are placed more or less vertically in a loose palisade-like tissue of which the interstitial spaces are filled by a hyaline, amorphous substance (Fig. 3 d). In freshly mounted, radial-longitudinal sections of the fruit-body in KOH-phloxine this substance could be seen as an unstained mass extruded from the section, in the otherwise bright pink colour of the mounting medium. In thin sections mounted in sterile distilled water, this substance could also be seen as a slightly darker mass, oozing out of the tissues, when observed by means of a phase contrast microscope. The thin-walled, tramal hyphae are clearly visible in extremely thin sections of about 5μ or less in thickness. This construction would explain Van der Bijl's (1922 a) observation that the tubes are "separable from the context as a thin elastic layer when moistened."

The hyphae of the fruit-body are all nodose-septate so that this fungus has a monomitic hyphal system as reported by Cunningham (1948 b) and Hansen (1956), but from the above description of the fruit-body, which agrees in most respects with that of Hansen (1956) it is evident that the thick-walled, nodose-septate hyphae of the context support the layer of thin-walled, interwoven hyphae from which the thin-walled, tramal hyphae and hymenium are suspended. These differences in hyphal morphology which is associated with differences of function, result in a much more complex construction of the fruit-body of *Polyporus dichrous* than that of fruit-bodies of species of *Thelephoraceae* which also possess monomitic hyphal systems (Talbot, 1951, 1954 b, 1958 b). Similar differences in morphology and function of hyphae were also found in the carpophores of some other species of poroid Hymenomycetes with monomitic hyphal systems such as *Polyporus adustus* (see previous section) and *Cerrena unicolor* (Van der Westhuizen, 1963).

The gelatinous tramal layer and hymenium which is fertile over the edges of the pores are important morphological characters of the carpophores of *Polyporus dichrous*. These characters are not found in any of the other species in Group 9 (Nobles, 1958 b) and are absent from most species of poroid Hymenomycetes. These

characters are found in species of the genera *Merulius* Hall. ex Fr., and *Gloeoporus* Montagne. The fruit-body of *Merulius tremellosus* Schrad. ex Fr., the type of the genus *Merulius*, also has a gelatinous layer under the hymenium and appears to resemble the fruit-body of *Polyporus dichrous* in construction (Burt, 1917). Cultures of *Merulius tremellosus*, however, were placed by Nobles in her Group 54 (1958 b) together with other species characterized by the presence of simple-septate hyphae in the advancing zone and nodose-septate hyphae elsewhere, a positive reaction for extra-cellular oxidase and the bipolar type of inter-fertility. Another species, *Merulius ambiguus* Berk. which also has a gelatinous layer under the hymenium, (Burt, 1917), differs in cultural characters from *Merulius tremellosus* by forming mycelial mats consisting of thin-walled, simple-septate hyphae, occasionally with multiple clamp connections and a negative reaction when tested for extra-cellular oxidase. *Merulius ambiguus* was placed by Nobles (1958 b) in Group 28, together with other species with similar cultural characters. Some other species, viz., *Merulius lacrimans* Wulf. ex Fr., the type of the genus *Serpula* Pers. ex S. F. Gray, (Cooke, 1959) *Poria incrassata* Berk. & Curt., the type of *Meruliporia* Murrill (Cooke, 1959), and *Poria taxicola* (Pers.) Bres. (Hansen, 1956) all have hymenia which are continuous over the edges of the dissepiments but they lack the gelatinous tramal layer in their fruit-bodies. (Burt, 1917).

No descriptions of the cultural characters of *Gloeoporus conchoides* Mont., the type of the genus *Gloeoporus* Mont., are available but the carpophores of *Polyporus dichrous* and *Gloeoporus conchoides* are so similar in morphology and anatomy that the two species can often be distinguished from each other only by the absence of clamps on the hyphae of the latter species according to Overholts (1953) and Bakshi & Singh (1961). Although this may be regarded as a difference of generic importance between the two species, some genera of Hymenomycetes are known to include species with as well as without clamps on their septate hyphae. Because these two species have so many other characters in common, it seems advisable to include *Polyporus dichrous* in the genus *Gloeoporus* Montagne.

The possession of an hymenium which is fertile over the edges of the dissepiments, excludes *Polyporus dichrous* as well as other species of *Gloeoporus* Mont. from the Polyporaceae. Donk (1964) advanced arguments for the inclusion of this genus together with the genus *Merulius* Fr. and other genera with similar characters in the family Corticiaceae Herter. The observations recorded here support this proposal.

5.3 Group 13

The mycelial mats of cultures of species in this group mostly develop brown, coloured areas due to the presence of brown pigment in the hyphal walls or contents. No extra-cellular oxidase enzymes are produced. The thin-walled hyphae have simple clamp connections at the septa and brown, aseptate fibre hyphae are formed in most of their cultures. Their basidiospores are brown and ovoid or ellipsoid-cylindric in shape. Interfertility is of the bipolar type.

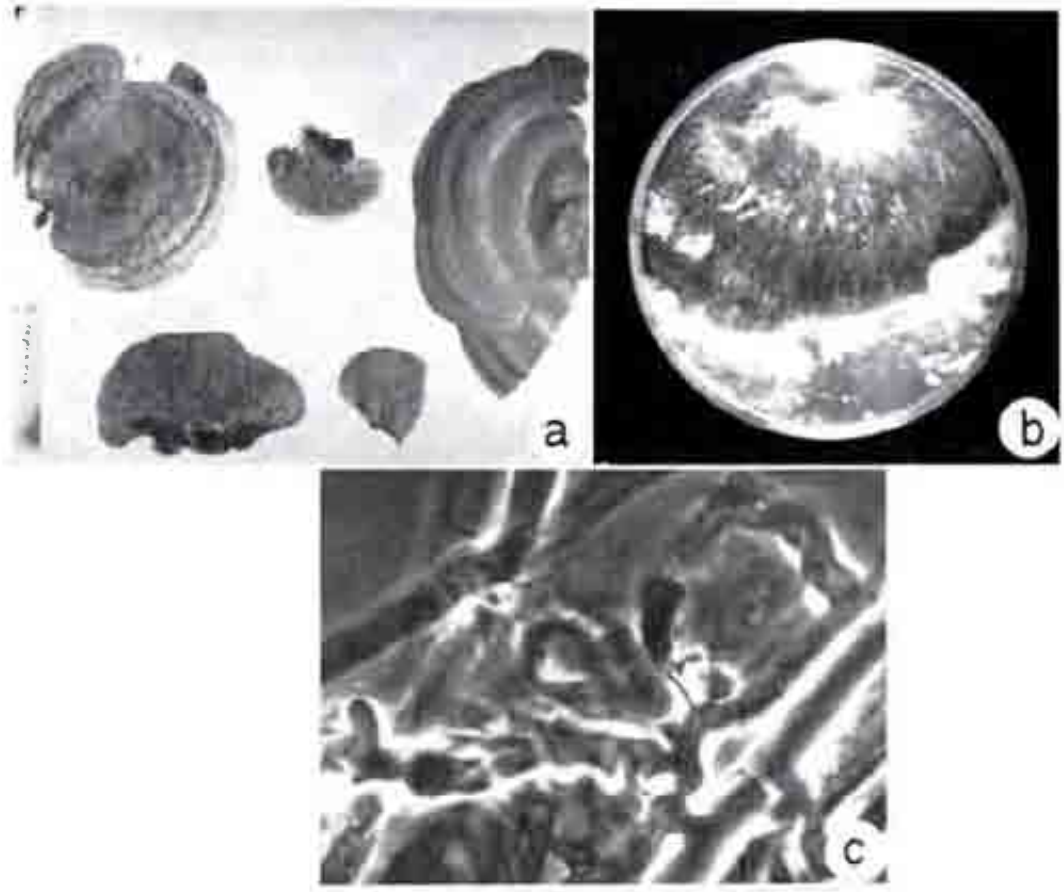

FIG. 5. — **Lenzites saepiaria.** (a) Carpophores of DOAM 22745; (b) culture of DAOM 22443 at six weeks; (c) nodose-septate hypha with lateral outgrowth with spiny projections in culture, × 1000 phase contrast.

Lenzites saepiaria *(Wulf. ex Fr.) Fr.* in Epicr. Syst. Myc. p. 407, 1838;

Daedalea saepiaria Wulf. ex Fr., Syst. Myc. 1, p. 332, 1821;

Gloeophyllum saepiarium (Wulf. ex Fr.) Karst., Finl. Hattso. II, p. 80, 1879.

Cultural characters

Growth moderately fast to slow, the mycelium covering the plate in three to seven weeks. The advancing zone is even; mat thin, appressed, becoming somewhat downy-farinaceous, or downy in younger parts with thin, sub-felty or irregular pellicular areas in the older parts of the mat, some of which may become slightly warted; mat white at first but turning "pale buff" changing to "warm buff" or "antimony yellow" or "honey yellow" to "tawny olive" or "snuff brown" to "umber brown" in patches. Occasionally mounds or ridges of raised, floccose, woolly mycelium appear, white at first, then darkening to "antique brown" or "snuff brown" and often with irregular patches of thin, collapsed mycelium between these mounds. Reverse unchanged or bleaching slowly; odour none or faint,

somewhat spicy. No diffusion zones on tannic acid and gallic acid agar and slight growth only on the latter.

Advancing mycelium: hyphae hyaline, thin-walled, nodose-septate, branching at the septa or from the clamp connections, 2.2 — 5.2μ in diameter (Fig. 6 a).
Aerial mycelium: (a) hyphae as in the advancing zone 2.0 — 3.5μ in diameter; (b) narrow, hyaline, nodose-septate hyphae, repeatedly branched, thin-walled at first, becoming thick-walled to solid, 1.0 — 2.5μ diameter, and with swollen projections or lateral outgrowths with numerous short, spiny projections or lateral outgrowths (Fig. 5c; 6b); (c) nodose-septate hyphae with thickened, brown walls and narrow lumina with staining contents, branching near the septa or from the clamp connections, 2.2 — 4.2μ in diameter (Fig. 6c); (d) fibre hyphae sub-hyaline to pale straw yellow, occasionally branched, walls thickened to sub-solid or solid, aseptate 2.2 — 3.6μ in diameter (Fig. 6d); (e) oidia long cylindrical, hyaline, thin-walled 6.0 — 13.0 x 3.0 — 4.2μ (Fig. 6e); (f) chlamydospores rare, ovoid to subglobose, terminal, 6.0 — 8.0 x 6.0 — 12.0μ (Fig. 6f). *Submerged mycelium:* (a) hyphae as in the advancing zone; (b) nodose-septate hyphae with walls thickened or solid, branched, numerous 1.2 — 3.6μ in diameter (Fig. 6b).

Carpophore characters

Carpophore lignicolous, solitary or grouped, annual or reviving; sessile, usually dimidiate occasionally effused-reflexed; pileus applanate to somewhat convex often laterally connate, occasionally imbricate, coriaceous when fresh, drying to rigid, 1.0 — 10.0 cm x 1.0 — 8 cm x 0.2 — 1.0 cm; upper surface hirsute-tomentose to fibrillose-tomentose or compactly tomentose at maturity, bright yellow-reddish brown to dark ferruginous; margin acute, thin or thick, entire, pale cream coloured to almost orange; pore surface yellowish brown to rusty brown, usually lamellate, occasionally daedaloid or poroid, lamellae often dentate, 0.5 — 1.0 mm apart and 2.0 — 5.0 mm broad; context up to 3 mm thick, umber to chestnut brown, darkening in KOH.

Hyphal characters: (1) nodose-septate hyphae hyaline or pale yellow, thin-walled, occasionally collapsed, branching frequently near the septa or from the clamp connections, 2.0 — 3.0μ in diameter (Fig. 6 g); (2) nodose-septate hyphae with thick, yellow-brown walls, and lumina narrow or solid, 2.5 — 4.0μ in diameter, with occasional thin-walled branches (Fig. 6 h); (3) fibre hyphae long, unbranched or occasionally branched, walls thickened, pale straw yellow to yellow brown with lumina narrow or occluded but widening towards the apex, aseptate or with one or two simple septa near the tip, 2.5 — 4.0μ in diameter (Fig. 6 k); (4) fibre hyphae pale brown, subsolid to solid, repeatedly branched, the branches short or long, flexuous, aseptate 1.5 — 3.0μ in diameter (Fig. 6 m).

Hymenium: basidia long-clavate, hyaline 20 — 32 x 4.0 — 5.0μ with four slender sterigmata 3.9 — 4.8μ (Fig. 6 n); basidiospores cylindrical, obliquely apiculate, hyaline, smooth, thin-walled, 7.0 — 10.0 x 2.0 — 4.0μ (Fig. 6 p); cystidioles fusiform resembling immature basidia but with slightly thicker walls 22.0 — 33.0 x 3.0 — 5.0μ, arising on basidial hyphae and protruding 5.0 — 7.0μ above the basidia (Fig. 6 q).

Construction. At the margin the pileus consists of long, unbranched fibre hyphae, aseptate, their walls partly thickened and sub-hyaline. The fibre hyphae lie parallel to the direction of growth of the pileus, are somewhat intertwined with their ends projecting outward to form the margin. Interwoven with the fibre hyphae and away from the extreme margin are numerous, hyaline, thin-walled, nodose-septate hyphae 2.2 — 3.5μ in diameter branching frequently at the septa or from the clamp connections. Behind the margin in the upper context, the fibre

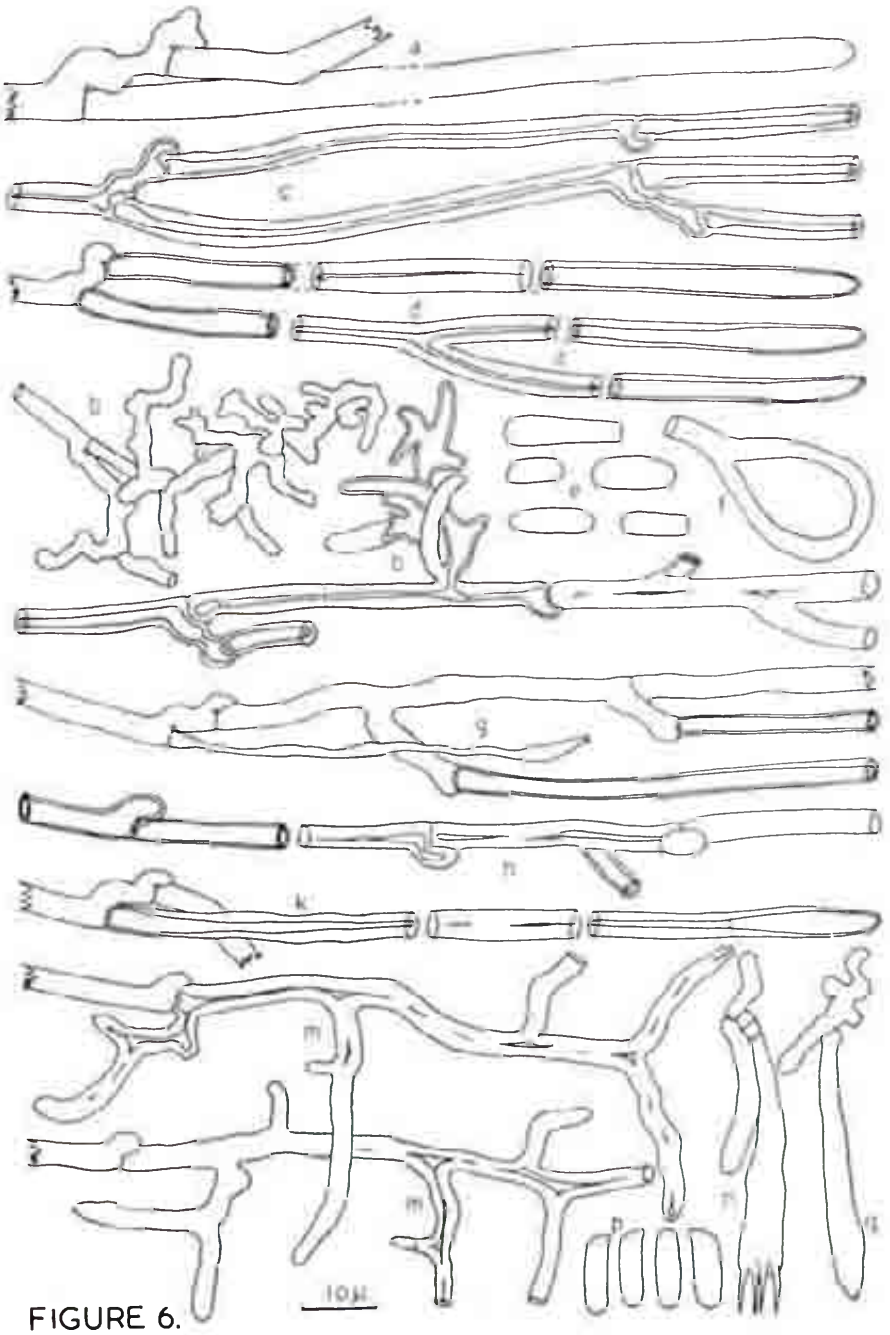

FIGURE 6.

FIG. 6. — **Lenzites sepiaria.** a - f. Hyphae and structures from cultures: (a) nodose septate from advancing zone; (b) nodose-septate hyphae with lateral outgrowths; (c) thick-walled, brown nodose-septate hyphae; (d) fibre hyphae; (e) oidia; (f) chlamydospores.
g - q. Hyphae and structures from carpophores: (g) nodose-septate hyphae; (h) thick-walled, nodose-septate hyphae; (k) fibre hyphae, unbranched; (m) fibre hyphae with short, flexuous branches; (n) basidium; (p) basidiospores; (q) cystidiole.

hyphae have thickened, pale, straw-yellow walls and narrow lumina. They are turned slightly upward towards the upper surface, are somewhat intertwined, 2.5 — 4.0μ in diameter with their tips free and projecting at a common level to form the pubescent, pale-coloured upper surface of the growing margin. Interwoven with these fibre hyphae are nodose-septate hyphae with thin, pale yellow walls, often collapsed, with deeply staining contents and branching freely or forming H-connections. In the dark-coloured part of the context the fibre hyphae are mostly sub-solid to solid, unbranched, 2.5 — 4.0μ in diameter, their walls dark yellow brown, the hyphae somewhat intertwined and turning upwards towards the upper surface of the pileus. At the upper surface these hyphal ends are agglutinated into tufts by a brownish, amorphous substance and bent over towards the margin to form the fibrillose-tomentose upper surface of the mature, dark-coloured part of the pileus. Below this fibrillose-tomentose layer, the fibre hyphae are agglutinated into a trichocutis by a thin layer of pale brownish substance. Below this layer and in the older parts of the context the nodose-septate hyphae are interwoven with the fibre hyphae, have thick, yellow-brown walls with the lumina narrow or occluded and the hyphae sub-solid or solid, 2.5 — 4.0μ in diameter (Fig. 6 h). Also present in the older parts of the context are fibre hyphae with pale brown, thickened walls, aseptate and branching repeatedly, the branches 1.5 — 5.3μ in diameter, short or long, tortuous, tightly interwoven with the other hyphae and binding them into a tough tissue (Fig. 6 m). Below the upper context the fibre hyphae turn downwards towards the trama of the pores. The fibre hyphae are similar to those of the upper context but remain somewhat narrower, 2.2 — 3.0μ in diameter and are more tightly intertwined and consequently more flexuous. Fibre hyphae with short, numerous branches with thickened walls are very numerous, binding all hyphae into a tough tissue. The nodose-septate hyphae in this part of the pileus mostly have thickened, pale brown walls and branch freely from the clamp connections or at the septa. In the trama and towards the hymenial surface these hyphae become more numerous, thin-walled, the walls sub-hyaline, and with deeply staining contents, branching freely and interwoven with the other tramal hyphae, finally protruding at the hymenial surfaces where they bear the basidia and cystidioles on short terminal branches.

Decay and hosts

Lenzites sepiaria causes a brown, carbonizing rot of dead coniferous wood or occasionally of hardwood.

Specimens examined

Herb. DAOM: *17240, on *Betula papyrifera*, Goose Bay, Lab., July, 1947; *17246, on *Pinus mariana*, Goose Bay, Lab., July, 1947; *22276, on *Populus tremuloides* log, Quesnel, B.C., Aug. 1949; *22442, on *Picea* stump Algonquin Park, Ont., Sept. 1950; *22443, on *Tsuga* or *Pinus* log, Dorset, Ont., Oct. 1950; *22745, Goose Bay, Labrador, Aug., 1949; 22761, on *Picea mariana* log, Goose Bay, Lab., May 1950; 30059, on *Picea glauca* log, Riding Mt. Nat. Park, July 1950; 31986, base of *Picea* sp. North Bay, Ont., Sept. 1955.
Herb. PRE: 41887 on *Picea canadensis*, ex Herb. J. R. Weir, Aug. 1917; 42141 on *Pinus* sp. log, Mac-Mac Falls, Transvaal, July, 1961, *42381 on coniferous log, Corkery Road, Ont., Aug. 1962.

Discussion

This fungus appears to be quite variable in culture. Snell (1922) reported that the fungus is recognizable in culture by its scant aerial mycelium and powdery appearance due to abundant oidia. Robak (1942) and Cartwright & Findlay (1946) confirmed this and reported patches of thicker, orange-brown, velvety mycelium on which flat, antler-like, basidia-bearing processes develop. Nobles (1948) described the farinaceous appearance and numerous oidia of the cultures but did

not mention fibre hyphae. Falck (1909) described two kinds of hyphae from cultures, viz.: (1) conducting hyphae in which the cross walls disappear at the clamp-connections and (2) hyphae with very thick walls and narrow lumina which give mechanical strength. These latter correspond to the fibre hyphae described above. Fibre hyphae were not present in all cultures studied and chlamydospores were present in cultures of DAOM 22442 and PRE 42381 only. All cultures however had abundant oidia while the thick-walled, nodose-septate hyphae were present in varying numbers in all the cultures. These hyphae may be identical to Falck's (1909) conducting hyphae. The variability of the cultural characters of this fungus makes its identification in culture rather difficult on occasion.

In this species, most of the types of hyphae formed in culture are also found in the carpophores. The peculiar lateral outgrowths of short branches and the roughened processes produced on the fibre hyphae and thick-walled, nodose-septate hyphae in culture, were not found in any of the carpophores.

Bourdot & Galzin (1928) described the hyphae from carpophores of *Lenzites sepiaria* as brownish and thick-walled. Cunningham (1948 h), considered this species to fall in the genus *Daedalea* Pers. ex Fr., as defined by him and thereby implied the presence of thin-walled, generative hyphae with clamp connections at the septa, and thick-walled, brown, aseptate skeletal and binding hyphae in the carpophores. Pinto-Lopes (1952) reported hyaline, thin-walled, nodose-septate, secondary hyphae and brownish, narrow, aseptate, subsolid or solid tertiary hyphae in the carpophores. Overholts (1953) stated: "hyphae mostly pale chestnut, rarely branched, thick-walled, with no crosswalls or clamps, 3 —— 5μ in diameter, a few hyphae paler or nearly hyaline, with clamps." Teston (1953 b) confirmed the existence of nodose-septate generative hyphae, aseptate, thick-walled, skeletal hyphae and narrow, sinuose, branched, binding hyphae in the carpophores of this species. The description given above thus agrees with those of earlier workers. The binding hyphae of this species are thus true binding hyphae as defined by Corner (1932 a, 1953). The brown, thick-walled, nodose-septate hyphae ("sclerified generative hyphae," Donk, 1964) which are fairly numerous in the older part of the context have not been mentioned before. The carpophores thus have the types of hyphae and construction of species with a trimitic hyphal system as defined by Corner (1932 a), Cunningham (1946, 1954) and Teixeira (1962 b).

Lenzites sepiaria was chosen as the type species of the genus *Gloeophyllum* by Karsten, (Donk, 1960) but Fries (1821) placed it in *Daedalea* Pers. ex Fries before transferring it to *Lenzites* Fries a few years later (1838). Cunningham (1948 h) considered this species to be congeneric with *Daedalea quercina* L. ex Fr. the type of the genus *Daedalea* Pers. ex Fr. (Cooke, 1959; Donk, 1960). Although Cunningham (1948 h) defined the genus *Daedalea* as having a trimitic hyphal system, it was found in the course of this work that *Daedalea quercina* does not have "binding hyphae" in the carpophores (c.f descriptions Group 25). Furthermore, cultures of *Daedalea quercina* do not form brown colours; the hyphae are all hyaline and the cultures are characterized by the presence of nodose-septate hyphae with irregularly thickened walls which are absent from cultures of *Lenzites sepiaria*. Because of these differences, *Lenzites sepiaria* cannot be placed in the genus *Daedalea* Pers. ex Fries.

Although *Lenzites betulina* (L. ex Fr.) Fries, the type species of the genus *Lenzites* Fries, has the trimitic type of hyphal system, (Cunningham, 1948 h; O. Fidalgo, 1957) it differs from *Lenzites sepiaria* by having hyaline hyphae in both the cultures and carpophores. Its cultures produce extra-cellular oxidase and the fungus causes a white rot. It also has the tetrapolar type of interfertility (Nobles, Macrae & Tomlin, 1957) while *Lenzites sepiaria* has the bipolar type (Mounce &

Macrae, 1936). It thus appears that *Lenzites sepiaria* is not well classified with species of *Lenzites* either and is best placed in the genus *Gloeophyllum* Karst. of which it is the type species (Donk, 1960).

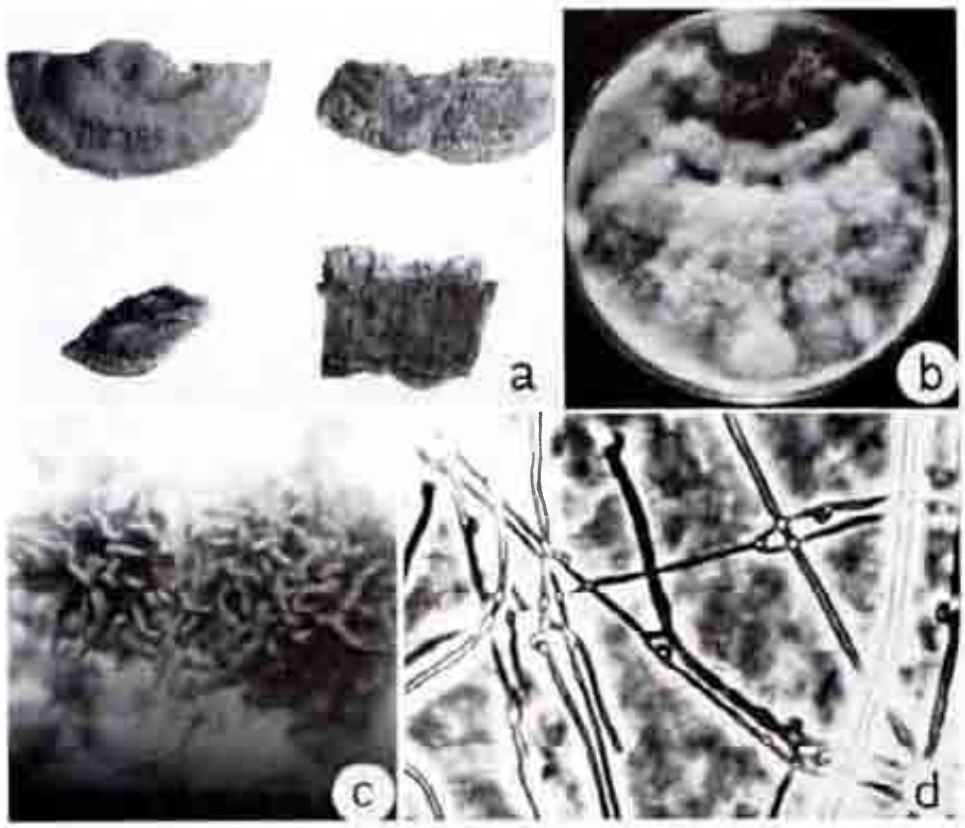

FIG. 7.—**Lenzites trabea.** (a) Carpophores of DAOM 22444; (b) culture of PRE 42457 at six weeks; (c) antler-like fructifications in culture; (d) wide and narrow nodose-septate hyphae from culture, × 1000 phase contrast.

Lenzites trabea *Pers. ex Fries*, Epicr. Syst. Myc. p. 407, 1838;
Daedalea trabea Pers. ex Fr., Syst. Myc. I, 335, 1821;
Trametes trabea (Pers. ex Fr.) Bresadola, Hym. Hung. Kmet. 27, 1897;
Gloeophyllum trabeum (Pers. ex Fr.) Murrill, Bull. Torr. Bot. Cl. 32, 370, 1905;
Coriolopsis trabea (Pers. ex Fr.) Bond. & Sing., Ann. Mycol. 39, 62, 1941;
Phaeocoriolellus trabeus (Pers. ex Fr.) Kotlaba and Pouzar, Ceska mykologie 9 (3) 152 — 170, 1957.

Cultural characters

Growth moderately fast, plates covered in 3-4 weeks, mycelial mat reaching a radius of about 30 mm after 1 week. Margin even, mycelium raised or in some cultures appressed, thin, downy, usually loose cottony to woolly at first, almost white to "light buff." Mat becomes progressively more woolly with age, darkening to "cream buff" or "light ochraceous buff" to "pale orange-yellow" with patches

of "orange buff" later turning to "apricot buff" or "ochraceous orange" and fans of mycelium growing over the lid of the Petri dish from the sides of the cultures. Fruiting bodies develop from the second week onward as dark "apricot buff" patches of compact, felty mycelium from which slender rounded spines, "apricot buff" in colour grow up, later expanding into flat, lamellate structures forming loose, irregularly poroid fructifications. At six weeks, mat mostly raised, woolly, radially and concentrically sulcate and "maize yellow" with darker fruiting or incipient fruiting areas, or, with large, irregular areas of thin, downy mycelium, or, sodden, appressed patches among areas of raised, woolly, "pale ochraceous buff" or "maize yellow" mycelium. Reverse bleaching slowly at first, then darkening in patches to "cadmium yellow," "deep chrome," "capucine orange" or "xanthine orange". Odour faint or strong, suggesting garlic. No diffusion zones are formed on gallic acid and tannic acid media; no growth on the latter medium but up to 20 mm diameter colonies on gallic acid media. No reaction occurs when gum guaiac solution is applied to the mat.

Advancing mycelium: hyphae hyaline, thin-walled, nodose-septate, branching from the clamp connections 3.0 — 4.5μ in diameter, (Fig. 8 a).

Aerial mycelium: (a) hyphae as in the advancing zone; (b) fibre hyphae rare, long, narrow, hyaline at first but turning yellowish gradually, unbranched or occasionally branched, the branches long, walls thickened, refractive, lumina narrow or occluded, aseptate, 2.0 — 3.0μ in diameter, (Fig. 8 b); (c) nodose-septate, narrow, much branched hyphae, thin-walled at first but becoming solid later, 0.7 — 1.5μ arising from normal thin-walled hyphae (Fig 8g); (d) oidia numerous or rare, cylindrical, thin-walled, hyaline 2.0 — 3.0μ in diameter and length variable (Fig. 8 h).

Fructifications: (a) thin-walled nodose-septate hyphae as in the advancing zone; (b) fibre hyphae numerous, long, unbranched, tortuous, yellowish-brown, walls thickened, lumina narrow or occluded, widening near the origins and tips, aseptate, 2.2 — 3.5μ (Fig. 8 b); (c) nodose-septate hyphae with pale-yellowish conspicuous walls, much branched and forming H-connections, 2.2 — 3.5μ in diameter, intertwined with other hyphae in the fructification (Fig. 8 c); (d) basidia hyaline, long-clavate to almost cylindrical 19.0 — 27.0 x 6.0 — 7.5μ, with 4 long, slender, straight sterigmata 4.5 — 6.0μ, borne in clusters of short branches from thin-walled, nodose-septate hyphae (Fig. 8 d); (e) basidiospores hyaline, cylindrical, obliquely apiculate, smooth, thin-walled 7.2 — 9.6 — (12) x 3.0 — 3.7μ (Fig. 8 e); (f) cystidioles hyaline, fusiform, often with peculiar branching, apical processes, 18.0 — 32.0 x 4.0 — 6.0μ arising from the basidial fascicles (Fig. 8 f).

Submerged mycelium: (a) hyphae hyaline, narrow, branched, with conspicuous clamp connections at the septa, thin-walled at first but walls thickening later, 1.2 — 2.0μ in diameter (Fig. 7d, 8k); (b) nodose-septate hyphae as in the advancing zone; (c) chlamydospores hyaline, ovoid to ellipsoid, thick-walled with deeply staining contents 10.0 — 23.0 x 6.0 — 10.0μ, intercalary or terminal (Fig. 8 m).

Carpophore characters

Carpophore annual or occasionally reviving, lignicolous, solitary or compound, sessile or effused-reflexed, applanate or dimidiate somewhat convex, often laterally connate, occasionally imbricate; coriaceous when fresh but harder and more rigid on drying, 1.0 — 10 x 1 — 4 x 0.2 — 0.8 cm; upper surface tomentose, velvety but becoming glabrous and rugose, azonate or concentrically sulcate, grayish-brown to cinnamon-brown or umber-brown; margin obtuse, thin, concolorous with pileus or somewhat paler, entire or somewhat lobed; pore surface concolorous or slightly paler than upper surface, lenzitoid to poroid or occasionally lamellate; tubes 1 — 4 mm deep, edges thin, entire, 2 — 3/mm; context fibrous, umber-brown, 1 — 4 mm thick.

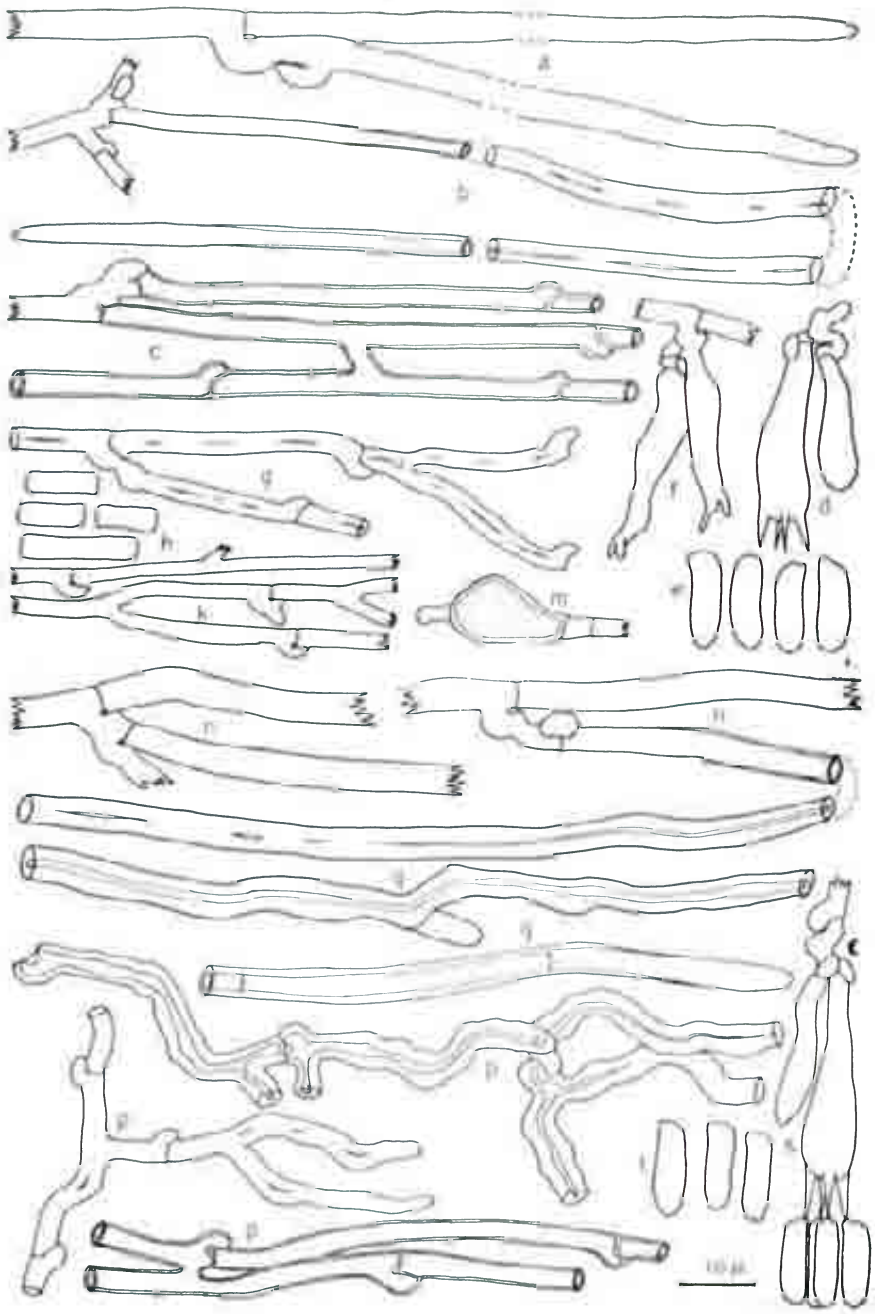

FIG. 8. — **Lenzites trabea.** a - m. Hyphae and structures from cultures: (a) hyphae from advancing zone; (b) unbranched, fibre hyphae; (c) thick-walled, nodose-septate hyphae with H-connection; (d) basidia; (e) basidiospores; (f) branched cystidioles; (g) thick-walled, sub-solid, nodose-septate hyphae; (h) oidia; (k) narrow, hyaline, nodose-septate, submerged hyphae; (m) chlamydospores.
n - t. Hyphae and structures from carpophores: (n) thin-walled, nodose-septate hyphae; (p) thick-walled, nodose-septate hyphae with tortuous branches; (q) unbranched fibre hyphae; (s) basidia; (t) basidiospores.

Hyphal characters. Carpophores consist of: (1) nodose-septate hyphae, thin-walled, hyaline, branching, often from the clamp connections, 2.4 — 4.0μ in diameter (Fig. 8 n); (2) nodose-septate hyphae with thickened sub-hyaline to brownish walls, narrowed or occluded lumina, branching and forming H-connections and forming short, tortuous, thin-walled or thick-walled to solid, nodose-septate, lateral branches 2.5 — 4.5μ in diameter (Fig. 8 p); (3) fibre hyphae long, straight or slightly flexuous, unbranched, pale brown, walls thickened, lumina narrow or occluded and usually widening towards the tip, aseptate, or with one or two simple septa towards the tip, 2.5 — 5.0μ in diameter (Fig. 8 q).

Hymenium: basidia long clavate, hyaline, 19.0 — 27.0 x 6.0 — 7.5μ, with four slender, straight sterigmata 4.5 — 6.0μ long (Fig. 8 s); basidiospores cylindrical, ends rounded, obliquely apiculate, hyaline, at first, later pale yellowish-brown, smooth ,thin-walled, 8.0 — 9.6 x 3.0 — 4.0μ (Fig. 8 t).

Construction. At the margin the carpophore consists of long, unbranched fibre hyphae with pale brown thickened walls and prominent aseptate lumina, subsolid in the middle portion, 2.4 — 3.6μ in diameter and arranged more or less parallel but somewhat intertwined in the direction of growth. Also intertwined with the fibre hyphae are long, hyaline, thin-walled, nodose-septate hyphae mostly branching from the clamp connections, 2.4 — 3.6μ in diameter, the branches interwoven with the other hyphae. In the context behind the margin the hyphae turn upward towards the upper surface. The fibre hyphae are lightly intertwined and similar to those of the margin but their lumina are narrower, often occluded and one or two simple septa may be present near their tips. Their ends are free and project upward to a common level to form the finely tomentose upper surface of the young parts of the pileus. Intertwined with these fibre hyphae, up to a position slightly below their tips, are numerous hyaline, nodose-septate hyphae similar to those in the margin, branching freely and forming frequent H-connections. In the older parts of the context the fibre hyphae are slightly darker in colour and their walls thickened for longer distances. Here the nodose-septate hyphae have thickened, pale brown walls with lumina narrowed and sections often solid and forming short, very tortuous, nodose-septate branches, tightly interwoven with the fibre hyphae (Fig. 8 p). In some specimens a greyish, glabrous cuticle may be present over this part of the carpophore. This may be up to 50μ thick and consists of hyaline or sub-hyaline hyphae with thick, gelatinous walls swelling in KOH, arising from the nodose-septate hyphae of the context, and lying prostrate and intertwined in all directions on the upper surface where they are agglutinated into a thin, smooth trichocutis (Lohwag, 1940). In the lower context the hyphae turn downwards into the trama Fibre hyphae resemble those of the upper context but they are narrower, mostly with very narrow lumina, more flexuous and tightly intertwined to form a denser tissue. In these parts, the nodose-septate hphae are thin-walled, hyaline, branching freely and interwoven with the fibre hyphae. Many branches of these nodose-septate hyphae are tightly intertwined with the fibre hyphae, become thick-walled or solid and bind the hyphal elements together into a tough tisue (Fig. 8 p). Many of these nodose-septate hyphae remain thin-walled and ramify though the hyphal elements in the tramal tissue to form numerous, short branches bearing clusters of basidia at the hymenial surfaces, each basidium subtended by a basal clamp connection (Fig. 8 s).

Decay and hosts

Lenzites trabea causes a brown rot of hardwood timbers but is also found on coniferous wood.

Specimens examined

Herb. DAOM: *F3823, on hardwood log, Ottawa, Ont., May 1934; F3838, on coniferous wood, St. Andrews, N.B., Aug. 1933; F3893, on *Acer* sp., Durham, Ont., Aug. 1937; F6482, on *Alnus incana,* Montgomery Lake, Ont., Sept. 1935; F8893, on *Acer* sp. log, near Durham, Ont., Aug. 1937; F9073, Mt. Mitutoge, Japan, Oct. 1933; *9507, on *Tsuga canadensis,* Toronto, Ont., 1939; *22444, on deciduous log, Waterbury Centre, Vt., Oct. 1950; *22630, ex Div. For. Prod. South Melbourne, Aust., 1939; *30929, on *Pinus sylvestris,* Suomsujorri Lieksa, Finland, 1951; *72285, Portage du Fort, Que., June 1961.
Herb. PRE: 31310; 31341, decayed wood, Stellenbosch, C.P., Nov. 1926; 31379, old posts, Stellenbosch, C.P., Aug. 1919; 31426, decaying logs, Stellenbosch, C.P., Sept. 1919; 36818, on *Pinus* sp. stumps, Harrismith, O.F.S., March 1948; 40222, on *Cupressus* sp. logs, Pretoria, Tvl., March 1952; 41679, Johannesburg, Tvl., 1954; *42457, on decaying hardwood log, Honeydew, Tvl., Jan. 1961.

Interfertility studies

Lenzites trabea has the bipolar type of interfertility with allelomorhps for heterothallism at one locus only (Mounce & Macrae, 1936). To determine whether the South African collection was interfertile and therefore conspecific with a Canadian strain, four cultures, each obtained from a single basidiospore of PRE 42457, were mated on malt agar slants in all possible combinations with each of four single spore cultures of the Canadian isolate DAOM 72285. The results are given in Table 4.

The formation of clamp connections on all the paired mycelia is regarded as positive proof that the South African and Canadian isolates are interfertile and therefore conspecific.

Discussion

This description of the cultural characters of *Lenzites trabea* agrees well with those of Snell (1922), Cartwright (1931), Cartwright & Findlay (1946) and Nobles (1948). Cultures of this species are readily recognized by their distinctive colour and texture, early fruiting, the brown fibre hyphae which are rare in the mycelial mat but abundant in the fruiting structures, and the very narrow hyphae with large conspicuous clamp connections which are found at the surface of the agar (Fig. 7 d).

From the descriptions it is evident that not all structures formed in culture are also present in the carpophores. The narrow hyphae with prominent clamp connections as well as the chlamydospores formed in the agar were not found in the carpophores. It is possible that these structures may be found in the wood decayed by the fungus but no specimens of decayed wood were available for examination. Chlamydospores have been found in wood decayed by species which form them in culture (Cartwright & Findlay, 1946). The nodose-septate hyphae and fibre hyphae formed in cultures are similar to those in the carpophores of *Lenzites trabea.*

From the above description it is evident that the carpophores of *Lenzites trabea* consist of two types of hyphae only, viz. unbranched, thick-walled hyphae mostly aseptate or occasionally with one or two simple septa (skeletal hyphae, Corner, 1932 a) and branching, nodose-septate hyphae either with thin, hyaline walls or with the walls coloured and thickened (sclerified generative hyphae, Donk, 1964). This observation agrees with the descriptions of the hyphae of this species by Pinto-Lopes (1952), Teston (1953 b) and Overholts (1953). According to the definitions of Corner (1932 a, 1953), Cunningham (1946, 1954) and Teixeira (1962 b) hyphae with clamp connections must be regarded as generative hyphae. The carpophore of *Lenzites trabea* thus has a dimitic hyphal system. But thick-walled elements of the nodose-septate hyphal system serve to bind the tissues of

the carpophores. This binding hyphal system, which admittedly is not well developed, thus consists of sclerified generative hyphae. The carpophores of *Lenzites trabea* differ in construction and hyphal characters from those of *Lenzites sepiaria*, a species with trimitic hyphal system (Cunningham, 1948 h; Teston, 1953 b) in which the binding system consists of "branched, aseptate, thick-walled hyphae of limited growth" that arise as differentiated terminal cells of lateral branches of nodose-septate generative hyphae (Corner, 1932 a). This difference is of fundamental importance in the anatomy of the carpophores of these two species, which therefore cannot be regarded as being congeneric.

Pinto-Lopes (1952), Corner (1954 a), Bondartseva (1961), Teixeira (1962 b) and Donk (1964) regard the absence or presence of different types of hyphae in carpophores as important at the generic or higher level. *Lenzites trabea* thus cannot be regarded as being congeric with *Lenzites sepiaria*, the type species of the genus *Gloeophyllum* Karsten (Cooke, 1959; Donk, 1960). For this same reason, *Lenzites trabea* cannot be congeric with any one of the three species *Polyporus occidentalis*, the type species of the genus *Coriolopsis* Murr., or *Lenzites betulina*, the type species of the genus *Lenzites* Fr., or *Trametes suaveolens*, the type species of the genus *Trametes* Fr. *Lenzites trabea* had been transferred to each of these three genera by various authors (loc. cit.) of which all have fruit bodies with trimitic hyphal systems (see descriptions Group 45).

Fries (1821) and Cunningham (1948 h) regarded *Lenzites trabea* as congeneric with *Daedalea quercina* Fr., the type species of the genus *Daedalea* Fr. But the nodose-septate hyphae with irregularly thickened walls which are present in cultures and carpophores of that species (Group 25) are not present in the cultures and fruit-bodies of *Lenzites trabea* and the two species can therefore not be regarded as congeneric.

Kotlaba & Pouzar (1957) created the new genus *Phaeocoriolellus* with *Lenzites trabea* as the type and only species. This genus is characterized by a dimitic hyphal system and was based on Bondartsev's (1953) and Teston's (1953 b) descriptions.

M. E. P. K. Fidalgo (1962) reported that hyphal analysis of *Trametes odorata* (Wulf. ex Fr.) Fries, the type species of the genus *Osmoporus* Sing., revealed this fungus to be dimitic, with the generative hyphae branched, hyaline, nodose-septate, characteristically thin-walled but often thick-walled or solid and skeletal hyphae unbranched, yellowish-brown to brown, aseptate, long, fibre-like. The nodose-septate hyphae were thin-walled in the growing region but often thick-walled and brownish in the older parts of the context and above the dissepiments. Fidalgo's descriptions of the hyphae, which confirmed the reports of Pinto-Lopes (1952) and Teston (1953 b), agree very closely with the description of the hyphae of *Lenzites trabea* as given above. These two species are thus very similar in hyphal characters, construction of the carpophore and other morphological features. These two species are thus congeneric and if the genus *Osmoporus* Sing. is accepted as valid, *Lenzites trabea* should be transferred to it.

Resumé.

From these descriptions it is evident that *Lenzites sepiaria* (Wulf. ex Fr.) Fr. and *Lenzites trabea* Pers. ex Fr. possess many characters which are common to both species in their cultures and their carpophores. The absence of some types of hyphae, which are present in the carpophores of *Lenzites sepiaria*, from carpophores of *Lenzites trabea*, indicates that the relationship between these species, which is suggested by these common characters, must exist at a supra-generic level.

5.4 Group 18

The mycelial mats of cultures of species in this group usually remain white or may develop pale pinkish or vinaceous tints. They do not produce extra-cellular oxidase. Their thin-walled hyphae have simple clamp connections at the septa and remain thin-walled but septate, thick-walled fibre hyphae are also formed in large numbers. Their basidiospores are globose, ovoid or ellipsoidal in shape. The interfertility of species of which this character is known, is of the bipolar type.

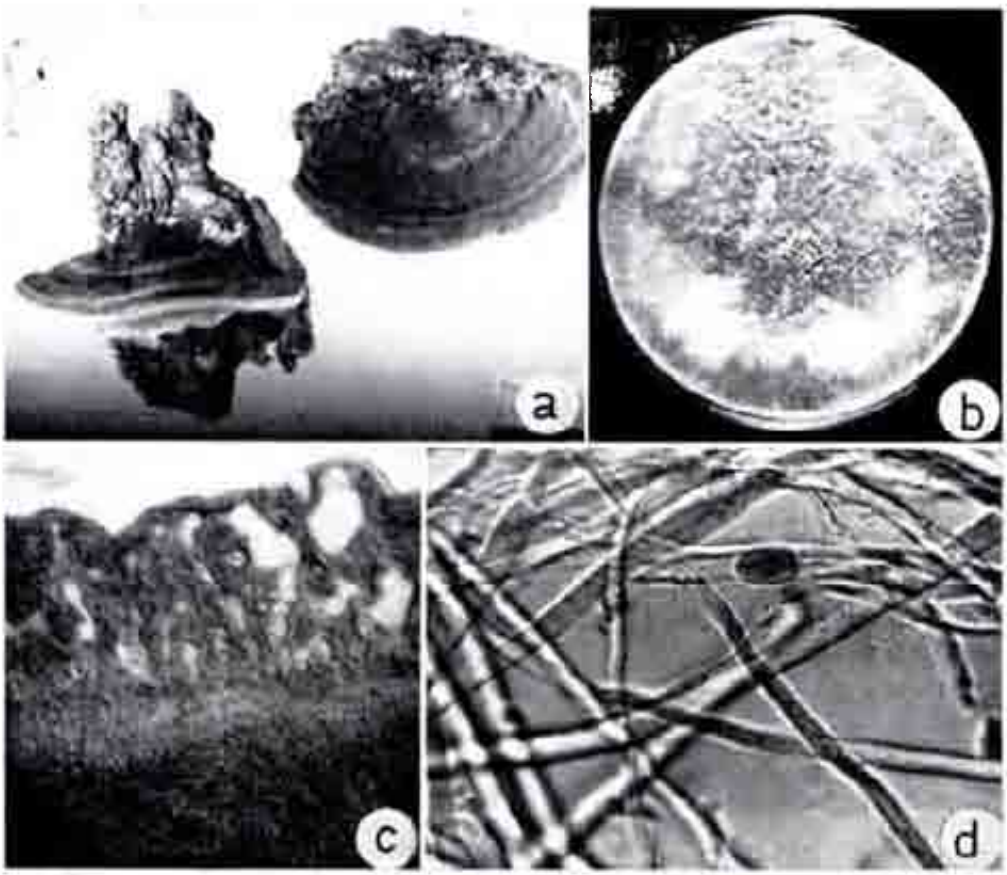

Fig. 9.— **Fomes pinicola.** (a) Carpophores of DAOM 22755; (b) culture at six weeks; (c) upper context and crust of fruit-body in radial-longitudinal section, × 100, in KOH; (d) inter-calary chlamydospore, thin-walled nodose-septate hyphae and fibre hyphae from carpophore.

Fomes pinicola *(Sw. ex Fr.) Cooke*, Grev. 14, 17, 1885;

Polyporus pinicola Sw. ex Fr., Syst. Myc. 1, 372, 1821;

Fomitopsis pinicola (Sw. ex Fr.) Karst., Bidr. Kanned. Finl. Nat. Folk, 48, 306, 1889.

Ungulina marginata (Fr.) Pat., Essai taxon. Hymen., p. 103, 1900.

Cultural characters

Growth is moderately fast to slow, the plates being covered in four to six weeks. Advancing zone even at first, thin, downy, appressed, later somewhat ragged but the mat becoming more dense towards the inoculum; white, raised, cottony-woolly, concentric zones develop or rounded lumps or nodules which slowly increase in size, appear on the zones of denser mycelium and may grow together as compact, uneven masses of tough, chamois mycelium near the sides of the plate; fruiting areas originating as shallow pores of which the sides grow upward to form tubes, resulting in pored areas with the oldest tubes in the centre, develop on the irregular lumps after five to six weeks. The cultures remain white or pale "cream color" over the fruiting areas. The reverse remains unchanged. No odour or a faint, fragrant odour is emitted. No colour change occurs when alcoholic gum guaiac is applied to the culture No diffusion zones are produced on gallic acid and tannic acid media but some mycelial growth occurs on both media.

Advancing mycelium: hyphae branching at or near the septa, hyaline, thin-walled, nodose-septate, 1.0 — 4.0μ in diameter (Fig. 10 a).

Aerial mycelium: (a) nodose-septate hyphae as in the advancing zone; (b) fibre hyphae hyaline, long, unbranched or occasionally branched, arising from nodose-septate hyphae, thin-walled near their origins and tips but walls thickened, lumina narrow or occluded, aseptate or with one septum near the tip, 1.0 — 4.0μ in diameter (Fig. 10 b); (c) chlamydospores, inter-calary or terminal, ovoid to sub-globose with thickened walls 6.0 — 18.0 x 6.0 — 9.0μ, mostly in young parts of mycelium (Fig. 10 c).

Fructification: (a) hyphae as in the advancing zone; (b) fibre hyphae as in the aerial mycelium but more freely branched, the branches long and tortuous, a number of branches often arising close together from a main branch and close to its origin, 1.0 — 4.0μ in diameter (Fig. 10 d); (c) basidia long clavate, 18.0 — 25.0 x 5.5 — 7.2μ with four sterigmata 2.4 — 3.0, and arising from short branches of thin-walled, nodose-septate hyphae in the dissepiments (Fig. 10 e); (d) basidio-spores hyaline, ovoid, or ellipsoidal with an oblique apiculum, thin-walled, smooth 4.8 — 6.0 x 3.3 — 4.0μ (Fig. 10 f); (e) hymenial cystidia hyaline, long cylindrical often tapering towards the tips and projecting somewhat beyond the basidia, 24.0 — 30.0 x 2.4 — 3.0μ, arising from the basidial fascicles (Fig. 10 g).

Carpophore characters

Carpophore perennial, lignicolous, solitary, sessile, dimidiate, convex to ungulate, hard corky to woody up to 15 x 20 x 10 cm; upper surface covered with a resinous layer, smooth, sticky and reddish brown at first, later dark gray to black, smooth or sulcate with age, hard; margin obtuse, thick, rounded, entire to lobate or undulate, pallid or lighter coloured than other areas; pore surface white to yellowish or pale buff where bruised; pores, rounded, 3 — 5 per mm, mouths entire, dissepiments thick, even; tubes concolourous, distinctly stratified, 3 — 7 mm long each season; context pale creamy to yellowish or pale brown, concentrically zoned, reddish brown in KOH, up to 2.0 cm thick.

Hyphal characters: carpohores consist of (a) hyaline, branching, thin-walled, nodose-septate hyphae, with deeply staining contents, or empty, 2.2 — 4.0μ in diameter, (Fig. 10 h); (b) fibre hyphae long, unbranched, hyaline to sub-hyaline with walls thick and refractive, lumina narrow, widening gradually towards the ends, aseptate or with one or two simple septa near the distal end, 3.0 — 9.0μ in diameter (Fig. 10 k); (c) chlamydospores hyaline, ovoid to ellipsoid, thick-walled, intercalary in nodose-septate hyphae, 7 — 12 x 10 — 24μ (Fig. 10 m).

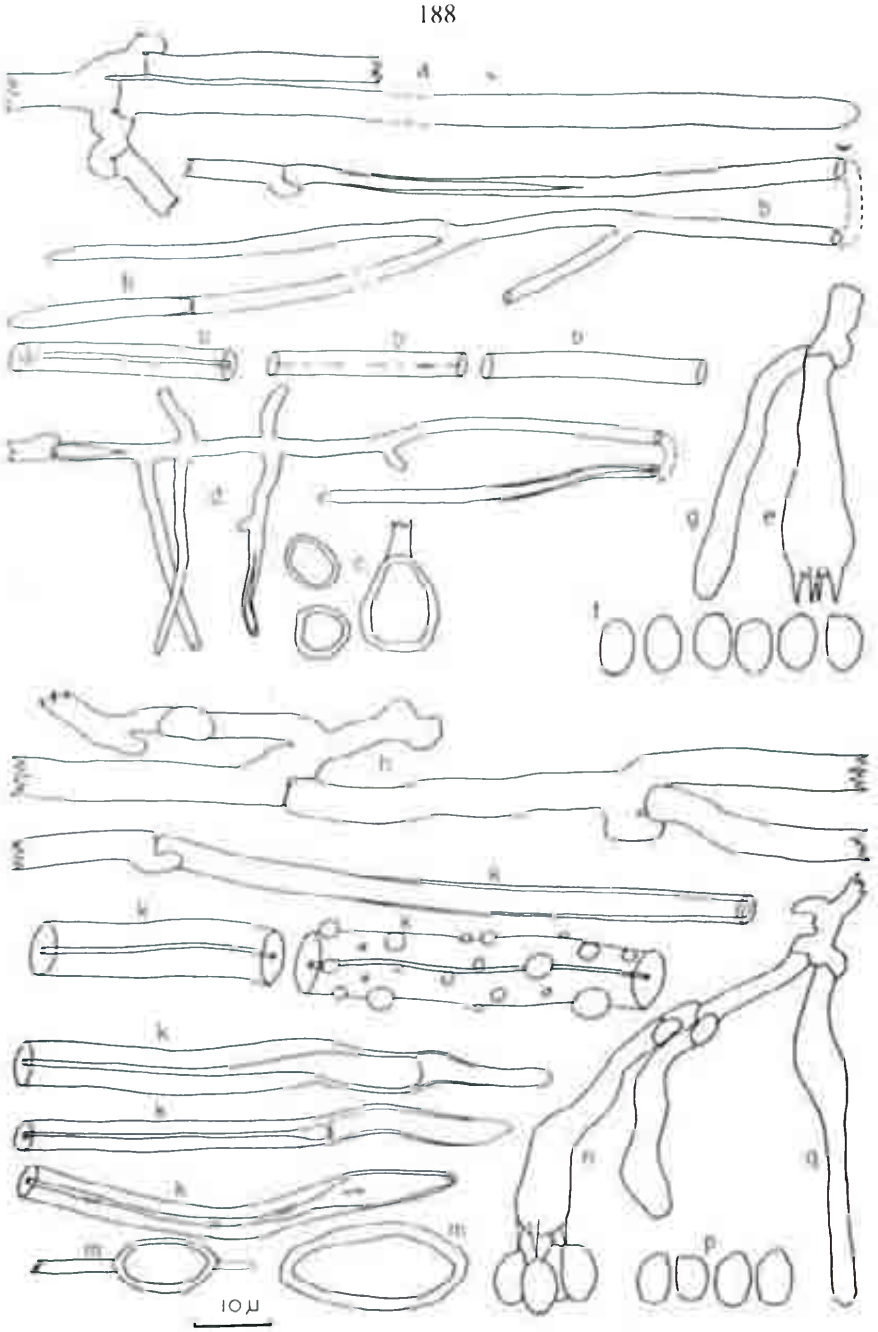

FIGURE 10.

FIG. 10.— **Fomes pinicola.** a - f. Structures from culture: (a) nodose-septate hyphae from advancing zone; (b) fibre hyphae; (c) chlamydospores; (d) fibre hyphae with long, tapering branches; (e) basidia; (f) basidiospores; (g) hymenial cystidium.
h - q. Structures from carpophores: (h) thin-walled, nodose-septate hyphae; (k) fibre hyphae; (m) chlamydospores; (n) basidia; (p) basidiospores; (q) hymenial cystidium.

Hymenium: basidia hyaline, long clavate 18.0 — 25.0 x 5.5 — 7.2μ with four slender, straight sterigmata 2.4 — 3.0μ (Fig. 10 n); basidiospores hyaline, ellipsoidal to ovoid, smooth, thin-walled, 4.8 — 6.0 x 3.3 — 4.0μ (Fig. 10 p); hymenial cystidia long, hyaline, tapering terminally, 24 — 30 x 2.4 — 3.0μ, projecting 10 — 12μ beyond the basidia (Fig. 10 q).

Construction: At the margin the carpophore consists of long, unbranched, thick-walled, fibre hyphae with narrowed lumina, arranged parallel to the direction of growth of the carpophore, somewhat intertwined and closely packed. Behind the margin in the context are numerous hyaline, thin-walled, nodose-septate hyphae, branching repeatedly and intertwined with the fibre hyphae, which arise from them. The context consists of long fibre hyphae, unbranched or occasionally branched, hyaline or sub-hyaline, sub-solid to solid, aseptate or occasionally with one or two simple septa at the distal end, 3.0 — 9.0μ in diameter and with globules of lacquer-like material adhering to them in the zones of growth of the pileus. These hyphae are mostly closely packed and slightly intertwined among themselves and with branching, hyaline, thin-walled, nodose-septate hyphae, some with deeply staining contents, others collapsed and empty, or, with intercalary thick-walled, ovoid to ellipsoid chlamydospores 7 — 12 x 10 — 24μ in the middle and lower context. At the upper surface the ends of fibre hyphae are bent over and become interwoven with one another and numerous branching, thin-walled, nodose-septate hyphae with deeply-staining contents, to form a sub-surface cortex (Lohwag, 1940). From these hyphae, a resin-like material is exuded which permeates the upper layer of the cortex and covers the surface of the pileus in a layer up to 1500μ thick (Fig. 9 c). From the lower context the fibre hyphae bend downward, remaining unbranched and intertwined towards the dissepiments. In the dissepiments the fibre hyphae are unbranched, tortuous, sub-solid, aseptate, narrower than in the context and tightly intertwined among themselves. Hyaline, nodose-septate hyphae are intertwined and interwoven with the fibre hyphae, branching freely and becoming increasingly numerous towards the hymenial surfaces where short branches project to bear fascicles of clavate basidia and long, tapering cystidia.

Decay and hosts

Fomes pinicola causes a brown rot of dead, standing or fallen coniferous and occasionally angiosperm timber, destroying both heartwood and sapwood.

Specimens examined

Herb. DAOM: *F3249, on *Populus balsamifera,* Victoria Beach, Man. May 1933; *F6895, on *Pinus yezoensis,* Hokkaido, Japan; *F6925, on *Picea glauca,* Hot Springs, Alaska, Aug. 1936; *F7120, on fallen *Picea exelsa,* Poland, Sept. 1936; *7121, on living *Prunus avium,* Poland, Sept. 1936; *8567, on *Picea sitchensis,* Kodiak Is., Alaska, Aug. 1938; *8568, on *Tsuga heterophylla,* Mt. Arrowsmith; *9937, on dead *A. saccharum,* Preston, Ont., Oct. 1959; *10787, on *Pyrus malus* stump, Kentville, N.S., Feb. 1942; 17924, on *Picea glauca,* Hudson Bay, Sask., Sept. 1947; 17926, on *Populus tremuloides,* Hudson Bay, Sask., Sept. 1947; 22358, ex Herb. J. Pinto-Lopes, Lisbon; 22711, on *Abies balsamea* log, Labrador, Aug. 1949; 22746, on *Picea sp.* logs, Moosehide Mtns., Yukon, Aug. 1949; 30023, on *Betula papyrifera,* Doré Lake, Sask., July 1948; 30064, on *Pinus contorta* slash, Spines Mill, Alta., Sept. 1950; 30152, on *Betula alba,* Uppsala, Sweden, Aug. 1952; 30157, on *Betula alba,* Uppsala, Sweden, Sept. 1952.

Discussion

The cultural characters as described above agree well with those described by Mounce (1929), Campbell (1938), Davidson, Campbell & Vaughn (1942), Cartwright & Findlay (1946) and Nobles (1948, 1965). There is a decided lack of distinguishing features in the gross appearance and hyphal characters of the mat formed in culture but the chlamydospores which occur in the newer parts of the mat but not in the older parts, may be a useful diagnostic feature.

From the above description it is clear that only thin-walled, branching nodose-septate hyphae and fibre hyphae, typically unbranched, are present in the carpophores. Lowe (1957) stated of *Fomes pinicola:* "context hyphae rarely branched, thick-walled, non-septate, 5 — 8μ in diameter with a small amount of thin-walled, clamped hyphae, 2.4μ in diameter; tramal hyphae similar except mostly 3 — 5μ in diameter". Overholts (1953) reported the thick-walled, aseptate hyphae but also found "hyphal complexes composed of hyaline hyphae 3 — 4μ in diameter, present in considerable numbers". Overholts usually reported such hyphal complexes in species in which branched binding hyphae are present (e.g. *Lenzites betulina).* Overholts did not describe the hyphae in these complexes. Teston (1953 b) figured narrow, thick-walled branched hyphae from the tubes of *Ungulina marginatus* (=*Fomes pinicola,* Bourdot & Galzin, 1928; Lowe, 1957) but stated that a few branched hyphae are found in the dissepiments of the carpophores of this species. No anatomical details of these hyphae were given however. It appears that Overholts' "hyphal complexes" and Teston's "branching hyphae" may correspond to the branched, nodose-septate hyphae, some of which have thickened walls, which are very numerous in the dissepiments of the specimens examined of this species. Structures resembling binding hyphae as described and defined by Corner (1932 a, 1953), Cunningham (1946, 1954), and Teixeira (1962 a, b) were never seen in any of the specimens examined. The above description thus agrees well with earlier reports on the hyphal characters of this species.

From the descriptions it is clear that structures found in the cultures, are also found in the carpophores. While the fibre hyphae of the carpophores are mostly unbranched, branched fibre hyphae are found in the fruiting areas formed in culture. The number of branches is however the only difference between these structures which are otherwise identical in all other respects. The chlamydospores found in some of the carpophores examined, are of interest since their occurrence in carpophores of Hymenomycetes have been reported only rarely, even in species in which they are abundantly produced in cultures. This is an indication that the absence or presence of chlamydospores in cultures, is at best of diagnostic value in the identification of cultures only.

Fomes pinicola has the hyphal characters, which are typical of species with the dimitic hyphal system as described by Corner (1932 a, 1953) and Cunningham (1946, 1954). Farinha (1964) reached a similar conclusion after a study of cultures and carpophores of this species. The large, perennial carpophores are however remarkably simple in construction. The fibre hyphae are straight and are more or less parallel to one another in the carpophore. Even in the dissepiments are they seldom very tortuous, suggesting a rather loose association of hyphae. There further appears to be little binding of the tissues by the nodose-septate hyphae as observed in *Lenzites trabea* and special binding hyphae or processes are lacking. This simplicity of construction is emphasized by the fact that sections of the carpophores, even from the dissepiments, are easily teased out with needles or even squashed when placed in KOH for microscopic examination.

The simple construction and dimitic hyphal system of fruit-bodies of *Fomes pinicola,* are in sharp contrast to the complex carpophores of *Fomes fomentarius* (L. ex Fr.) Kickx the type of the genus *Fomes* (Fr.) Kickx (Donk, 1960) as described by Teixeira (1962 a). According to Teixeira (1962 a), the fruit-bodies of *Fomes fomentarius* are characterized by the dark brown context, consisting of nodose-septate generative hyphae, dark-brown, thick-walled skeletal hyphae and much branched binding hyphae and are covered by an indurate layer of agglutinated ends of skeletal hyphae. Because of this great difference in hyphal composition

and construction of the carpophores of *Fomes fomentarius* and *Fomes pinicola*, these two species cannot be regarded as congeric.

Although *Fomes fomentarius* (L. ex Fr.) Kickx is the type species of the genus *Fomes* (Fries) Kickx, Donk (1960) presented strong evidence in favour of his view that this species is also the type of the genus *Ungulina* Pat. and that the latter genus is an isonym of the genus *Fomes* (Fr.) Kickx. If this view is accepted, it will mean that *Fomes pinicola* cannot be included in either of the genera *Fomes* (Fr.) Kickx or *Ungulina* Pat. but may be best placed in the genus *Fomitopsis* Karsten of which it is the type species (Cooke, 1959; Donk, 1960).

Fomes pinicola has not been recorded from South Africa. The species however occupies an important taxonomic position as the type of the genus *Fomitopsis* Karst., to which a number of species, including some found in South Africa, had been referred. It furthermore appeared to be a good example of a species with dimitic hyphal system, of which the construction had not been described, to include in this study in order to have a sound basis for future comparison with possibly related species.

5.5 Group 25

Cultures of species in this group form white, pale yellow or rose coloured mycelial mats which do not produce extra-cellular oxidase enzymes. Their thin-walled hyphae have simple clamp connections at the septa. Thick-walled, aseptate fibre hyphae are also formed. Characteristic hyphae with numerous clamp connections and their walls irregularly thickened, and the lumina much reduced but staining deeply in phloxine, are present to a greater or lesser extent. Their basidiospores are cylindrical or allantoid. Their interfertility, where known, is of the bipolar type.

Daedalea quercina *L. ex Fr.*, Syst. Myc. 1, 333, 1821.
Lenzites quercina (L. ex Fr.) Quélet, Ench., 153, 1886;
Trametes quercina (L. ex Fr.) Pilát, Atl. Champ. Eur. 3, 329, 1936.

Cultural characters

Growth is slow, the mat reaching a radius of about 30 mm in two weeks and covering the plate only after six weeks. The advancing margin is even with the hyphae raised to the limit of growth. The mat is white, at first woolly with fine strands radiating from the inoculum. From 3 — 4 weeks the older mycelium tends to become appressed and patches of denser felty mycelium with an overgrowth of sparse, erect, cottony mycelium begin to form on the agar in the older parts of the mat and along the sides of the dish. Over these patches, fruiting areas may appear as granules which later develop into coarse, warty or spine-like columns of dense white or creamy mycelium which may become connected to each other by ridges or strands of similar dense mycelium. At six weeks the cultures have a thin, radiating, woolly mat with vague, radiating and concentric depressions with the dense mycelium of the fruiting areas mostly over the older parts and against the sides of the dish. Rhizomorphic strands may run from the inoculum to the fruiting areas. The reverse remains unchanged. At 4 — 6 weeks a pleasant, fruity odour is given off by the culture. No reaction is evident when tested for extra-cellular oxidase enzymes with gum guaiac solution.

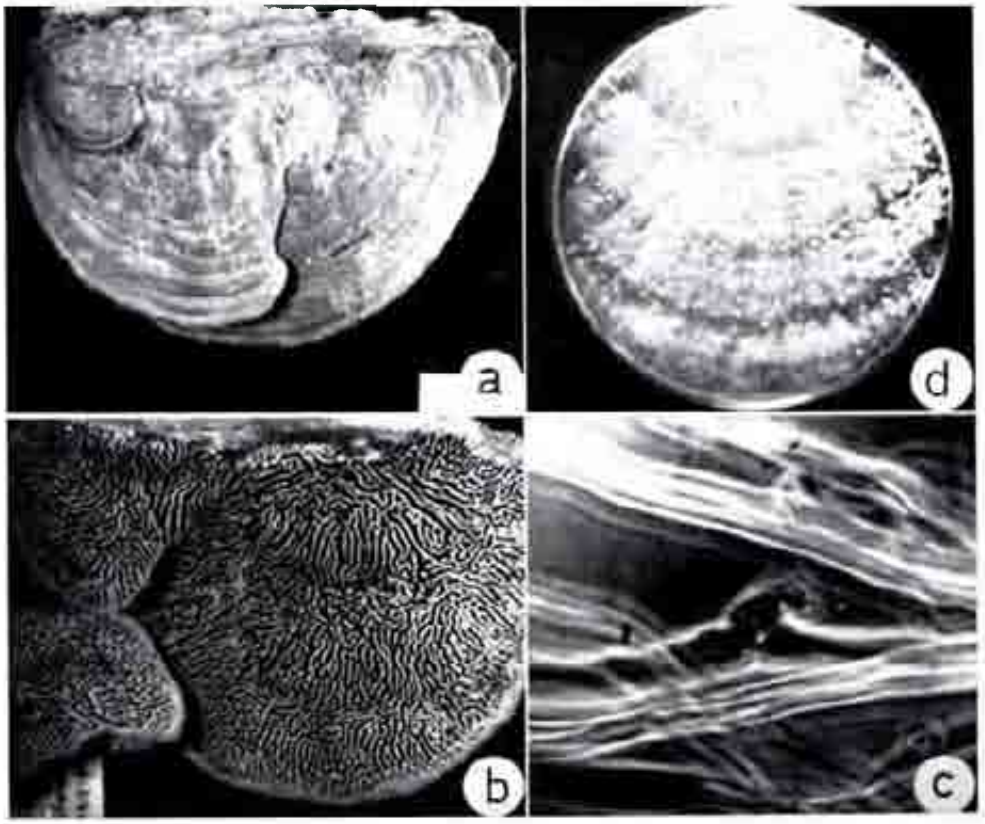

FIG. 11.— **Daedalea quercina.** (a) Carpophore of PRE 31394, upper surface and (b) hymenial surface; (c) nodose-septate hyphae with irregularly thickened walls from carpophore, × 1000; (d) culture of PRE 42366 at 6 weeks.

Advancing mycelium: hyphae hyaline, thin-walled, nodose-septate, branching at or near the septa or from clamp connections 2 — 6μ in diameter (Fig. 12 a).

Aerial mycelium: (a) nodose-septate hyphae as is the advancing zone; (b) nodose-septate hyphae with the walls irregularly thickened and with deeply staining contents in the lumina, either very narrow 1.5 — 2.0μ in diameter, branching and solid in parts or wide, up to 6μ in diameter and mostly unbranched and tending to break at the clamp connections (Fig. 12 b). The latter type is abundant in the felty mycelium on the surface of the agar; (c) fibre hyphae hyaline, unbranched or occasionally with branches, the walls thick, refractive and lumina narrow or almost occluded, aseptate and widening only at the ends, 1.5 — 4.0μ in diameter (Fig. 12 c). They arise from thin-walled, nodose-septate hyphae and nodose-septate hyphae with irregularly thickened walls.

Fructifications: (a) nodose-septate, thin-walled hyphae; (b) nodose-septate hyphae with irregularly thickened walls, and (c) fibre hyphae as described above. Basidia hyaline, long-clavate 22 — 36 x 4.5 — 6μ, with 4 straight sterigmata 3.6 — 4.5μ long (Fig. 12 d), borne in clusters on repeatedly branched thin-walled, nodose-septate hyphae (Fig. 12 d); basidiospores, short cylindrical, hyaline, smooth, thin-

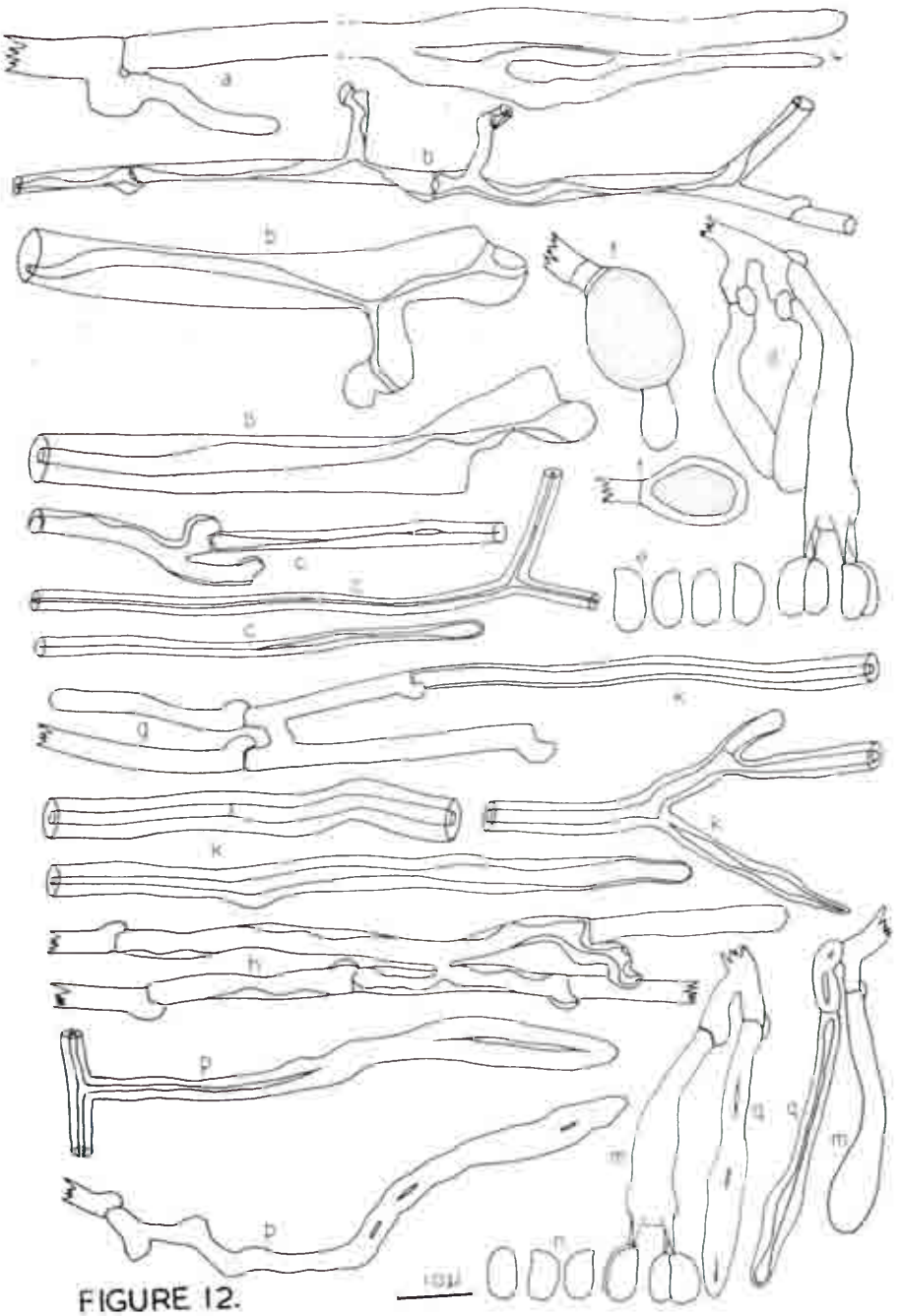

FIG. 12. — **Daedalea quercina.** a - f. Structures from culture: (a) hypha from advancing zone; (b) nodose-septate hyphae with irregularly thickened walls; (c) fibre hyphae; (d) basidia; (e) basidiospores; (f) chlamydospores.
g - q. Structures from carpophores: (g) thin-walled, nodose-septate hyphae; (h) nodose-septate hyphae with irregularly thickened walls; (k) fibre hyphae; (m) basidia; (n) basidiospores; (p) tramal cystidia; (q) skeletal cystidia.

walled, 4.5 — 6.5 x 2.4 — 3μ (Fig. 12 e). Ends of fibre hyphae project into the hymenium and slightly beyond it from the underlying tissues, appearing as hyaline cystidia, 3 — 3.6μ in diameter.

Submerged mycelium: (a) hyaline, thin-walled, nodose-septate hyphae as in the advancing zone; (b) nodose-septate hyphae with irregularly thickened walls as in the aerial mycelium; (c) chlamydospores intercalary and terminal, hyaline, ellipsoidal, thick-walled 6 — 20 x 4 — 8μ (Fig. 12 f).

Carpophore characters

Carpophores perennial, lignicolous, solitary or grouped, sessile, dimidiate; pileus applanate, occasionally connate, imbricate; hard corky or rigid up to 15 x 20 x 8 cm; upper surface at first finely tomentose, soon glabrous, uneven to zonate, somewhat furrowed, finally somewhat incrusted with age, at first whitish, later umbrinous to black; margin obtuse, entire, pallid; pore surface creamy white to pale amber or avellaneous, poroid at first but soon labyrinthiform and about 1 mm wide, dissepiments even, 0.75 — 1.5 mm wide; tubes up to 3 cm deep, somewhat decurrent, concolourous with the pore surface; context whitish to pale brown, 0.2 — 1.5 cm thick, corky, zonate, with concentric zones of darker and lighter colour, smooth, fibrous texture and darkening with KOH.

Hyphal characters: (i) thin-walled, nodose-septate hyphae hyaline, branched, with frequent H-connections, 1.8 — 3.0μ in diameter (Fig. 12 g); (ii) nodose-septate hyphae with irregularly thickened, refractive walls hyaline, branched, forming occasional H-connections and contents staining deeply in phloxine, 1.8 — 3.6μ in diameter, rare (Fig. 12 h); (iii) fibre hyphae long, more or less straight, or flexuous, unbranched, or, with one or two branches often with pointed ends sub-hyaline to pale brown, the walls thickened towards the middle with extremities thin-walled lumina prominent, staining, aseptate, or with one or two simple septa near the tips, widest at the ends, or, walls much thickened, with lumina narrowed or occluded and reduced to a thin interrupted line, expanding only towards the ends, 2.5 — 5.5μ in diameter (Fig. 12 k).

Hymenium: basidia long clavate 20.0 — 30.0 x 4.5 — 6.5μ bearing four short, slender, straight sterigmata 2.5 — 3.0μ (Fig. 12 m); basidiospores hyaline, long ellipsoid to cylindrical and flattened on one side, thin-walled, smooth 4.8 — 6.5 x 2.4 — 3.0μ (Fig. 12 n); tramal cystidia hyaline, ob-clavate, thick-walled to sub-solid 30.0 — 50.0 x 4.0 — 6.0μ or longer, arising in the hymenium or in the trama below (Fig. 12 p).

Construction. At the margin the fibre hyphae are mostly long, straight and unbranched with prominent lumina, their ends often thin-walled and collapsed. These hyphae are arranged more or less parallel to and loosely intertwined with each other and with the numerous branched, thin-walled, nodose-septate hyphae from which they arise. The older parts of the context are similar but the fibre hyphae have thicker walls, becoming sub-solid and few thin-walled, nodose-septate hyphae are present. In the upper part of the context the fibre hyphae bend upwards gradually, are mostly branched, sub-solid, up to 5.5μ in diameter more or less straight and loosely intertwined, and arranged with their apices closely packed and imbricate at a common level, to form the finely pubescent upper surface. Thin-walled, nodose-septate, branching, hyaline hyphae mostly 2.5μ in diameter are intertwined with the fibre hyphae just below the level of the upper surface. From the lower part of the margin and context, fibre hyphae turn downward towards the dissepiments. These fibre hyphae are narrower, mostly 2.2 — 4.0μ in diameter with more prominent lumina, often very tortuous and more frequently branched, the branches long and flexuous and becoming tightly interwoven in all

directions with each other and with the numerous nodose-septate hyphae into a denser and more compact tissue than the upper context. Some fibre hyphae remain more or less straight. Intertwined with the fibre hyphae are nodose-septate hyphae, mostly thin-walled but occasionally with their walls irregularly thickened and refractive, branching repeatedly and becoming increasingly numerous towards the surface of the dissepiments where they branch freely to form the numerous, short, closely packed, tightly intertwined, nodose-septate branches which bear the basidia. The ends of fibre hyphae from the trama of the dissepiments may protrude through this layer and beyond the basidia as tramal cystidia. Short fibre hyphae, 50.0 — 90.0μ in length, arising from thin-walled, nodose-septate hyphae in the trama, or, as lateral branches of fibre hyphae and mostly narrow, 1.8 — 2.2μ, near their origin and for part of their length, but then widening suddenly into spear-shaped ends (Fig. 12 p), may also project as skeletal-cystidia into the hymenium (Fig. 12 q). Thick-walled cystidia arise from the basidial fascicles on the same level as the basidia.

Decay and hosts

Daedalea quercina causes a brown rot of hardwood timber and trees where it lives saprophytically on dead parts (Cartwright & Findlay, 1946).

Specimens examined

Herb. DAOM: *F676, Quercus sp., Ottawa, Ont., Sept. 1926; *F2278, on red oak, Morton, Ont., June 1932; F6848, on hardwood stump, Mt. Burnet, Que., Nov. 1935; F6888, on*Quercus* sp., Chelsea, Que., Nov. 1935; F10198, on *Quercus* sp., Ile Perrot, Que., Aug. 1941; 17933, on *Quercus robur,* Bavaria, Sept. 1946; 22351, on *Eucalyptus* sp., Portugal, ex Herb J. Pinto-Lopes; 52788, on *Quercus borealis,* Wickham, New Brunswick; 53418, on *Quercus* sp., Gatineau, Que., Nov. 1950; 72046, Fungi Scandinaviae, Ellensvide, Sweden; *72510, Gatineau Park, Que., Oct. 1961.
Herb. PRE: 1480, Kirstenbosch, C.P., June 1921; 15552, on *Quercus* stump, ex Herb. L. O. Overholts; 22846, Falkenberg, Germany, Leg. Plogel; 24207, on *Quercus* sp. ex Hollos, Hungarian Fungi; 31394, Stellenbosch; 36573, on stump, Falcourt, Sussex, England, Aug. 1947; 34551, on *Quercus* sp., Cape Town; 41570, on *Eucalyptus* stump, ex Herb. J. Pinto-Lopes; *42366, on decayed hardwood, Pakenham, Ont., Aug. 1962.
Herb. STE: 1397, Kirstenbosch, C.P.; 1674, Kirstenbosch, C.P., July 1924; 2521, Kirstenbosch, C.P., June 1928; 2742, East London, C.P., Sept. 1932.

Discussion

In the cultures, fibre hyphae are present mainly in the tough, felty, fertile areas. On the other hand, the nodose-septate hyphae with irregularly thickened walls, which are so characteristic of cultures of this group, are not very numerous in the fertile parts of the culture. Instead, these hyphae make up a large proportion of the soft aerial mycelium where they may develop into solid hyphae with solid clamp connections.

This description of the cultural characters agrees well with those of Humphrey & Siggers (1933), Cartwright & Findlay (1946) and Nobles (1948) but the thin-walled swollen, globose cells, either single or in chains, usually "common in fragile, cinnamon-buff mycelium from the upper part of the culture in test tube cultures 6 — 8 weeks old", reported by Davidson *et al.* (1942) were not seen.

From the descriptions it is evident that three kinds of hyphae are present in carpophores of *Daedalea quercina,* viz.: nodose-septate hyphae with thin walls, nodose-septate hyphae with irregularly thickened walls and fibre hyphae which are mostly unbranched. The carpophores also possess extra-hymenial structures but are on the whole rather simple in construction despite their usual large size.

Thin-walled, nodose-septate hyphae have been reported in the carpophores of *Daedalea quercina* by Cunningham (1948 h), Pinto-Lopes & Farinha (1950),

Pinto-Lopes (1952), Overholts (1953), Teston (1953 b) and Teixeira (1960). The nodose-septate hyphae with irregularly thickened walls have been reported from cultures only by Nobles (1948, 1958 b), but these hyphae, which are so abundant in the cultures have not been reported form the carpophores before. They are present in the carpophores in small numbers only and were found only after prolonged and careful searching. It was noticed in the cultures that these hyphae were most numerous in areas away from the fibre hyphae and fructifications. It is therefore possible that these hyphae may be more abundant in the decayed wood, under the carpophores. In support of this view, it may be added here that large numbers of such hyphae were seen on the surface and in the vessels of a specimen of wood decayed by an unknown fungus which was recently examined by the author. This fungus displayed all the hyphal characters of cultures of species in group 25 (unpublished data).

Cystidia were not reported from the carpophores by Overholts (1953) but Bourdot & Galzin (1928) and Talbot (1954 a) figured fusiform, thick-walled cystidia which they regarded as hyphae projecting into the hymenium from the underlying tissues. Many of these projecting hyphae were seen in some specimens and some of these pseudo-cystidia (Lentz, 1954) or tramal cystidia (Donk, 1964) were rather characteristic in form (Fig. 12 p). They resemble normal fibre haphae in all characters except in their length and appear to be stunted fibre hyphae. Some of these structures were seen to be borne in the same position as the basidia on the same nodose-septate hyphae. These are regarded as skeleto-cystidia and have thick, refractive walls and narrow, aseptate lumina like fibre hyphae but lack their length. They fit the description of skeleto-cystidia given by Donk (1964, p. 234) very well.

The fibre hyphae from the carpophores are slightly darker in colour and generally larger in diameter than those from the cultures but are in other respects closely similar. As described here, they agree well with the descriptions by Cunningham (1948 h), Pinto-Lopes (1952), Overholts (1953) and Teston (1953 b) who stated that the fibre hyphae are more or less straight and unbranched or rarely branched.

From the above descriptions it is evident that the structures formed in culture are also present in the carpophores from which they were made. No chlamydospores were seen in the carpophores but they have been reported in hyphae present in the decayed wood (Cartwright & Findlay, 1946).

Cunningham (1948 h), in his characterization of the genus *Daedalea* Pers. ex Fr. stated that *Daedalea quecina*, the type species, has a trimitic hyphal system with the "binding hyphae aseptate, commonly of the bovista type". Teston (1953 a) and Kotlaba & Pouzar (1957) agreed. Teston (1953 a) reported that the binding hyphae were narrower more tortuous and branched more frequently than the skeletal hyphae. Teston's figures (1953 b, P14: 8) show hyphae which resemble the branches of fibre hyphae as illustrated here in Fig. 12 k. These branches perform a binding function but they are morphologically similar to and continuous with the straight fibre hyphae. These branches contribute to the binding system, as described by Corner (1932 a) in the case of some skeletal hyphae in the fruit-body of *Polystictus xanthopus* but they differ morphologically from the true binding hyphae from the fruit-body of *Polystictus xanthopus* (Corner 1932 a) or those of *Fomes fomentarius* (Teixeira, 1962 a) in their limited branching and unlimited growth. These branches can thus not be regarded as true binding hyphae. Nor were binding hyphae of the bovista type as described by Cunningham (1948 h), found in the tissues of the specimens examined. Donk (1964) furthermore accepted Corner's (1953) view that Cunningham's (1946) "binding hyphae of the bovista type"

are branched skeletals. This agrees with the observations described above. For these reasons the fruit-bodies of *Daedalea quercina* must be regarded as having a dimitic hyphal system in the sense of Corner (1932 a, b), Cunningham (1946) and Teixeira (1962 b). This conclusion contradicts the reports by Cunningham (1948 h) and Teston (1953 b).

Fidalgo (1957) discussed the nomenclatural status of *Daedalea* Pers. ex. Fr. and related genera. He concluded that the only distinction between the genera *Daedalea* Pers. ex Fr., *Lenzites* Fr. and *Trametes* Fr. is in the hymenial configuration, a character which is so variable in species of this group, as to be without significance. *Daedalea* Pers. ex Fr., *Trametes* Fr. and *Lenzites* Fr. are thus synonyms in his view; but comparison between the descriptions of *Daedalea quercina* on the one hand and *Trametes suaveolens* (L. ex Fr.) and *Lenzites betulina* (L. ex Fr.) Fr., the type species of *Trametes* Fr. and *Lenzites* Fr. respectively (Donk, 1960) on the other hand, shows that clear and significant distinctions in hyphal characters and construction exist between these species, viz.: hyphae with many, short, tortuous, thick-walled, aseptate branches, arising from thin-walled, nodose-septate hyphae and binding the tissues together (Fig. 23 d; 26 g) are abundant in the carpophores of *Trametes suaveolens* and *Lenzites betulina* but entirely absent from those of *Daedalea quercina*. The nodose-septate hyphae with irregularly thickened walls which are found in the carpophores, and, more abundantly, in the cultures of *Daedalea quercina* are entirely absent from the carpophores and cultures of *Trametes suaveolens* and *Lenzites betulina*. Furthermore, *Daedalea quercina* causes a brown rot (Overholts, 1953) and its cultures do not produce extra-cellular oxidase while cultures of *Trametes sauveolens* and *Lenzites betulina*, which cause white rots (Overholts, 1953), produce extra-cellular oxidase (see Group 45). These differences in hyphal composition, construction of the carpophores and biochemical activity of these two species indicate important phylogenetic differences which must necessarily outweigh all taxonomic considerations based on superficial similarities such as form, texture and colour of the carpophores. For these reasons the genus *Daedalea* Pers. ex Fr. is not congeric with the genera *Trametes* Fr. and *Lenzites* Fr. but constitutes a distinct and well-marked generic entity. *Daedalea quercina* thus is the type species of the genus *Daedalea* Pers. ex Fr. which is characterized by carpophores having a dimitic hyphal system consisting of nodose-septate generative hyphae with thin walls, nodose-septate hyphae with irregularly thickened walls, and sub-solid to solid, aseptate, skeletal hyphae unbranched or occasionally branched.

These results must influence the taxonomic positions of a large number of species of polypores because the genus *Daedalea* Pers. ex Fr. is one of the oldest genera accepted by Fries (1821). Together with *Daedalea quercina*, Nobles (1958 b) included a number of other species with similar cultural characters in Group 25. Among these were seven species of the genus *Coriolellus* Murrill, including the type *Coriolellus sepium* (Berk.) Murr. Sarkar (1959) in a study of six of these species, showed that the structures formed in their cultures were also present in their carpophores so that these six species formed a homogenous group which she placed in the genus *Coriollelus* Murr. From her descriptions it is evident that the hyphal characters of these species of *Coriolellus* are very similar to those of *Daedalea quercina* as described above. Other carpophore characters such as spore shape, carpophore texture, upper surface and attachment as well as the type of decay and host range also agree in many respects. The main differences are the absence of the daedaloid hymenial surface of *Daedalea quercina* and the presence of nodose-septate hyphae with uniformly thickened walls in its carpophores. Such hyphae were interpreted as "early stages of fibre hyphae" by Sarkar (1959) and were found in all the species of *Coriolellus* Murr. described by her. It thus appears

that the genus *Coriolellus* Murr. has so many characters in common with the type species of the genus *Daedalea* Pers. ex Fr. that these six species described by Sarkar (1959) should be transferred to the genus *Daedalea* Pers. ex Fr. Certain workers, however, consider the absence or presence of certain types of hyphae in fruit-bodies to be of importance at the genus level (Bondartseva, 1961; Teixeira, 1962b; Fidalgo & Fidalgo, 1963, 1966), and these hyphae described as "early stages of fibre hyphae" by Sarkar (1959) are absent from the carpophores of *Daedalea quercina*. Although the hyphal characters of too small a number of species have been studied with sufficient care and accuracy to properly evaluate the significance of a difference of this nature, it appears that the transfer of these six species of *Coriolellus* to the genus *Daedalea* Pers. ex Fr. by Aoshima (1967), is acceptable.

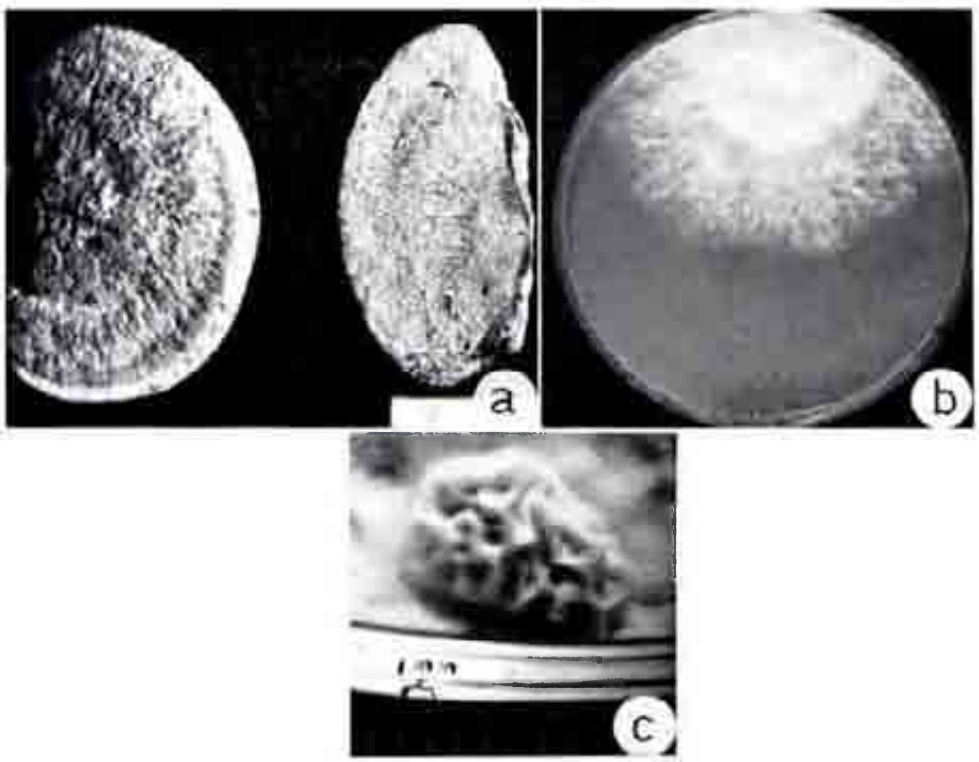

FIG. 13.— **Trametes moesta.** (a) Carpophores of PRE 42241 upper and hymenial surfaces; (b) culture of PRE 42241 at 6 weeks; (c) fructification in culture, × 4.

Trametes moesta *Kalchbrenner*, Fungi Macowaniana, Grevillea 10, 56, 1881.

Cultural characters

Growth is slow the mat reaching a radius of up to 25 mm in two weeks and up to 50 mm in six weeks. The margin is bayed and somewhat ragged with the hyphae raised to the limit of growth, cottony at first, becoming woolly and finely farinaceous, white, with small patches of felty mycelium developing on the surface of the agar, the patches increasing in size but becoming granular towards the inoculum and coalescing to form a dense, felty, mat around the inoculum and against the sides of the dish. Fertile areas appear as small depressions or irregular

ridges on these parts, after 5-6 weeks. At six weeks faint, radiating grooves may be seen in the younger more woolly mycelium with small, elongated tufts of dense mycelium over this part. Mat white, with occasionally "pale ochraceous buff" tinges on the felty patches. The reverse is bleached and a faint, slightly fragrant odour is given off. The oxidase reaction is negative when tested with gum guaiac solution.

Advancing mycelium: hyphae hyaline, nodose-septate, clamp connections simple, branching mostly near the septa, 2.2 — 5.5μ in diameter, the contents staining deeply in phloxine (Fig. 14 a).

Aerial mycelium: (a) thin-walled, nodose-septate hyphae as in the advancing zone; (b) nodose-septate hyphae with irregularly thickened walls and contents staining deeply in phloxine, branching or unbranched 1.5 — 5.0μ in diameter (Fig. 14 b); (c) fibre hyphae hyaline, long, unbranched or branching occasionally, solid or sub-solid with slight beadlike swellings with prominent lumina in those parts and the ends usually thin-walled, 1.5 — 5.2μ near the origin and widening gradually to 4 — 5μ at the widest part; others narrow, 0.7 — 1.0μ in diameter for some distance then widening suddenly to 4 — 5μ with the lumina more prominent and continuous or in a series of ellipsoidal spaces with deeply staining contents (Fig. 14 c).

Fructification: (a) thin-walled, nodose-septate hyphae as above; (b) fibre hyphae as in aerial mycelium but usually narrower, 2.5 — 3.5μ; (c) basidia long clavate 20 — 27 x 5.5 — 7.5μ with 4 straight sterigmata, 3 — 4μ long (Fig. 14 d); (d) basidioles 1.2 — 4μ wide, often with narrow branches, thin-walled, hyaline, arising from the basidial fasicles (Fig. 14 e); (e) basidiospores hyaline, long ellipsoidal to cylindrical and flattened on one side, with a marked apiculum, smooth, thin-walled, 6.0 — 8.5 x 3.0 — 4.2μ (Fig. 14 f).

Submerged mycelium: a thin-walled, nodose-septate hyphae as in the advancing zone; (b) chlamydospores abundant, hyaline, subglobose to ellipsoidal, intercalary or terminal, thick-walled, borne on thin-walled, nodose-septate hyphae 4.5 x 6.0 — 8.0μ (Fig. 14 g).

Carpophore characters

Carpophores perennial, lignicolous, solitary or grouped, sessile, dimidiate; pileus applanate to thick convex, single, laterally connate or imbricate, rigid, hard, corky, up to 12 x 7 x 3 cm; surface at first finely tomentose to sub-glabrous, smooth or somewhat rugulose and slightly rimose in age, at first creamy white, darkening to "pinkish buff" later to "avellaneous" in mature specimens or blackish in oldest parts; margin obtuse, thick, entire, creamy white when fresh, darkening to "pale pinkish buff" or "pinkish buff"; pore surface creamy white when fresh drying to somewhat dirty white or umber in older parts, poroid to daedaloid; pores elongate, angular, 0.5 — 1.0 mm wide; dissepiments dentate, thin; tubes whitish 0.5 — 12 mm deep, becoming stuffed with white hyphae; context "wood brown", zonate, fibrous, 1 — 10 mm thick, darkening with KOH.

Hyphal characters: (i) nodose-septate hyphae hyaline, branching, forming H-connections, thin-walled, contents staining in phloxine, 1.2 — 3.0μ in diameter (Fig. 14 h); (ii) nodose-septate hyphae with irregularly thickened walls, lumina irregularly narrowed and deeply staining contents, branching and forming H-connections, 2.4 — 4.5μ in diameter, rare (Fig. 14 k); (iii) fibre hyphae long, sub-hyaline to pale brownish, straight or flexuous, unbranched or with one to three branches, narrow near the origin but widening towards the middle, walls thickened, refractive, lumina narrow or obliterated often visible as interrupted lines, prominent towards the

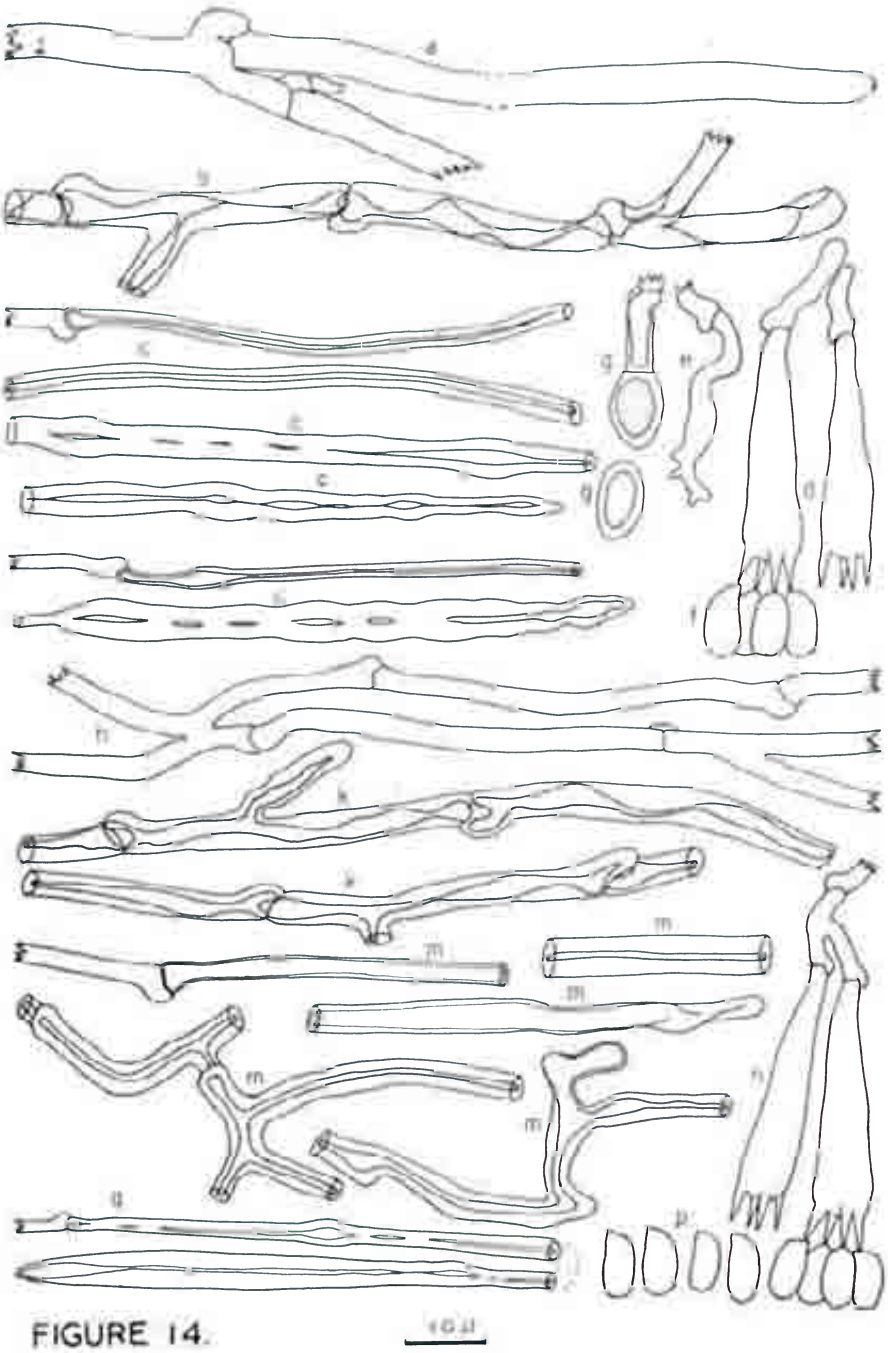

FIG. 14.— **Trametes moesta.** a - g. Structures from cultures: (a) thin-walled, nodose-septate hyphae from advancing zone; (b) nodose-septate hyphae with irregularly thickened walls; (c) fibre hyphae; (d) basidia; (e) basidioles; (f) basidiospores; (g) chlamydospores.
h - q. Structures from carpophores: (h) thin-walled, nodose-septate hyphae; (k) nodose-septate hyphae with irreguarly thickened walls; (m) fibre hyphae; (n) basidia; (p) basidiospores; (q) tramal cystidium.

extremities, aseptate or with occasional simple septa near the tips, 2.5 — 6.0μ in diameter (Fig. 14 m).

Hymenium: basidia long clavate, 22.0 — 30.0μ long, bearing four, straight, slender sterigmata 2.5 — 3.0μ (Fig. 14 n); basidiospores hyaline, cylindrical, thin-walled, smooth 7.2 — 9.8 x 3.3 — 4.2μ (Fig. 14 p); tramal cystidia sub-hyaline, tapering towards the tips, thick-walled, with narrow lumina, 3.0 — 6.0μ in diameter projecting up to 40μ beyond sub-hymenium, arising from trama as widened terminal portion, 50 — 80μ long, of short, narrow, fibre hyphae 1.5 — 3.0μ in diameter (Fig. 14 q).

Construction. At the margin the tissues consist of long, unbranched, hyaline fibre hyphae usually with prominent lumina and thin-walled extremities, often collapsed 3.0 — 4.0μ in diameter. These fibre hyphae are arranged more or less parallel to the direction of growth of the carpophore and loosely intertwined with each other and the numerous narrow, branching, thin-walled, nodose-septate hyphae from which they arise. In the older parts of the context the construction is similar but the fibre hyphae are darker in colour, their walls are thicker, the lumina are often reduced to narrow interrupted lines and the hyphae are of greater diameter, up to 6.0μ. Few nodose-septate hyphae are present. In the upper context the fibre hyphae are mostly sub-solid, more or less parallel to and intertwined with each other and with their ends closely packed at a common level to form the finely pubescent upper surface. Near the upper surface thin-walled, nodose-septate hyphae are fairly numerous, intertwined with the fibre hyphae and branching freely between them and across their direction of growth. In the older tissues thin-walled, nodose-septate hyphae are rather rare. In the lower context some fibre hyphae turn downwards to form the trama of the dissepiments. The fibre hyphae are somewhat narrower, 2.4 — 4.5μ, with wider lumina than in the upper context and more flexuous, often with a somewhat beaded appearance and many with one to three long branches, of similar appearance. These hyphae and their branches are tightly intertwined with each other as well as thin-walled, branching, nodose-septate hyphae and occasional nodose-septate hyphae with irregularly thickened walls to form the dense tissues of the lower context and trama. The nodose-septate, thin-walled hyphae become very numerous by repeated branching towards the hymenial surfaces where abundant, short, narrow branches produce the basidia. From the tramal tissues short fibre hyphae with narrow lower portions which suddenly increase in diameter towards the upper part (Fig. 14 q) and 50 — 90μ in length, project into the hymenium as tramal cystidia. Some branches of fibre hyphae may also project into the hymenium.

Decay and hosts

This species causes a brown rot of stumps of hardwood trees.

Specimens examined

Herb. PRE: 11288, coll. A. Roberts, May 1915; 34391, on indigenous hardwood, Hluhluwe Game Res., Oct. 1935; *42241, on *Acacia mearnsii* stump, Kaapse Hoop, Tvl., Feb. 1961; *42242, on *Acacia mearnsii* stump, Kaapse Hoop, Tvl., Feb. 1961; *42442, on *Acacia mearnsii* stump, Kaapse Hoop, Tvl., Feb. 1961.
Herb. STE: 538, as *Daedalea moesta* Kalchbrenner.

Interfertility studies

In order to test the possibility of conspecificity between this species and *Daedalea quercina,* which is very similar to *Trametes moesta,* four cultures made from single spores obtained from a fructification formed in culture by *Trametes moesta* PRE 42241, were paired on agar slopes in all possible combinations with

four cultures made from single spores of *Daedalea quercina* DAOM 2278. Four days after the mycelia had met on the slopes, the cultures were examined for the presence of clamp connections.

No clamp connections were found in any of the cultures thus indicating that *Daedalea quercina* and *Trametes moesta* are two different species.

Discussion

This species was described by Kalchbrenner (loc. cit.) from a collection by Tyson which could not be located for examination The specific epithet of the specimens examined in this study is based on Van der Bijl's description (1922 a), the collection PRE 11288 cited by him, and collection No. 538, *Daedalea moesta* Kalch. in the P. A. van der Bijl Herbarium, University of Stellenbosch. The other specimens cited above agree very well with Van der Bijl's description and specimens.

This species is not well-known in South Africa and the collections cited above are the only records of its occurrence. The three collections from Kaapse Hoop, are probably part of the same population of this fungus in that region since they were made from different hosts in a fairly small area. It is probable that the species may be much more widely distributed than these records would indicate.

The cultural characters of *Trametes moesta* had not been described before In culture the fungus forms nodose-septate hyphae, some with irregularly thickened walls, and fibre hyphae, whilst no extra-cellular oxidase is produced. This species thus displays all the characteristics of species included in Group 25 by Nobles (1958 b).

In cultural characters *Trametes moesta* resembles *Daedalea quercina* very strongly but differs from it in a slower growth rate, even margin, generally smoother topography of the mat and the formation of granular, fertile areas from which ridges more delicate than those in cultures of *Daedalea quercina*, arise. Cultures of *Trametes moesta* differ from those of species of the genus *Coriolellus* Murr., as described by Sarkar (1959) in the absence of the refractive projections from their nodose-septate hyphae with irregularly thickened walls. In most respects their cultures appear to be strikingly similar however, but the differences mentioned here may serve to distinguish cultures of *Trametes moesta* from those of other species if considered together with host and locality records if available.

Van der Bijl (1922 a) described the hyphae in carpophores of *Trametes moesta* as "simple, 2 — 4μ in diameter". This agrees to some extent with the description given above as the bulk of the hyphae in the carpophore are thick-walled, aseptate, fibre hyphae mostly unbranched or occasionally branched. Nodose-septate, thin-walled hyphae are abundant in the growing margin, tramal tissues and, to a lesser extent, near the upper surface of the carpophore. Nodose-septate hyphae with irregularly thickened walls were found in small numbers in the lower context and tramal tissues. Since hyphae with clamp connections at their septa must be regarded as generative hyphae, according to Corner (1953), Teixeira (1962 b), and Donk (1964), only two kinds of hyphae, generative and skeletal hyphae are present in the carpophores of *Trametes moesta*. This species thus has a dimitic hyphal system (Corner, 1932 a, b; Cunningham, 1946, 1954).

The structures that were found in the cultures of *Trametes moesta* were also present in the carpophores. The fibre hyphae were somewhat larger in diameter in the carpophores than in the cultures and were pale brownish rather than hyaline or sub-hyaline as in the cultures. The thin-walled, nodose-septate hyphae were abundant in the margin and dissepiments of the carpophores but the nodose-septate hyphae with irregularly thickened walls, were seen only rarely and occurred

mostly in mounts made from the older parts of the lower context just above the dissepiments.

The peculiarly branched structures seen in the hymenia of some fructifications formed in culture, were not seen in the carpophores. It was noticed at the time that the cultures in which these occurred, showed signs of dessication. Since these structures were formed on the basidial hyphae in the hymenium, they were regarded as deformed basidia formed under dry conditions as described by Bose (1943) in carpophores of *Polyporus sanguineus* and *Ganoderma lucidum*.

The carpophores of *Trametes moesta* are strikingly similar to those of *Daedalea quercina* in hyphal composition, construction and morphology. The types of hyphae found in *Daedalea quercina* were also found in carpophores of *Trametes moesta*. In both species the fibre hyphae, which make up the bulk of the carpophores are arranged in parallel and slightly intertwined and unbranched in the upper context. They are more frequently branched and tightly interwoven in the lower context and dissepiments. In both species short fibre hyphae or branches of fibre hyphae project as tramal cystidia from the tramal tissues of the carpophores. Both species cause brown rots in hardwood stumps or logs, but the non-appearance of clamp connections when single spore mycelia of these two species were mated, indicate that they are not conspecific.

Although carpophores of these two species are so strikingly similar in morphology and anatomy, small but consistent differences are present, viz.: the upper surface of carpophores of *Trametes moesta* have pale reddish-brown colours not common in *Daedalea quercina;* the pore surface of *Trametes moesta* is mostly poroid with the angular pores much smaller and dissepiments more delicate than those of *Daedalea quercina*. The basidiospores of *Trametes moesta* are longer and more markedly cylindrical than those of *Daedalea quercina*. Differences of this nature do not outweigh the great similarity in cultural characters and carpophore anatomy and are regarded by most workers as of interspecific value only. Therefore, these two species must be congeneric and *Trametes moesta* Kalch. should be transferred to the genus *Daedalea* Pers. ex Fr. as typified by *Daedalea quercina* L. ex Fr.

Trametes roseola Patouillard & Hariot, in Journal de Botanique 14, 239, 1900.

Cultural characters

Growth is slow, the mat reaching a radius of 27 mm in two weeks and covering the plate in 5 weeks. The margin is even, with mycelium appressed for about 1 mm, then raised, white, cottony behind the margin but becoming woolly towards the inoculum. After 3 weeks small, rounded, lumps of dense mycelium form along a narrow zone and on the sides of the plate, later covering the younger part of the mat in distinct zones of pebbly mycelium alternating with zones of smooth, felty mycelium. After six weeks the plates are covered, the mats raised, woolly, with a deep, wide, concentric groove in the newest growth and with successive narrow, concentric coarsely farinaceous to pebbly zones, often with "light ochraceous buff" colours and traversed by shallow radial grooves. About halfway across the mat and towards the inoculum, the texture is cottony-woolly. Mat is white at first, but turns a very pale "seafoam yellow" colour. Lumps of compact mycelium "light ochraceous buff" or "cinnamon buff" or "dresden brown" in colour appear on the surface after 3 — 4 weeks and later may develop minute pores over the surface. The reverse is unchanged at first but bleaching after 4 — 5 weeks. A faint, fragrant odour is given off. The oxidase reaction is negative when tested with gum guaiac solution.

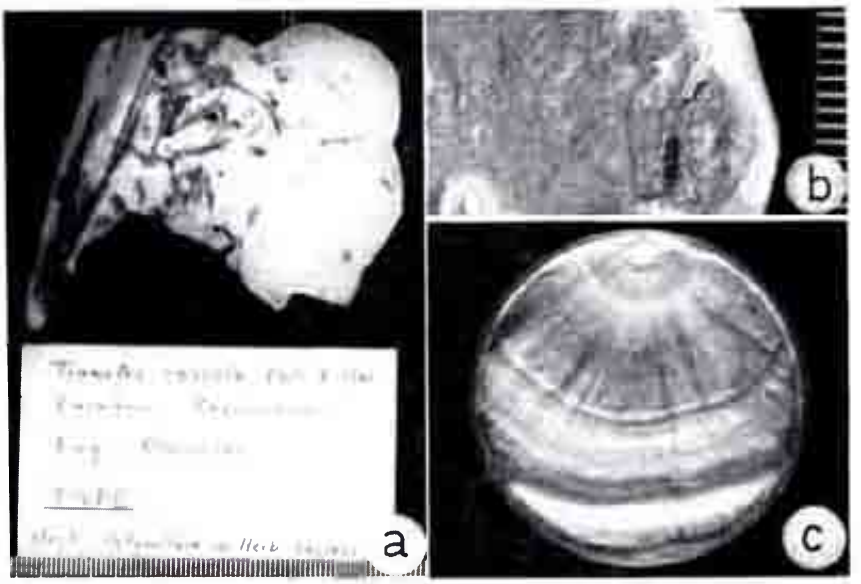

FIG. 15.— **Trametes roseola.** (a) Carpophore of type specimen, upper surface and (b) hymenial surface; (c) culture of PRE 42443 at 6 weeks.

Advancing mycelium: hyphae hyaline, simple or branching near the septa, nodose-septate with deeply staining contents 2.2 — 4.5μ in diameter (Fig. 16 a).

Aerial mycelium: (a) hyphae as in the advancing zone; (b) nodose-septate hyphae with irregularly thickened walls, often solid and refractive in parts, branched or unbranched 2.5 — 4.5μ in diameter (Fig. 16 b); (c) fibre hyphae hyaline at first, later subhyaline, unbranched or very occasionally branched, walls thick and refractive, lumina narrow, widening near the tips, aseptate or occasionally with one or two simple septa, 2.5 — 3.5μ, arising from thin-walled, nodose-septate hyphae and of fairly slow growth (Fig. 16 c).

Submerged mycelium: (a) hyphae as in the advancing zone; (b) nodose-septate hyphae with irregularly thickened walls as in aerial mycelium; (c) chlamydospores terminal or intercalary, ovoid or ellipsoid with thick, refractive walls 18.0 — 30.0 x 9.0 — 12.0μ (Fig. 16 d).

Carpophore characters

Carpophore annual or perennial, lignicolous, solitary, sessile, pileus conchate to somewhat spathulate, soft corky, drying to corky, up to 5.5 x 6.0 x 1.2 cm; surface finely pubescent, smooth, mat, azonate, "pale ochraceous buff" to "light pinkish cinnamon" or becoming fuscous in parts in older specimens; margin obtuse, entire, thick and rounded, concolorous with upper surface; pore surface "seashell pink" darkening to "vinaceous cinnamon" or "buff brown" and cracking on drying; pores rounded or slightly angular, 5 — 8 mm, dissepiments even; tubes pale yellowish, 0.5 — 1.0 mm deep, stratified in some specimens, decurrent at point of attachment; context pale "ochraceous buff" to "light pinkish cinnamon" floccose or somewhat fibrous, with occasional concentric, darker zones, and darkening in KOH.

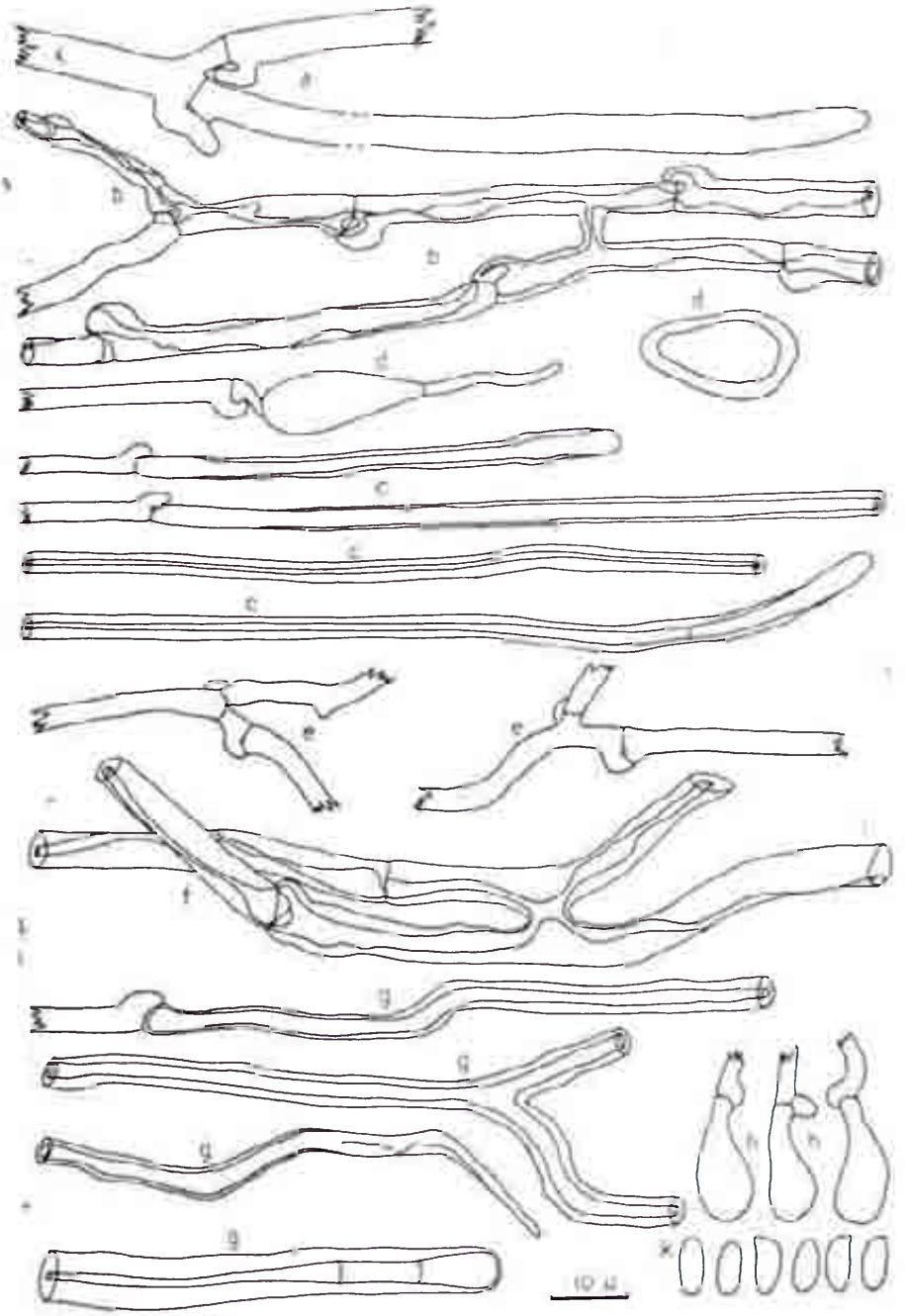

FIG. 16.— **Trametes roseola.** a - d. Structures from cultures: (a) thin-walled nodose-septate hyphae from advancing zone; (b) nodose-septate hyphae with irregularly thickened walls; (c) fibre hyphae; (d) chlamydospore.
e - k. Structures from carpophores: (e) thin-walled, nodose-septate hyphae; (f) nodose-septate hyphae with irregularly thickened walls; (g) fibre hyphae; (h) basidia; (k) basidiospores.

Hyphal characters: (i) nodose-septate hyphae hyaline, thin-walled, with deeply staining contents and branching near the septa 2.0 — 3.0μ in diameter (Fig. 16 e); (ii) nodose-septate hyphae with walls irregularly thickened and refractive, hyaline, branching near the septa, forming H-connections, 3.0 — 6.0μ in diameter (Fig. 16 f); (iii) fibre hyphae sub-hyaline to pale brownish, straight or flexuous, mostly unbranched, occasionally branched, thick-walled the lumina prominent or narrow, seldom occluded, aseptate or occasionally with one or two simple septa near the thin-walled tips, narrow and thin-walled towards the origin, arising from thin-walled, nodose-septate hyphae, 2.2 — 7.0μ in diameter (Fig. 16 g).

Hymenium: basidia hyaline, clavate 8.0 — 15.0 x 4.5 — 6.0μ with short, straight sterigmata 1.5 — 2.2μ (Fig. 16 h); basidiospores hyaline, long ellipsoidal to cylindrical, smooth, thin-walled 4.8 — 6.0 x 2.2 — 2.8μ (Fig. 16 k).

Construction. The margin consists of long, straight, unbranched fibre hyphae, walls subhyaline to pale brownish, arranged more or less parallel to or somewhat intertwined with each other, their tips projected forward to form the margin of the pileus. Branching, narrow, hyaline, thin-walled, nodose-septate hyphae, from which the fibre hyphae arise, are intertwined and interwoven with them just behind the margin. Towards the upper context the fibre hyphae are darker in colour, with thicker walls and are of larger diameter than in the margin but also parallel to each other and turning upwards towards the upper surface where their thin-walled ends are closely packed at a common level to form the finely pubescent to subglabrous upper surface. Just below the upper surface, narrow, thin-walled, branching, nodose-septate hyphae, intertwined with the fibre hyphae, are fairly numerous. In the older tissues few nodose-septate hyphae are present. The lower context consists of long fibre hyphae, straight or flexuous, 3.0 — 4.0μ in diameter, occasionally branched, walls thickened, but lumina prominent, more or less parallel to one another and slightly intertwined with one another and with small numbers of thin-walled, branching, nodose-septate hyphae from which they arise and occasional nodose-septate hyphae with irregularly thickened walls, 3.0 — 6.0μ in diameter. From the lower context the hyphae turn downwards into the dissepiments where the fibre hyphae are narrower and become very flexuous and more tightly interwoven than higher up in the context. Thin-walled, nodose-septate hyphae with deeply staining walls are numerous, branching frequently and anastomosing parallel to and across the direction of growth of the fibre hyphae and turning outwards toward the pore surfaces with increased branching to form the tightly interwoven, short, nodose-septate branches of the sub-hymenium bearing the basidia. Also in the dissepiments are occasionally portions of nodose-septate hyphae with irregularly thickened walls, continuous with the thin-walled, nodose-septate hyphae.

Decay and hosts

Trametes roseola causes a brown rot of broad-leaved trees. Hopkins (1939, 1943) reported this species as the cause of stem rot of living trees in Rhodesia.

Specimens examined

Herb. PRE: 26709, on *Eucalyptus ficifolia,* Pietermartizburg, 1934; 28560, on *Acacia mearnsii,* Impolweni Natal, Sept. 1934; 30191, on *Acacia mearnsii,* Melmoth, March, 1935; 30634, on living *Prunus persica,* Rhodesia, June 1937; 30204, on *Acacia mearnsii* wood, Melmoth, Natal 1935; 24116, on dead wood, Albert Falls, Natal; 39016, on dead wood, ex Herb. Timber Res. Lab., Johannesburg; *42443, on decayed hardwood log, Bushbuckridge, Tvl., Feb. 1961. *Herb.* Patouillard in FH: Sheet no. 2853, 3 collections in packets marked: "Caraban (Casamance) Leg. Chevalier"; "313, sur branche mort, Reserve forestiêr de Compong Chnang, Cambodge, Juillet 1921, M. Perclot;" "Madagascar, M. Decary 1920."

The specimen from Caraban on Patouillard's sheet no. 2835, agrees with the collection data mentioned in the original description (Patouillard & Hariot, 1900) and must therefore be designated the type specimen (Fig. 15 a, b).

Discussion

The presence of aseptate fibre hyphae and nodose-septate hyphae, some with irregularly thickened walls, and the absence of extra-cellular oxidase enzymes in its cultures, place *Trametes roseola* in Group 25 (Nobles, 1958 b). Its cultural characters agree well with those of other species in this group but the pale yellowish-green colour of the mycelial mat, the colour of the poroid, felty lumps in the cultures and the slow-growing fibre hyphae are unique in cultures of *Trametes roseola* and serve to distinguish this species from others in Group 25. This species had not been described in culture before.

The South African collections of this fungus agree very well in morphological and hyphal characters with Patouillard's collections, one of which is designated as the type. All the carpophores were rather small, with minute pores barely visible to the naked eye, fairly thick dissepiments and with a soft, "trametoid" feel and appearance. To the type specimen is attached a small piece of hardwood, from which it grew, showing a characteristic brown rot. No spores could be found on the type specimens but young basidia were very numerous. There is no doubt that the South African specimens are conspecific with Patouillard's collections.

From the description it is evident that the carpophores of *Trametes roseola* are simple in construction. They consist of three types of hyphae only, viz. thin-walled, nodose-septate hyphae, nodose-septate hyphae with irregularly thickened walls and fibre hyphae. The fibre hyphae are mostly unbranched and lightly intertwined. The nodose-septate hyphae are branched but not tightly interwoven with the fibre hyphae. There is an almost total absence of a binding function in the hyphal elements so that the fruit-bodies feel soft and somewhat fragile.

From the descriptions, it is evident that the vegetative structures formed in culture are also present in the carpophores. As in other species of this group, the nodose-septate hyphae with irregularly thickened walls were very numerous and prominent in the cultures but rare in the carpophores. In one carpophore, PRE 42443, however, these hyphae were fairly abundant in a narrow zone between two layers of tubes and towards the middle of the carpophore where they were visible as a faintly greenish patch in the otherwise apricot-coloured context tissue.

In gross morphological features and texture of its carpophores, *Trametes roseola* resembles *Trametes suaveolens* (L. ex Fr.) Fr., the type of *Trametes* Fr., very closely. Comparison of their hyphal characters, however, reveals that this resemblance is entirely superficial since the short, much branched fibre hyphae (or binding hyphae), present in carpophores of *Trametes suaveolens*, are absent from the carpophores of *Trametes roseola*. Nodose-septate hyphae with irregularly thickened walls are present in carpophores and cultures of *Trametes roseola* but not in those of *Trametes suaveolens*.

The similarities in cultural characters and hyphal characters of their carpophores indicate close affinities between *Trametes roseola, Daedalea quercina* and species of the genus *Coriolellus* Murr. described by Sarkar (1959). The small fruit-bodies of these *Coriolellus* species however, contain hyphae described by Sarkar as "immature fibre hyphae" or "incompletely differentiated fibre hyphae." These hyphae, from her figures, are thick-walled, nodose-septate or "sclerified generative hyphae" (Donk, 1964) which are also formed in cultures of these fungi. Such hyphae are absent from cultures and carpophores of both *Trametes roseola* and *Daedalea quercina*. Because it is not known at present whether the formation of thick-walled, nodose-septate hyphae, in species of which the carpophores consist mainly of aseptate fibre hyphae, takes place as a result of the influence of

environmetal factors or genetic factors, it appears to be advisable not to group *Trametes roseola* with these species of *Coriolellus* Murr. Donk (1966) recently transferred these *Coriolellus* spp. described by Sarkar (1959), to the genus *Antrodia* Karsten. The type species of *Antrodia* Karst., *Trametes mollis* (Sommerf.) Fr., however, lacks nodose-septate hyphae with irregularly thickened walls in its cultures. Nobles (1958 b) placed cultures of this species in her Group 48 which differ from cultures of Group 25 by the presence of a brown mycelial mat and the production of extra-cellular oxidase enzymes.

Although the cultural characters and hyphal characters of the fruit-bodies of *Trametes roseola* resemble those of *Daedalea quercina* in so many respects, their fruit-bodies do not appear to be so markedly similar in gross morphology. Fruit-bodies of *Trametes roseola* are smaller, of different colour and softer in texture than those of *Daedalea quercina* and have small pores rather than daedaloid dissepiments. They also lack tramal or skeleto-cystidia. On the other hand, the fruit-bodies of *Trametes roseola* are constructed in the same way and of the same types of hyphae as those of *Daedalea quercina* and further have the same thick dissepiments, anoderm surface, cylindrical spores and context darkening in KOH. Furthermore, fruit-bodies of *Trametes roseola* with a daedaloid hymenial surface were figured and reported by Lloyd (1922, p. 1145) from North Borneo. The differences in gross morphology of the carpophores of these two species thus appear to be of minor importance. Many workers (e.g. Teixeira, 1962 b; Furtado, 1965 a, b) regard hyphal characters as important at the generic level. As the carpophores of these two species agree in so many hyphal and micromorphological characters, the differences between them appear to be of interspecific nature only and *Trametes roseola* appears to be congeneric with *Daedalea quercina*, the type species of the genus *Daedalea* Fr.

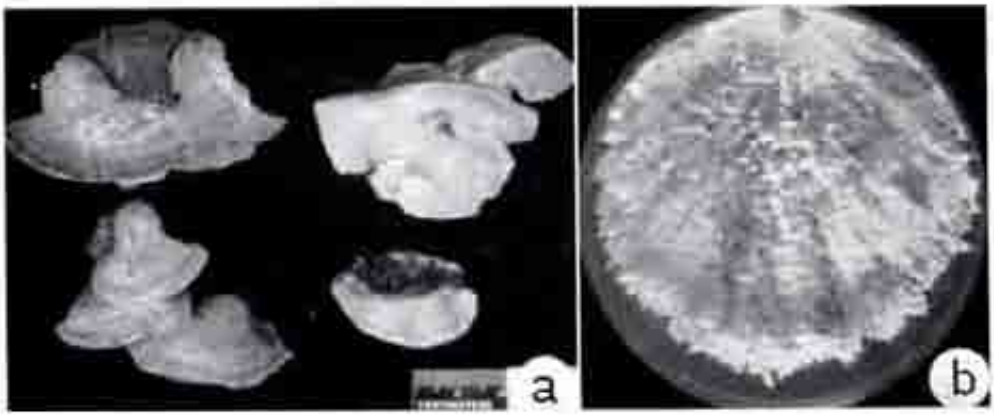

FIG. 17. — **Fomes cajanderi.** (a) Carpophores of DAOM 31973; (b) culture of DAOM 31973 at 6 weeks.

Fomes cajanderi *Karsten*, Finska Vet.-Soc. Ofv. Forh. 46 (11), 8, 1904.

Trametes subrosea Weir, Rhodora 25, 217, 1923;

Fomitopsis subrosea (Weir) Bond. & Sing., Ann. Mycol. 39, 55, 1941;

Fomitopsis cajanderi (Karst.) Kotlaba & Pouzar, Ceska mykologie 9, 157, 1957.

Cultural characters

Growth moderately fast to slow the colony reaching a radius of about 40 mm in two weeks covering the plates in 4 to 5 weeks. Margin even to slightly bayed with mycelium raised to limit of growth. Behind the margin mat is thin, cottony, raised but collapsing to sub-felty, or, more compact to almost velutinate around the inoculum, white at first but soon developing "seashell pink" to "pale salmon color" tints near the inoculum. Later the areas of more compact mycelium develop irregular, pellicular-felty patches which gradually enlarge and coalesce to form smooth or vaguely, radially, grooved patches of raised, felty mycelium on which angular pores, labyrinthiform at first, develop. These patches gradually become seashell pink", "pale congo pink" or "hydrangea pink", expanding continually, with the older, coloured areas darkening gradually to "vinaceous pink" or "vinaceous fawn", and "Roods brown" in the oldest tubes. Fruiting areas enlarge gradually by the formation of new tubes around the periphery. The reverse remains unchanged and a faint, sweet odour is emitted. No diffusion zones are formed on gallic acid and tannic acid agar but colonies op to 3.0 cm on the former medium and up to 1.5 cm on the latter, are formed A negative reaction is obtained when gum guaiac solution is applied to the culture.

Advancing mycelium: hyphae hyaline, nodose-septate, branching at or near the septa, with contents staining deeply, 1.5 — 3.5μ in diameter (Fig. 18 a).

Aerial mycelium: (a) thin-walled hyphae as in the advancing zone, 1.2 — 3.0 — (3.5) μ; (b) nodose-septate hyphae with walls irregularly thickened and refractive and occasionally with refractive projections, lumina irregularly narrowed and staining deeply 1.5 — 4.5μ in diameter, branching freely, numerous in the pellicular areas (Fig. 18 b); (c) fibre hyphae long, straight, unbranched, sub-hyaline or hyaline, solid with lumina visible at the narrower thin-walled ends or sub-solid with very narrow lumina, aseptate, up to 3.0μ in diameter along middle portion (Fig. 18 c); (d) solid, refractive, branching hyphae with hyaline walls and prominent, solid clamp connections, the lumina lacking or reduced to an interrupted line 1.5 — 3.0μ in diameter arising from thin-walled, nodose-septate hyphae or nodose-septate hyphae with irregularly thickened walls (Fig. 18 d).

Fructifications: (a) basidia clavate 10.5 — 18.0 x 4.2 — 5.1μ with four slender sterigmata 2.4 — 3.1μ (Fig. 18 e); (b) basidiospores long-cylindrical or allantoid, obliquely apiculate, hyaline, smooth, thin-walled 4.8 — 6.0 x 1.6 — 2.1μ (Fig. 18 f); (c) fibre hyphae as in the aerial mycelium; (d) nodose-septate hyphae with irregularly thickened walls as in aerial mycelium rare.

Submerged mycelium: (a) thin-walled, nodose-septate hyphae as in the advancing zone 1.5 — 3.0μ in diameter; (b) nodose-septate hyphae with irregularly thickened walls as in the aerial mycelium 1.5 — 6.0μ; (c) chlamydospores rare, intercalary or terminal, ovoid to ellipsoidal, walls slightly thickened, 8.0 — 20.0 x 6.0 — 8.0μ

Carpophore characters

Carpophore annual or reviving a second season, lignicolous, solitary or compound, sessile or effused-reflexed; pileus conchate to applanate, imbricate, often laterally connate, coriaceous to corky, drying rigid, up to 5.0 — 10.5 x 1.7 cm; upper surface at first velvety tomentose but later radially fibrillose or nearly glabrous, smooth or somewhat rugose often zonate, pinkish red at first but soon pinkish brown in age and occasionally with a thin, dark, brittle crust; margin acute, thin, entire, concolourous with upper surface; pore surface "vinaceous" to "orange vinaceous", poroid; pores rounded or angular 3 — 5 mm, dissepiments even; tubes whitish, up to 3 mm deep, stratified; context soft corky, "hydrangea pink" to "congo pink", indistinctly zonate, up to 12 mm thick.

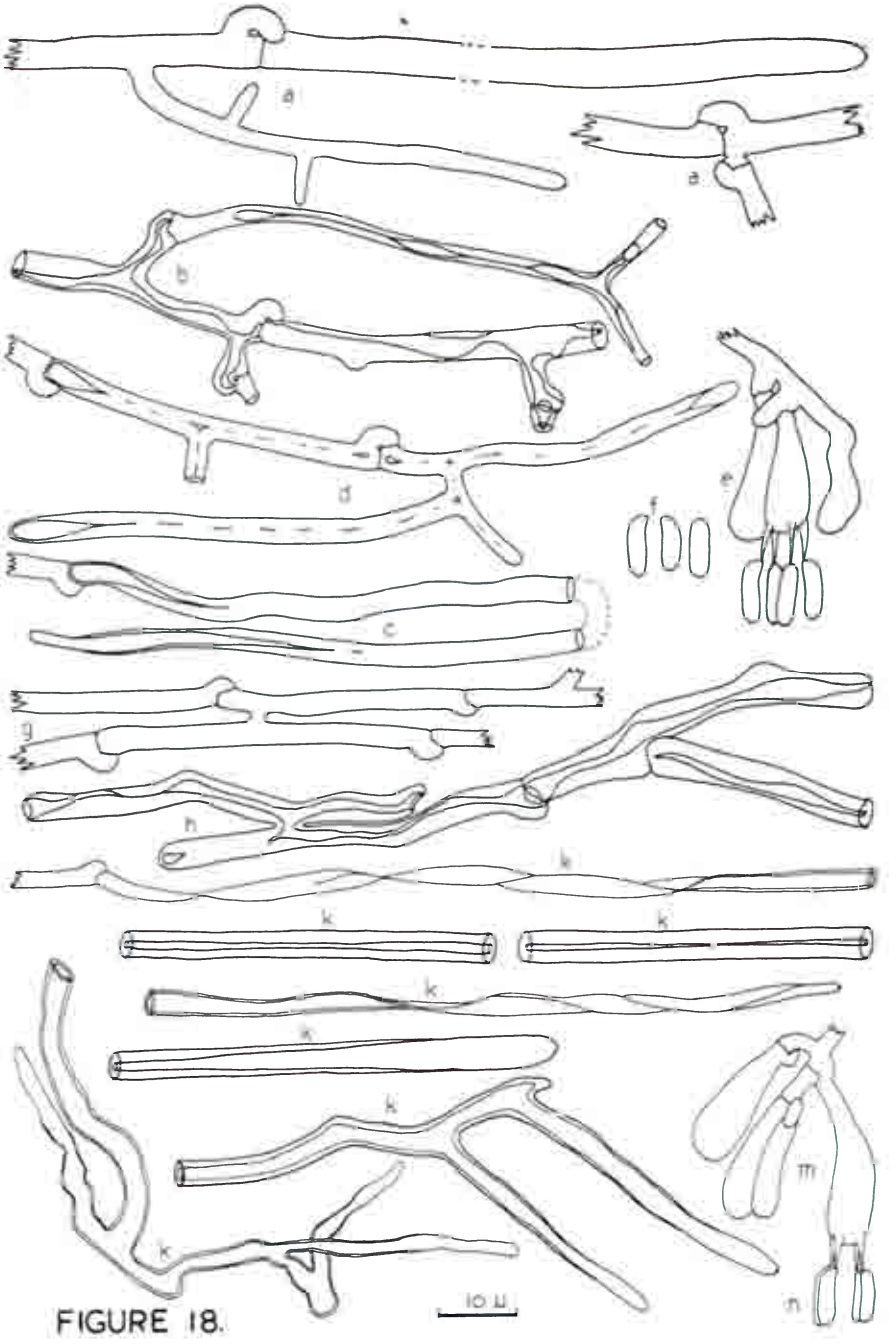

FIGURE 18.

FIG. 18.— **Fomes cajanderi.** a - f. Structures from cultures: (a) hyphae from advancing zone: (b) nodose-septate hyphae with irregularly thickened walls; (c) fibre hyphae; (d) thick-walled or subsolid, nodose-septate hyphae; (e) basidia; (f) basidiospores.
g - n. Structures from carpophores: (g) thin-walled, nodose-septate hyphae; (h) nodose-septate hyphae with irregularly thickened walls; (k) fibre hyphae; (m) basidia; (n) basidiospores.

Hyphal characters: (i) nodose-septate hyphae thin-walled, hyaline, branching at or near the septa, with deeply staining contents, 1.5 — 3.0μ in diameter (Fig. 18 g); (ii) nodose-septate hyphae with irregularly thickened walls hyaline, branched or unbranched, rare, 2.4 — 4.5μ in diameter (Fig. 18 h); (iii) fibre hyphae long, unbranched, or with one or two branches towards the tip, straight or tortuous, thick-walled, sub-hyaline to pale brownish, lumina narrow, aseptate, occasionally occluded, always prominent towards the ends which are thin-walled and often collapsed, 1.5 — 5.0μ in diameter (Fig. 18 k).

Hymenium: basidia narrowly clavate, 12.0 — 15.0 x 4.0 — 5.5μ bearing four short sterigmata 2.1 — 2.4μ (Fig. 18 m); basidiospores long narrow-cylindrical to somewhat allantoid, apiculate, hyaline, smooth, thin-walled, 5.0 — 7.0 x 1.8 — 2.4μ (Fig. 18 n).

Construction. At the margin the carpophore consists mainly of long, straight, unbranched, sub-hyaline fibre hyphae with prominent lumina and thin-walled ends sometimes collapsed, arranged parallel to or slightly intertwined with each other and with numerous, narrow, branching, thin-walled nodose-septate hyphae from which they arise. Behind the margin and in upper context the fibre hyphae have thicker and darker walls and turn upward towards the upper surface but are still more or less parallel to and slightly intertwined with one another and thin-walled, branching, nodose-septate hyphae, mostly empty and collapsed. Occasional lengths of nodose-septate hyphae with irregularly thickened walls are also present, intertwined with the others. At the upper surface the ends of the fibre hyphae may be arranged parallel to each other and packed at a common level to form a finely pubescent surface or, frequently the ends may be tangled and intermingled with numerous, tortuous, thin-walled, nodose-septate hyphae and agglutinated with a thin layer of lacquer-like substance into a glabrous trichoderm with resinous crust (Lohwag, 1940). Subsequent growth of the hyphae may result in a succession of similar layers which may be up to 500μ thick. In the lower context the fibre hyphae are similar to those in the upper context but turn downwards into the trama of the dissepiments. Towards the tramal tissues the fibre hyphae become generally more tortuous, one or two branches are often formed, the branches being long and similar to the parent hyphae. All hyphae become more tortuous and tightly interwoven and bound into a dense tissue. Below the context towards the trama, thin-walled nodose-septate hyphae with deeply staining contents and branching frequently and repeatedly, become increasingly numerous and tightly intertwined with the fibre hyphae. Nodose-septate hyphae with irregularly thickened walls, some apparently solid, are also fairly numerous in this region and intertwined with the other hyphae. The thin-walled, nodose-septate hyphae branch repeatedly towards the surface of the dissepiments where the basidia are borne in clusters on their numerous branches, 1.8 — 2.4μ in diameter. No accessory structures are present.

Decay and hosts

Fomes cajanderi causes a brown rot of coniferous wood.

Specimens examined

Herb. DAOM: *10278, on *Picea mariana,* Champlain Co., Que.; 17029, on coniferous stump, St. Aubert, Que.; 17164, on *Pseudotsuga taxifolia,* Saanichton, B.C., No. 1959; *17522, on *Picea mariana* slash, Lake Sasiginigate Man., Aug. 1947; 17528, on *Picea glauca* log, Wasagaming, Man., Sept. 1947; *17529, on *Picea glauca* log, Wasagaming, Man., Sept. 1947; 17572, on *Picea sp.,* Rocky Mt. House, Alta., Oct; 22380, on *Picea sp.,* Harricanaw Riv., Que., June 1946; 22729, on *Abies balsemea,* Tweedie Brook, N.B., July 1949; 30061, on *Picea glauca,* Riding Mt. Nat. Park, Man., July 1950; 31849, on *Pseudotsuga taxifolia,* Cathedral Grove, B.C., May 1948; *31973, on *Tsuga canadensis,* Warrensburg, N.Y., Oct.

1955; 53725, on *Picea* sp., Victoria Park, N.S.; *72322, on *Pseudotsuga taxifolia*, Beacon Hill, Vict., B.C.; *72652, on *Picea mariana*, Warrensburg, N.Y., Sept. 1961; 72742, on *Picea glauca*, Laird River, N.T.; *73183, on coniferous log, S. Santion Highway, Oregon, Aug. 1962.

Discussion

Cultural characters of this species as described here, agree well with the descriptions by Campbell (1938), Davidson *et al.* (1938), Cartwright & Findlay (1946) and Nobles (1948, 1958 b). It fits well into Group 25 and its cultures differ from those of other species in this group mainly in the presence of pinkish colours.

The hyphae of the carpophores of this species have been described by Overholts (1953) who stated: "hyphae pale brown in KOH, long and flexuous, simple, with no cross walls or clamps 2.5 — 5.0μ in diameter". Lowe (1957) later stated that these hyphae were "mixed with a small amount of thin-walled, clamped hyphae, 3 — 5μ in diameter". Farinha (1946) reported clamped hyphae with walls very slightly thickened up to 6μ in diameter in addition to thick-walled, aseptate occasionally branching hyphae from carpophores of this species. None of these authors mentioned the presence of nodose-septate hyphae with irregularly thickened walls in the carpophores as described here and first reported from cultures by Nobles (1948).

From the above descriptions it is evident that the structures formed in the cultures are also present in the carpophores with the exception of the chlamydospores. These may probably be found in decayed wood associated with the carpophores as in the case of *Daedalea quercina* (Cartwright & Findlay, 1946). As in the other three species described here in Group 25, the nodose-septate hyphae with irregularly thickened walls were not very abundant in carpophores of this species either but were nevertheless present in sufficient numbers in the older tissues above the pores to ensure their rapid detection. Basidia and spores are virtually identical in both cultures and carpophores.

The hyphal characters and construction of the carpophores of *Fomes cajanderi* Karst. resemble those of *Daedalea quercina* L. ex Fr. as described above, quite closely. This resemblance indicates a close phylogenetic relationship between these species although morphological differences between them are evident. *Fomes cajanderi* has a poroid hymenium, rose-coloured context and a type of upper surface not found in *Daedalea quercina*. In these characters, *Fomes cajanderi* and *Daedalea quercina* appear to be of interspecific importance only and are outweighed by the similarity in hyphal characters and construction with the carpophores of *Daedalea quercina*.

Fomes cajanderi has been described as *Trametes subrosea* by Weir (1923) but comparison of its hyphal characters with those of *Trametes suaveolens* (L. ex Fr.) the type of *Trametes* Fr. (Donk, 1960) reveals important differences. Carpophores of *Trametes suaveolens* have much branched, fibre hyphae with short tortuous branches, (binding hyphae, Corner, 1932 a; Cunningham, 1946, 1954) in addition to the thin-walled, nodose-septate hyphae and unbranched fibre hyphae. Carpophores of *Fomes cajanderi* lack "binding hyphae" and instead have thick-walled, nodose-septate hyphae with irregularly thickened walls which are not present in the carpophores of *Trametes suaveolens*. Any similarity between the two species, is thus entirely superficial.

Overholts (1953) transferred *Fomes cajanderi* (as *Trametes subrosea* Weir) to the genus *Fomes* (Fr.) Kickx on account of its stratified pores. Teixeira (1962 a) in a study of three species of *Fomes* (Fr.) Kickx which included the type, *Fomes*

fomentarius (L. ex Fr.) Kickx, showed that the carpophores of species of this genus have solid or sub-solid, aseptate "binding hyphae" in addition to unbranched fibre hyphae and thin-walled nodose-septate hyphae in the context, but lack the nodose-septate hyphae with irregularly thickened walls which are present in carpophores of *Fomes cajanderi*. Furthermore, the upper surface of *Fomes fomentarius* is completely different from that of *Fomes cajanderi*. Because of these differences, *Fomes cajanderi* thus cannot be regarded as congeneric with *Fomes fomentarius*.

Bondartsev & Singer (1941), Bondartsev (1953) and Kotlaba & Pouzar (1957) included *Fomes cajanderi* Karst. in the genus *Fomitopsis* Karsten together with the type species *Fomes pinicola* (Sw. ex Fr.) Cooke. There are however great differences in hyphal characters between these two species. Carpophores and cultures of *Fomes pinicola* lack the nodose-septate hyphae with irregularly thickened walls which are present in the carpophores and cultures of *Fomes cajanderi*. Furthermore, the fibre hyphae of *Fomes pinicola* are seldom branched and very slightly intertwined. The rigidity of the carpophore is due to a certain amount of agglutination of the hyphae. This is not evident in carpophores of *Fomes cajanderi* which are thus more complex in construction and of different texture. A certain amount of similarity in the nature and construction of the crustose upper surface of certain specimens of *Fomes cajanderi* and those of *Fomes pinicola* is evident. Lohwag (1940), however, reported similarities in the upper surfaces of *Fomes pinicola* and a number of other species of the genus *Ungulina* Pat. which were later placed in different groups on the basis of their hyphal and cultural characters by Nobles (1958 b). Therefore, the similarity in the upper surfaces of the carpophores of *Fomes cajanderi* and *Fomes pinicola* must be regarded as of lesser importance than the dissimilarity in their hyphal characters and *Fomes cajanderi* cannot be regarded as congeneric with *Fomes pinicola*.

Kotlaba & Pouzar (1957) suggested that *Fomes cajanderi* is transitional between *Fomitopsis* Karst. and *Coriolellus* Murr. From the above descriptions and discussions it is clear that there are few similarities between *Fomes cajanderi* and *Fomes pinicola*. Sarkar (1959) showed that six species of the genus *Coriolellus* Murr., including the type species, *Coriolellus sepium* (Berk.) Murr. which also have the cultural characters of Group 25 (Nobles, 1958 b) have hyphal characters and carpophores constructed very much like those of *Fomes cajanderi*, but she described the thick-walled, nodose-septate hyphae, which she called "incompletely differentiated fibre hyphae", in the carpophores of these species of *Coriolellus*. Such hyphae, which appear to be sclerified generative hyphae (Donk, 1964), were not found in the carpophores of *Fomes cajanderi*.

The carpophores of *Fomes cajanderi* thus differ from those of these species of *Coriolellus* Murr. in respect of the types of hyphae present in them. On the other hand, it was shown before, that many similar characters and structures exist in carpophores of *Daedalea quercina* L. ex Fr., the type of the genus *Daedalea* Pers. ex Fr., and *Coriolellus sepium* (Berk.) Murr., the type of the genus *Coriolellus* Murr. It was suggested that the six species of *Coriolellus* Murr. as described by Sarkar (1959), and which included the type species, should be included in the genus *Daedalea* Pers. ex Fr. The carpophores of *Coriolellus sepium* (Berk.) Murr., however, differ from those of *Daedalea quercina* L. ex Fr. in the same characters as carpophores of *Fomes cajanderi* differ from those of *Daedalea quercina*. In cultural characters too, there is as much similarity between cultures of *Fomes cajanderi* and *Daedalea quercina* as exists between cultures of the latter species and those of *Coriolellus sepium*. For these reasons it seems safe to suggest that *Fomes cajanderi* Karst. should be included in the genus *Daedalea* Pers. ex Fr.

Resume.

The four species of polypores included in Group 25 in the present study have many characters in common. In the cultures and carpophores of all four species, thin-walled, nodose-septate hyphae and nodose-septate hyphae with irregularly thickened walls are present together with aseptate, thick-walled fibre hyphae which are mostly unbranched. Their basidiospores are cylindrical. Their relatively thick, anoderm carpophores have thick dissepiments and are similar in construction. Their cultures do not produce extra-cellular oxidase enzymes and they all cause brown rots in their respective hosts. They differ from each other in respect of hymenial configuration, carpophore texture and host preferences. These appear to be minor differences however which are overshadowed by the many similar characters in these species. It thus appears that these species may be regarded as congeneric with the type species of the genus *Daedalea* Pers. ex Fr.

5.6 Group 32

Cultures of species in this group form white mycelial mats which produce extra-cellular oxidase enzymes. Their thin-walled hyphae have simple clamp connections at the septa and are undifferentiated except for occasional swellings or incrusted portions. Their basidiospores are sub-globose to ovoid or ellipsoid and less than 8μ in length. Their interfertility is of the tetrapolar type.

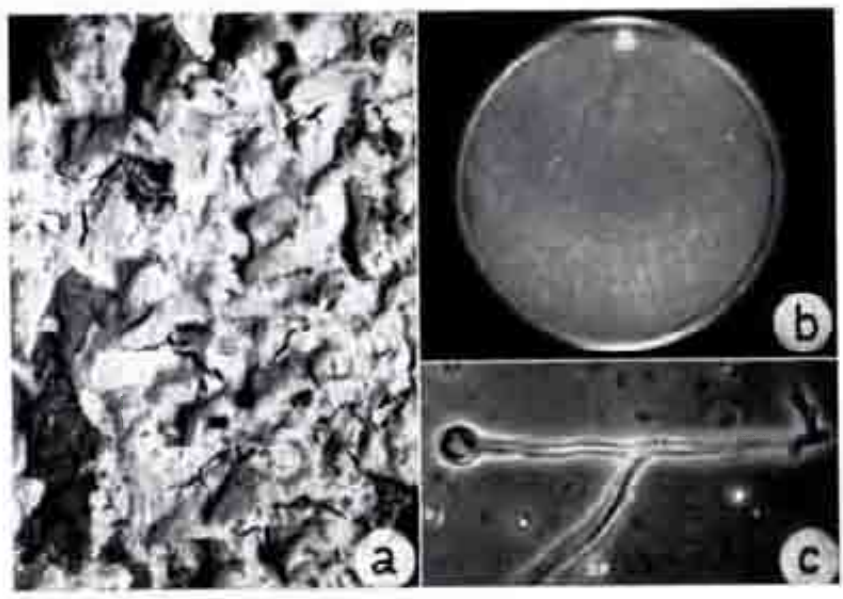

Fig. 19. — **Polystictus subiculoides.** (a) Carpophore of PRE 35331; (b) culture of PRE 42155 at six weeks; (c) vesicle on thick-walled, nodose-septate hypha from carpophore. × 500 phase contrast.

Polystictus subiculoides *Lloyd*, C. G., in Mycological Notes No. 73, 1331, 1924.

Cultural characters

Growth is moderately fast the mat reaching a radius of 50 mm after two weeks and covering the plates in 3 to 4 weeks; margin even to slightly bayed, hyphae raised to limit of growth; mat white, thin, downy to cottony, azonate, with

a smooth, even, radially combed appearance and remaining so for many weeks; reverse bleaching slowly after two weeks. Oxidase reaction positive with gum guaiac solution; weak diffusion zone and slow growth, colony diameter 10 mm after one week on gallic acid agar, no growth or diffusion zone on tannic acid agar. *Advancing mycelium:* hyphae hyaline, unbranched or branching, nodose-septate, thin-walled, 2.2 — 4.5μ in diameter (Fig. 20 a).

Aerial mycelium: (a) hyphae as in the advancing zone; (b) vesicles obovate or pyriform, hyaline, 7 — 10 x 15 — 20μ arising terminally on short lateral projections from hyphae (Fig. 20 b); (c) narrow thin-walled, hyaline nodose-septate hyphae, 1.5μ in diameter, with sub-globose, terminal vesicles 3.0 — 5.0μ in diameter (Fig. 20 c).

Submerged mycelium: hyphae as in the advancing zone but more frequently septate. Crystals hyaline, amorphous, numerous in the medium.

Carpophore characters.

Carpophore annual, lignicolous; pilei small, sessile to effused-reflexed, imbricate, often connate and arising from broad subiculum, soft corky, drying to hard corky 0.1 — 0.4 x 0.3 — 1.2 x 0.1 — 0.2 cm; surface minutely pubescent, smooth or slightly rugose, azonate, acuticulate, "cream color" or with small "cinnamon" patches; margin thin, acute, entire, concolorous with surface; pore surface concolorous or slightly buff coloured, poroid; pores angular, 4 — 7 per mm, mouths entire, dissepiments thin, decurrent on the subiculum, tubes 0.5 — 3 mm deep. Context white to pale "cream color" drying isabelline, up to 3.0 mm thick.

Hyphal characters: hyphae hyaline, branched nodose-septate with clamp connections often on one side only, thin-walled in young parts (Fig. 20 e); vesicles thin-walled, ovoid or sub-globose 4.5 — 12.0μ in diameter borne terminally on short lateral or terminal hyphae, arising at clamp connections (Fig. 19 c, 20 f).

Hymenium: basidia hyaline, broadly clavate, 8 — 12 x 4.5 — 6.0μ with four short straight sterigmata 1.5 — 2.2μ (Fig. 20 h); basidiospores hyaline sub-globose to ovoid, smooth, thin-walled 3.0 — 3.5 x 3.2 — 4.2μ (Fig. 20 k); vesicles as in the context, occasionally incrusted, small; acicular, encrusted hyphal tips projecting into hymenium narrow, 1.5 — 2.5 x 12 — 20μ (Fig. 20 n).

Construction. The cream-coloured subiculum which is up to 5 mm thick consists mainly of hyaline, thick-walled, nodose-septate hyphae together with thin-walled, nodose-septate hyphae, somewhat intertwined, and growing perpendicularly out of the substrate, with vesicles scattered throughout the subiculum and hyphal contents discoloured at different levels to form the darker zones visible in vertical section.

The pilei are formed by thick-walled, nodose-septate hyphae which grow out beyond the level of the subiculum and by repeated branching form intertwining hyphae which turn upward towards the upper surface of the pilei where their ends are densely packed at a common level to form the pubescent upper surface. In the same way these thick-walled, nodose-septate hyphae turn downward and by repeated branching produce intertwining hyphae which form the lower context. In the trama of the tubes the branches of these hyphae are mostly thin-walled, short and form a dense, even layer which bear the small basidia on the hymenial surfaces lining the cavities of the tubes only. In the lower context vesicles are more numerous than in the upper context. The margins of the pilei consist of the terminal sections of thick-walled, nodose-septate hyphae from the context, mostly unbranched, often somewhat elongated to over 100μ in length and resembling short, fibre hyphae with thin-walled tips (Fig. 20 g).

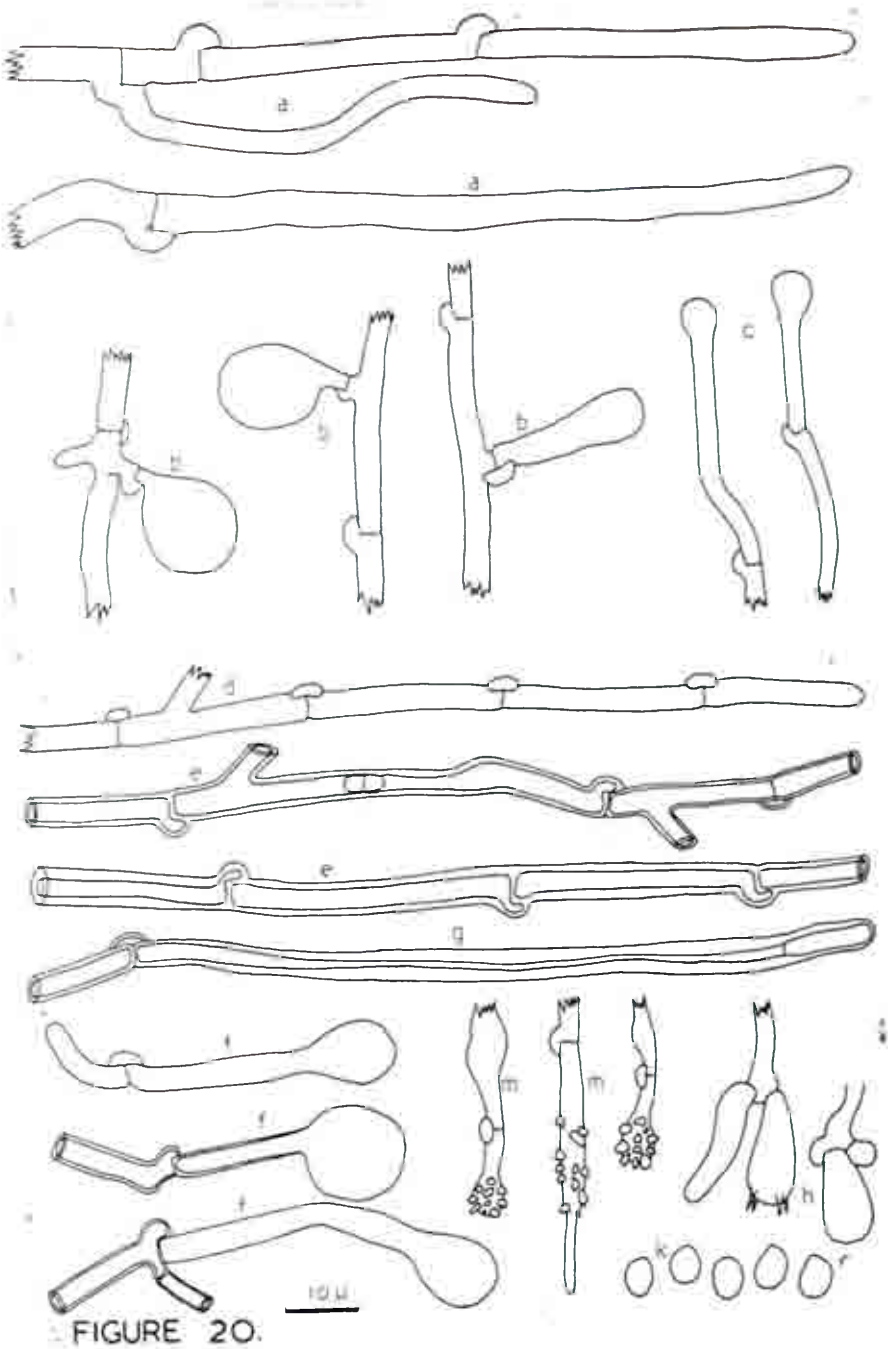

FIGURE 20.

FIG. 20.— **Polystictus subiculoides.** a - c. Structures from cultures: (a) thin-walled, nodose-septate hyphae from advancing zone; (b) lateral vesicles; (c) terminal vesicles.
d - m. Structures from carpophores: (d) thin-walled, nodose-septate hyphae from margin; (e) thick-walled, nodose-septate hypha from context; (f) hyphae with terminal vesicles; (g) thick-walled nodose-septate hypha with lengthened, terminal cell; (h) basidia; (k) basidiospores; (m) acicular and vesicular encrusted hyphal tips.

Decay and hosts

Polystictus subiculoides causes a white rot of living hard-wood trees and dead deciduous and coniferous wood.

Specimens examined.

Herb. PRE: 1357, on *Grevillea robusta*, Pietermartizburg, Natal, April 1911. (TYPE); 27651, on bark of dead stump, Pietermaritzburg, Natal, 1934; 27775, Pietermaritzburg, Natal, 1934; 28649, indigenous wood, Pietermaritzburg, Natal, Sept. 1934; 28472, on *Grevillea robusta*, Pietermartizburg, Natal, Sept. 1934; 28556, on gum tree, Pietermartizburg, Natal, Sept. 1934; 28559, on *Acacia mollissima*, Impolweni, Natal Sept. 1934; 28772, on *Quercus* sp., Johannesburg, 1936; 30171, on indigenous wood Umgeni Forest, Natal, March 1935; 30179, on indigenous wood, Umgeni Forest, Natal, March 1935; 30742, on bark, Deepwalls, Knysna, Apr. 1939; 35331, on *Quercus* sp., Pietermaritzburg, Natal, 1943; 36692, on *Acacia* sp. stump, Lions River, Natal, May 1948; 39195, Pietermartizburg, Natal, Jan. 1946; *42155, on *Bridelia macranthra*, F. C. Erasmus Nat. Reserve, Feb. 1961; *42157, on dead stump, F. C. Erasmus Nat. Res. Tvl., Feb. 1961; 42199, on dead wood, Pretoria, Nov. 1961; 42291, on dead *Pinus* sp., Saasveld, C.P., Nov. 1962; *42359, on dead *Pinus* sp., Entabeni Forest Reserve, Tvl., Apr. 1964.

Discussion

Polystictus subiculoides has not been described in culture before. Cultures of this species are distinguished by the weakly positive oxidase reaction, hyaline-white, radiating, silky, mycelial mat, and thin-walled, nodose-septate, undifferentiated hyphae bearing thin-walled vesicles on short, lateral branches. As the terminal vesicles may be conveniently regarded as swellings of the hyphae a basis for the inclusion of *Polystictus subiculoides* in Group 32 is provided, but this species is not well placed in Group 32 because the lateral vesicles are not simple swellings on hyphae and as no provision is made other than for undifferentiated nodose-septate hyphae and differentiated fibre hyphae, no other alternative group is available in which this species may be better placed.

Vesicles are regarded as gloeocystidia by Lentz (1954), Talbot (1954 a) and Van der Westhuizen (1958) but the characteristic staining reaction for gloeocystidia was not seen when mycelium from a growing culture of *Polystictus subiculoides* was mounted in sulphuric-anisaldehyde and sulphuric-benzaldehyde as used by Slysh (1960) for species of *Peniophora*. The vesicles of *Polystictus subiculoides* thus do not appear to be gloeocystidia. Allocysts were described from cultures of *Flammula alnicola* and *Flammula conissans* by Denyer (1960). The vesicles of *Polystictus subiculoides* resemble these allocysts very closely.

Nobles (1965) included *Flammula alnicola* and *Flammula conissans* under Key Code 2.3.26 of a key devised as an aid for the identification of cultures of Basidiomycetes isolated from decayed wood. As cultures of *Polystictus subiculoides* have a positive reaction for extra-cellular oxidase, consistently nodose-septate, thin-walled hyphae, and "swellings on hyphae" similar to those of *Flammula alnicola* and *Flammula conissans*, *Polystictus subiculoides* may be included in Key Code 2.3.26. Cultures of *Polystictus subiculoides* may be distinguished from cultures of these two *Flammula* spp. by the higher growth rate and more uniform texture of the mat together with the geographical distribution of the species.

Cultures of *Collybia velutipes*, *Aporpium caryae*, *Polyporus volvatus* and *Polyporus fumosus* were also included by Nobles (1965) in Key Code 2.3.26. Cultures of these species may however be readily distinguished from those of *Polystictus subiculoides* as they lack the characteristic vesicles of this fungus. Cultures of *Polystictus subiculoides* also resemble those of *Odontia bicolor* (Nobles, 1953) in many ways but differ by having thinner, silky mycelium while the vesicles of *Polystictus subiculoides* are larger than the cystidia of *Odontia bicolor* and lack the latter's typical, large crystalline incrustations.

The carpophores of *Polystictus subiculoides* are most interesting morphologically as well as anatomically. The pilei arise as reflexed portions of a well-developed subiculum. The pilei are integral parts of the subiculum and, except for the presence of hymenial layers in the minute tubes, anatomically undifferentiated and virtually indistinguishable from it microscopically. Both structures are remarkable for their simple construction of nodose-septate hyphae with partly thickened walls, arranged more or less parallel to one another and perpendicular to the substrate. Of all the species included in this study, *Polystictus subiculoides* has the simplest construction of its pilei and the least differentiation in morphology and function of its hyphae.

From the descriptions it is evident that only one type of hypha is found in both the cultures and carpophores. The vesicles which are so characteristic in the cultures, are found throughout the tissues of the carpophores and subiculum. Differences in the thickness of the walls of hyphae from the cultures and hyphae from the carpophores had been seen in other species as well (cf. Groups 7 & 9) and appears to be a modification which usually occurs under natural conditions during fruit-body formation. All structures formed in cultures are thus present in the carpophores as well.

Few species of poroid Hymenomycetes are known to have similar vesicles or gloeocystidia in their carpophores. Notable among these are *Poria versipora* (Pers.) Romell (Cunningham, 1946; Lowe, 1946) and *Polyporus borealis* Fr. (Ames, 1913; Overholts, 1953). These structures are found in *Poria versipora* in the hymenium only but they are present in the context of specimens of *Polyporus borealis*. Nobles (1958 b) placed cultures of these species in Group 32, but did not indicate whether vesicles were formed. Since the other species in Group 32 are known to form vesicles in culture, it is assumed that *Poria versipora* and *Polyporus borealis* agree in this respect with the other species and that the vesicles formed in their carpophores are ontogenetically or physiologically different from those of *Polystictus subiculoides*.

Pilát (1946) described conical, immersed cystidia in carpophores of *Poria fissiliformis* and Nobles (1958 b) included cultures of this species in Group 32, but this species differs from *Polystictus subiculoides* by having fibre hyphae in its carpophores.

Vesicles and gloeocystidia of various forms are present in the cultures and carpophores of many species of lower Hymenomycetes notably in the genera *Corticium* Pers ex Fr. *Odontia* Fr., *Peniophora* Cke. and *Stereum* Pers. ex Gray (Lentz, 1954; Talbot, 1954 a; Nobles, 1948, 1965; Cunningham, 1963). In *Odontia bicolor* capitate vesicular gloeocystidia are formed in cultures (Nobles, 1953) and in the spines of the carpophore (Talbot, 1958 b). In *Peniophora utriculosa* G. H. Cunn. the small deeply-staining vesicles are borne on short lateral branches of the intermediate layers of the fruit-body, and are not subtended by clamp connections (Cunningham, 1963). In *Peniophora vesiculosa* G. H Cunn. and *Peniophora utriculosa* G. H. Cunn. the vesicles are larger and subtended by clamp connections and situated in the intermediate layers of the carpophores. In both species encrusted metuloids are also present in the tissues (Cunningham, 1963). The vesicles of *Stereum purpureum* are also present in the intermediate zone of the fruit-body but this fungus differs from the others by having fibre hyphae in culture (Van der Westhuizen, 1958) and in the carpophore (Talbot, 1954; Cunningham, 1963). These species of these three genera agree in the morphology and positions of the vesicles in the tissues of their carpophores. The vesicles of *Polystictus subiculoides* are similar in morphology and disposition in the tissues to the vesicles of these four species. The carpophores also show similarities with those of the thelephoraceous

species by virtue of their simple construction of one type of hypha only. *Polystictus subiculoides* also occurs mainly on angiosperm wood and has a weakly positive oxidase reaction. These similarities appear to indicate that *Polystictus subiculoides* has affinities with these species and should be regarded as a poroid member of a group of Hymenomycetes with thelephoraceous carpophores.

5.7 Group 45

The cultures of species in this group form mycelial mats which mostly remain white or develop patches of pale, bright colours. Extra-cellular oxidase enzymes are produced. Their thin-walled hyphae have simple clamp connections at the septa and usually remain thin-walled but thick-walled, aseptate, fibre hyphae are formed in large numbers. Their basidiospores are cylindrical and their interfertility is of the tetrapolar type.

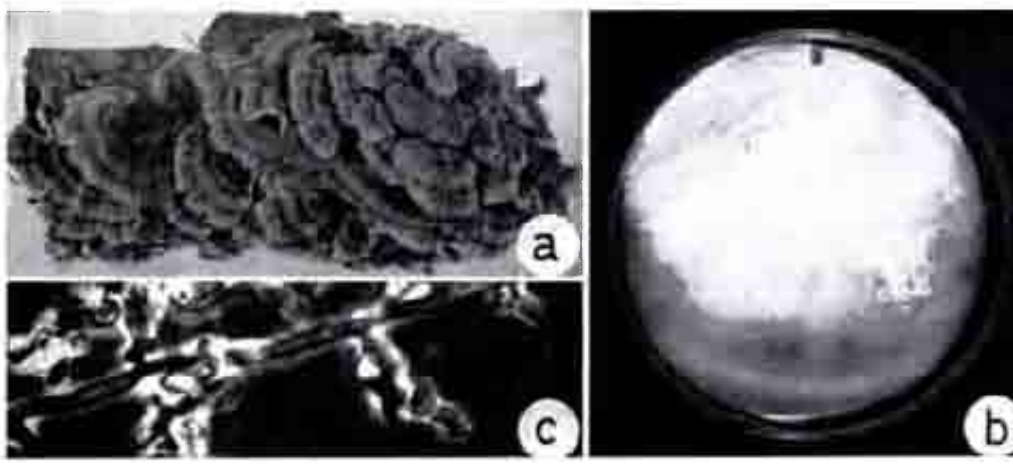

Fig. 21.— **Polyporus versicolor.** (a) Carpophores of DAOM 83052; (b) culture of PRE 42370 at six weeks; (c) nodose-septate hypha with irregular projections from culture, × 500 phase contrast.

Polyporus versicolor *L. ex Fr.*, Syst. Mys. 1, 368, 1821;
Coriolus versicolor (L. ex Fr.) Quel., Ench. Fung., 175, 1886;
Trametes versicolor (L. ex Fr.) Pilát, Atl. Champ. Eur. III, 261, 1939.

Cultural characters

Growth is rapid to moderately rapid the colonies reaching radii of 30 — 50 mm in one week and covering the plates in two to three weeks. The margin is even, appressed, thin, hyaline. Behind the margin the young mat may be raised, cottony, with vague radiating grooves, or floccose, or finely farinaceous, white, but becoming collapsed over the older part where thin, pellicular patches of dense mycelium start forming after 2 — 3 weeks. The pellicular areas become sub-felty, increase in size and coalesce while in some parts they change from white or "cream color" to smooth, hard, crustose areas of various shades of brown, turning finally "saccardo's umber" or "sepia." In some isolates these pellicular areas may become more felty and increase in thickness eventually developing "natal

brown" or "saccardo's umber" patches. In others the pellicular areas never develop but the mat remains thin, white, downy-farinaceous with fine, white, farinaceous striae radiating from the inoculum. Fruiting may occur in some cultures. Shallow, smooth depressions appear on dense, pellicular areas of mycelium or on rounded lumps of dense mycelium. Minute, acicular projections develop in these depressions, bearing normal, fertile basidia and basidiospores. A white spore deposit is soon formed under these structures in inverted cultures. The reverse is bleached after two to four weeks but patches of "wood brown", "army brown" or "natal brown" may develop in the agar under the coloured areas. Odour may be strong mushroomy or somewhat unpleasant, fishy.

On gallic and tannic acid agars the diffusion zones are dark and wide while growth of mycelium extends up to 2.0 cm and 3.0 cm in diameter on gallic acid and tannic acid media respectively. When an alcoholic solution of gum guaiac is applied to the mycelium the colour changes rapidly to bright blue.

Advancing mycelium: hyphae hyaline, branching, thin-walled, nodose-septate, with deeply staining contents, 2.0 — 4.0μ in diameter (Fig. 22 a).

Aerial mycelium: (a) hyphae as in the advancing zone; (b) fibre hyphae long, unbranched hyaline, sub-solid to solid with the lumina visible mostly at the tapering ends only, up to 4.5μ in diameter at the widest part, (Fig. 22 b); (c) fibre hyphae long, narrow, hyaline, branching repeatedly the branches long and flexuous and tapering towards the ends, 1.2 — 3.0μ in diameter, (Fig. 22 c); (d) nodose-septate hyphae with slightly thickened, hyaline walls and without contents, 2.5 — 3.5μ in diameter, and with many, short, lateral branches, either thick-walled or solid and refractive, and stained brown by a lacquer-like substance secreted in the brown areas (Fig. 21 c, 22 d); (e) nodose-septate hyphae with thickened, brown walls, 2.5 — 3.5μ in diameter, embodied in brown, resin-like material present in the brown areas (Fig. 22 e); (f) very narrow, hyaline hyphae, 0.5 — 0.8μ in diameter and profusely, dichotomously branched, forming a network among the other hyphae in the pellicular areas.

Fructifications: basidia clavate, hyaline, 12.0 — 20.0 x 3.6 — 4.6μ with four long, slender, somewhat curved sterigmata, 2.8 — 3.3μ; basidiospores hyaline, cylindrical, slightly curved, rounded at the ends, obliquely apiculate, smooth, thin-walled, 4.2 — 5.4 x 1.8 — 2.2μ (Fig. 22 f); occasionally branched cystidioles present among the basidia.

Submerged mycelium: (a) nodose-septate hyphae as in the advancing zone; (b) nodose-septate hyphae with thickened, brown walls and numerous, short, lateral branches as in the aerial mycelium.

Carpophore characters

Carpophore annual often reviving, lignicolous, grouped or compound; pileus dimidiate, sessile, often with a reduced base, or, effused-reflexed, occasionally imbricate, laterally connate or forming rosettes, up to 6.0 x 8.0 x 0.1 — 0.3 cm; tough, coriaceous, drying to hard coriaceous; surface velutinate to villose, concentrically zonate with alternate zones finally glabrous, and zones variously coloured

FIG. 22.— **Polyporus versicolor.** L. ex Fr. a - f. Structures from cultures: (a) hyphae from advancing zone; (b) unbranched, fibre hyphae; (c) fibre hyphae with long, flexuous branches; (d) nodose-septate hyphae with numerous, thick-walled or solid, lateral branches; (e) thick-walled, brown, nodose-septate hyphae; (f) basidia and basidiospores.
g - p. Structures from carpophores: (g) thin-walled, nodose-septate hyphae; (h) tuft of agglutinated, thick-walled, nodose-septate hyphae; (k) fibre hyphae; (m) fibre hyphae with short, tortuous, lateral branches; (h) fibre hyphae with long, tapering branches; (p) basidia and basidiospores.

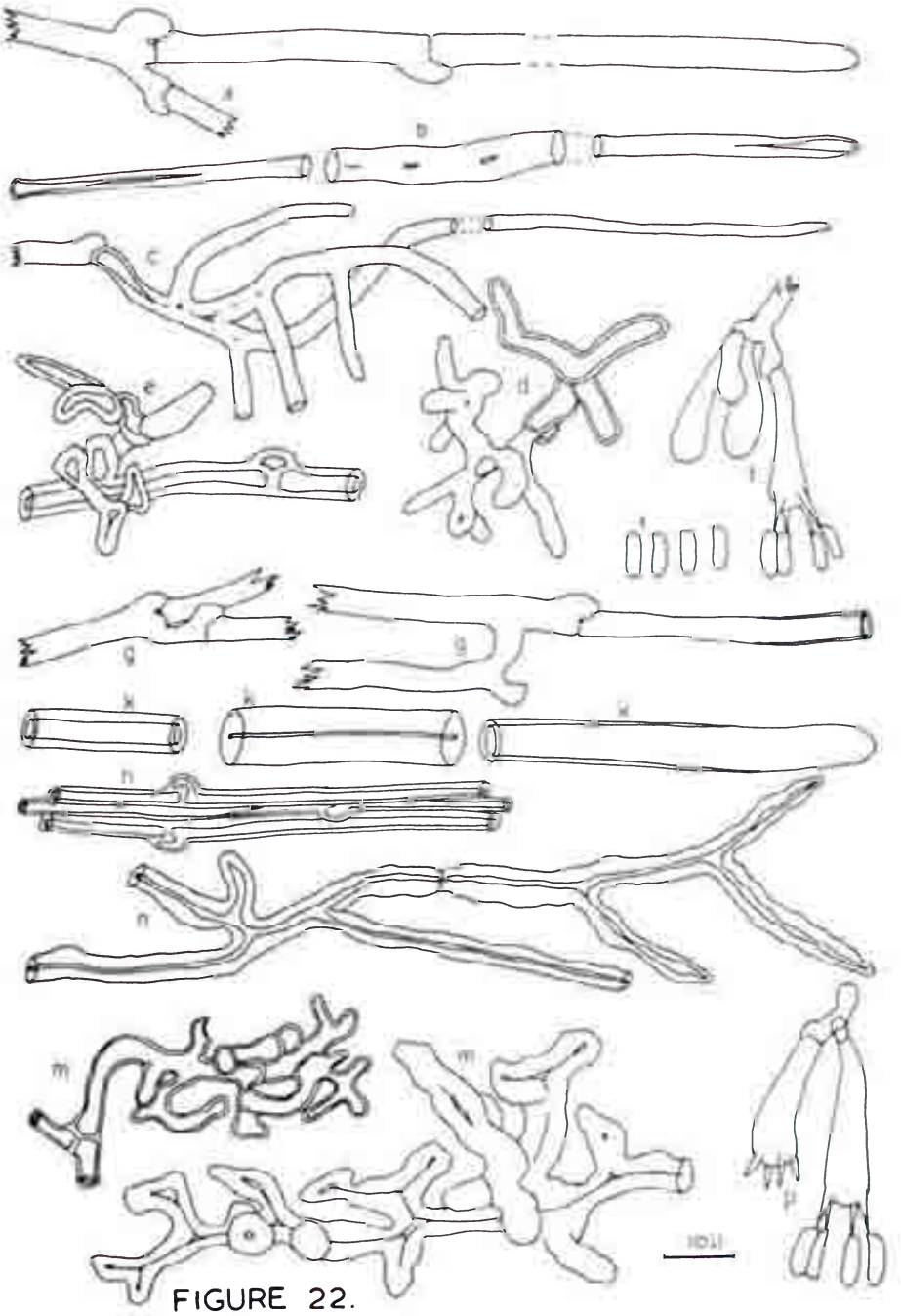

FIGURE 22.

from white to yellow brown, reddish, greenish, blueish and blackish; margin acute, entire, occasionally undulate or lobed, white or pale yellowish; pore surface white or pale cream drying to deep cream or brownish yellow, often glistening; pores 3 — 5 per mm, angular, entire; dissepiments even, thin-walled, tubes concolorous or pale up to 2 mm deep. Context white or pale cream-coloured, floccose, thin, 0.5 — 2.5 mm.

Hyphal characters: (i) nodose-septate hyphae hyaline, branching freely, thin-walled, contents staining deeply, 2.0 — 3.5μ in diameter (Fig. 22 g); (ii) nodose-septate hyphae mostly agglutinated into tufts or strands the walls at first hyaline, soon pale brown, thickened, the lumina narrowed to two thirds or one half the total diameter of the hyphae, and with deeply staining contents, 1.5 — 2.4μ in diameter (Fig. 22 h); (iii) fibre hyphae long, straight, unbranched, hyaline with thick refractive walls and lumina wide at the tips, but narrowed along the middle sections where they are visible as thin interrupted lines only, aseptate or with an occasional simple septum near the tips, contents usually deeply staining often discoloured to brownish or dark brown towards the distal ends, 3.0 — 8.0μ in diameter (Fig. 22 k); (i) fibre hyphae short, with numerous short, intricately flexuous lateral branches, hyaline, with walls thickened and lumina narrowed, with deeply staining contents, aseptate, or solid, 1.5 — 3.0μ in diameter and arising from thin-walled, nodose-septate hyphae (Fig. 22 m), binding hyphae sensu Corner (1932 b); (v) fibre hyphae with fairly numerous branches, the branches mostly long and tapering rather abruptly at the tips, or similar to the "binding hyphae", the walls thickened, hyaline, the lumina narrow but prominent with deeply staining contents, aseptate, 2.2 — 3.2μ in diameter (Fig. 22 n).

Hymenium: basidia short, hyaline, narrowly clavate, 9.0 — 15.0 x 3.6 — 4.5μ, with four, straight, slender sterigmata, 1.5 — 2.5μ (Fig. 22 p); basidiospores long, cylindrical, slightly curved or allantoid, hyaline, smooth, thin-walled, 4.5 — 6.5 x 1.2 — 2.0μ (Fig. 22 p); hyphal pegs broadly conical, sterile, projecting up to 40μ beyond the level of the hymenium, not numerous.

Construction. The margin consists mainly of hyaline, long, unbranched, fibre hyphae mostly with fairly wide lumina and arranged more or less parallel to and slightly intertwined with one another. In between them are numerous fibre hyphae with partly thickened walls and a profusion of short, contorted branches growing across the direction of growth of the fibre hyphae and binding them together into a tough tissue. Both these types of hyphae arise from branches of narrow, thin-walled, nodose-septate hyphae with deeply staining contents, which are interwoven with the other two types. Behind the margin the upper context is similar in construction but the fibre hyphae develop thicker walls and lumina are narrower. Much branched fibre hyphae (binding hyphae), mostly solid, are abundant towards the upper surface, where they bind the long fibre hyphae and numerous branching, thin-walled, nodose-septate hyphae into a tough, dense, layer of tissue up to 60μ thick and coloured brownish by a resinous or lacquer-like substance. Through this layer the ends of long fibre hyphae from the context protrude to form the pubescence of the upper surface. Most of these fibre hyphae have brownish contents of the lumina which widen gradually towards the rounded ends (Fig. 22 k). Arising from thin-walled, nodose-septate hyphae in this dense layer, are numerous narrow, thick-walled, nodose-septate hyphae, with the walls pale brown and luminal contents staining deeply. These hyphae are either agglutinated into tufts or strands (Fig. 22 h) or closely appressed to and agglutinated with fibre hyphae into tufts by means of a brown, lacquer-like substance. The smooth, brown zones of the upper surface are formed by this brown, lacquer-like substance agglutinating the fibre hyphae and nodose-septate hyphae into a brown, smooth cuticle of resupinate elements.

Below this dense upper layer the context tissues are less dense consisting of long, unbranched, hyaline, solid or sub-solid, fibre hyphae in more or less parallel arrangement, small numbers of thin-walled, nodose-septate hyphae and intertwined with hyaline, fibre hyphae (binding hyphae) with long, flexuous branches with characteristically tapering ends (Fig. 22 n).

The lower context is like the middle context but the fibre hyphae (binding hyphae) with numerous short, hyaline, solid, branches (Fig. 22 m) become very numerous and form a dense layer. From the lower context, long unbranched fibre hyphae turn downward into the dissepiments and become flexuous, narrower and tightly intertwined, with numerous "binding hyphae" of the short, much branched type as well as the other type with longer branches and which may become indistinguishable from the short type, into a very tough and dense tissue. In between the fibre hyphae, numerous thin-walled, nodose-septate hyphae, with deeply staining contents and branching repeatedly, are present. At the surfaces of the dissepiments, the branches of the nodose-septate hyphae bear the basidia in a dense, even stand.

The hyphal pegs in the hymenium consist of the ends of fibre hyphae, in parallel arrangement, projecting into and beyond the hymenium from the underlying tissue.

Decay and hosts.

Polyporus versicolor causes a white rot of dead wood of a wide variety of species of deciduous trees.

Specimens examined

Herb. DAOM: *F8183, on *Juglans* sp. Saanichton, B.C., June 1938; 11781, on decayed wood, Burnet, Que., Aug. 1944; 11782, on hardwood, Gatineau Park, Que., Aug. 1944; *11783, on *Betula* sp. Gatineau Park, Que., Aug. 1944; *21150, on *Betula papyrifera* log, Dorset, Ont., July 1948; 21196, on decayed *Acer* log Dorset, Ont., July 1948; *21767, on decayed *Podocarpus spectatus*, Rotorua, N.Z., Nov. 1948; *22296, on *Alnus rubra*, Cowichan Lake, B.C., June 1948; 22342, on decayed hardwood, Ottawa, Sept. 1949; 22348, on deciduous host, ex herb. J. Pinto-Lopes, April 1950; 22357, on *Eucalyptus* sp. ex herb. J. Pinto-Lopes, April 1950; *22586, on *Eucalyptus*, Seven Oaks, Surrey, Sept. 1950; *22794, on roots of *Betula lutea*, Bells Corners, Ont., July 1949; *30588, on *Quercus robur* stump, Norway, Nov. 1953; *30589, on *Acer* sp., Norway, Nov. 1953; *31926, on *Betula papyrifera*, Calabogie, Ont., Aug. 1955; 52102, Gainesville, Fla., Sept. 1954; *53899, on dead wood, Wakefield, Que., July 1952; 53900, on *Acer* sp., Cantley, Que, July 1952; *69694, on hardwod, Walker, La., Aug. 1960; 72326, on deciduous wood, Sargent Camp, N.H., Aug. 1956.

Herb. PRE: 1332, on *Acacia decurrens*, Pietermartizburg, Natal, Apr. 1911; 14838, Kirstenbosch, C.P., June 1929; 20603, Knysna, C.P., Jan. 1925; 21877, on *Fagus* sp., Krieger, Schädliche Pilzen, Sept. 1905; 22072, Boschberg, C.P. Sept. 1876; 22857, Falkenburg, Germany, Sept. 1873; 23482, Mont-aux-Sources, Natal, 1937; 24202, Hollos, Hungarian Fungi No. 320; 24830, dead logs, Kirstenbosch, C.P., June 1929; 24847, on stumps, Kirstenbosch, C.P., June 1929; 27278, Groote Schuur, C.P., Aug. 1933; 27608, Town Bush Valley, Pietermartizburg, 1934; 28754, dead wood, Pilgrim's Rest, Tvl., Oct. 1936; 30522, Pretoria, Tvl., Feb. 1939; 30722, dead wood, Pretoria, Tvl., 1939; 30726, Xumeni Forest, Natal, 1937; 30739, Deepwalls, C.P., April 1939; 30848, Margawa Forest, Natal, June 1939; 31336, Town Bush Valley, Pietermartizburg, June 1939; 31427, old logs, Stellenbosch, C.P., Sept. 1919; 31429, Stellenbosch, C.P., Sept. 1919; 31550, Moodies, Natal, August 1915; 34071, dead wood, Mariepskop, Tvl., May 1943; 35651, dead wood, ex Herb. Hort. Bot. Reg., Kew, Oct. 1938; 36874, dead wood, Umtali, S.R., July 1948; 41536, dead wood, Hogsback, C.P., May 1956; *42370, on maple log, Packenham, Ont., June 1962; *42813, on dead wood, Stellenbosch, C.P., Aug. 1959; *42956, on hardwood stump, Warrensburg, N.Y., Aug. 1962.

Herb. STE: 124, Kirstenbosch; 159, on *Salix* sp. log, Nottingham Rd., Natal; 199, on dead stumps and logs, Natal Midlands; 291, on dead stumps and logs, Barberton, Tvl.; 714, op dooie hout, Knysna, Jan. 1922; 882, on *Alnus tenuifolia* ex Herb. J. R. Weir; 1480, droe hout, Houtbos, Tvl., Julie 1924; 2647, on *Alnus tenuifolia*, ex Herb. C. J. Humphrey.

Discussion

The cultural characters as described above, agree well with the descriptions by Fritz (1923), Jay (1934), Refshauge & Proctor (1936), Davidson, Campbell & Vaughn (1942), Cartwright & Findlay (1946) and Nobles (1948, 1965). The thick-walled, brownish, nodose-septate hyphae and the short hyphae with numerous, short, lateral branches have not been reported before. These hyphae do not form wrinkled, pseudoparenchymatous, crustose areas which are characteristic of cultures of the species in Nobles' Group 53 (1958 b) although there appears to be some superficial resemblance to "hyphae with interlocking projections" (Nobles 1948, 1958 b). Instead, these hyphae from the cultures of *Polyporus versicolor* are found mostly in the mycelial mat among the fibre hyphae or occasionally agglutinated with brown, lacquer-like material in brown areas of some isolates of this species (Nobles, 1965). In view of their position, morphology and development and the fact that the binding hyphae in the carpophores of *Polyporus versicolor* apparently develop in the same way, they are regarded as homologous with the binding hyphae, which are so numerous in the carpophores of *Polyporus versicolor*. These structures are quite characteristic and may serve to distinguish this species from others in this group of which the cultural characters are otherwise very similar.

From the description it is evident that the carpophores of *Polyporus versicolor* consist of five kinds of hyphae. Thin-walled, nodose-septate hyphae are present in the growing regions and hymenial areas while thick-walled, nodose-septate hyphae are associated with the unbranched fibre hyphae on the upper surface and in other parts of the context where they bind other hyphae into tough, dense tissue. The branched fibre hyphae of the lower context together with the branched, tortuous, binding hyphae constitute the binding system in the lower part of the tissues. The carpophores thus have a trimitic hyphal system with generative, skeletal and binding hyphae as reported by Cunningham (1948 c), Teston (1953 b), Kotlaba & Pouzar (1957), Teixeira (1960) and Farinha (1964), but these authors, with the exception of Teixeira (1960) and Farinha (1964), who described thick-walled, nodose-septate hyphae from carpophores of *Polyporus versicolor*, mentioned only three kinds of hyphae in the carpophores. Corner (1932 a), however, stated that such thick-walled, nodose-septate (or generative) hyphae may contribute to the binding hyphal system of some species, thus confirming the above observations. The fibre hyphae with branches towards the distal ends have not been reported from *Polyporus versicolor* before but similar hyphae, termed "arboriform hyphae" by Teixeira (1962 b) were reported from the fruit-bodies of *Ganoderma* spp. by Hansen (1958) and Furtado (1965 a) where they also assist in binding the tissues of the carpophores. In the carpophores of *Polyporus versicolor*, morphologically and ontogenically different hyphae thus contribute to the different hyphal systems of the trimitic fruit-bodies.

From the above descriptions, it is clear that most of the structures formed in cultures of *Polyporus versicolor* are also present in the carpophores from which the cultures were made. Only very narrow hyphae which form a network in the pellicular areas of the cultures, were not found in the carpophores. It is not known whether such hyphae are present in wood decayed by *Polyporus versicolor*. No decayed wood was available for study.

Polyporus versicolor is regarded as the type species of the genus *Coriolus* Quél. (Cooke, 1959; Donk, 1960). This species was transferred to the genus *Trametes* Fr. by Pilát (1936) who was followed by Kotlaba & Pouzar (1957) in this. There is indeed great similarity in hyphal characters and carpophore construction between *Polyporus versicolor* and *Trametes suaveolens* Fr. the type of the genus *Trametes* Fr. (Donk, 1960). These similarities and their implications will be discussed below.

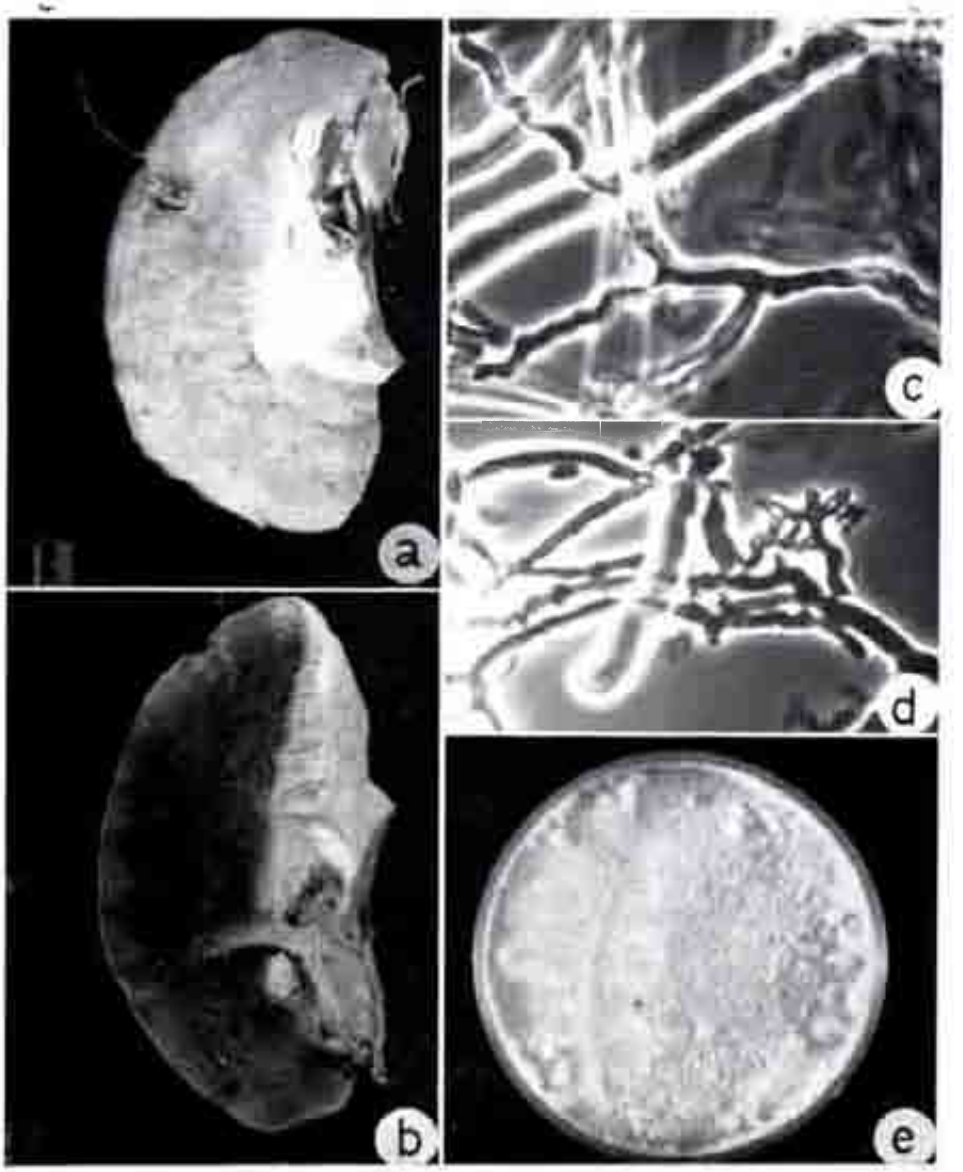

FIG. 23.— **Trametes suaveolens.** (a) Carpophore upper surface and (b) hymenial surface of DAOM 31500; (c) branched fibre hypha from upper context of fruit-body; (d) same from context above tubes, X 1000 phase contrast; (e) culture of DAOM F1964 at six weeks.

Trametes suaveolens *(L. ex Fr.) Fries*, Epicr. Syst. Myc., 491, 1838.

Cultural characters

Growth is moderately fast, the mat reaching a radius of 20 — 30 mm after one week and covering the plates in 2 to 4 weeks. Margin even, mycelium raised to limit of growth or appressed. Mycelium white, dense cottony to woolly in newest growth occasionally somewhat lacunose but collapsing in older parts, becoming more cottony and forming irregular sub-felty or woolly areas interspersed in some cultures by patches of sodden mycelium, or, mat fairly evenly thin, woolly, with elongated lumps or ridges of more compact, felty mycelium developing pale, yellowish or brownish tints and placed on vague ridges radiating from the inoculum. Around the inoculum may be an area of farinaceous-downy or farinaceous, thin, sub-felty mycelium. A ring of woolly mycelium may gradually develop against the side of the dish in some isolates. The reverse is bleached rapidly and a sweet fragrant, odour is emitted. On gallic acid and tannic acid media, strong diffusion zones are formed and a trace of growth takes place on tannic acid agar only. A strong blue colour is formed when a drop of alcoholic gum guaiac solution is applied to the culture.

Advancing mycelium: hyphae hyaline, thin-walled, with deeply staining contents, nodose-septate, branching between the septa, 2.4 — 4.5μ in diameter (Fig. 24 a).
Aerial mycelium: (a) hyphae thin-walled, nodose-septate, hyaline as in the advancing zone; (b) fibre hyphae hyaline, unbranched, solid or sub-solid, with lumina aseptate and visible only at the extremities, 2.0 — 4.0μ in diameter (Fig. 24 b), or, branching freely, often from a short main stem and tapering towards the ends, narrow, thick-walled to sub-solid in parts, 1.5 — 3.0μ (Fig. 24 c). Some fibre hyphae may have spear-shaped ends (Fig. 24 d).

Submerged mycelium: (a) nodose-septate hyphae as in the advancing zone: (b) chlamydospores terminal and intercalary, broadly ovoid to somewhat cylindrical, thin-walled or thick-walled, 7.5 — 16.0 x 4.0 — 6.0μ (Fig. 24 e).

Carpophore characters

Carpophore annual, occasionally reviving, lignicolous, solitary or compound, sessile, dimidiate or occasionally effused-reflexed; pileus convex above, occasionally imbricate or laterally connate, soft spongy and watery when fresh drying to tough or corky, anise-scented when fresh, up to 10 x 16 x 4 cm; surface velutinous, to villose-tomentose or glabrous, azonate or occasionally slightly radially rugose, mat, white or greyish to isabelline or drying yellowish; margin obtuse, entire, somewhat involute and concolorous with upper surface; pore surface white at first then greyish-brownish or smoky, drying yellowish or dark smoky; pores entire, rounded occasionally angular or elongated, 1 — 3 per mm; dissepiments thick, even or somewhat dentate; tubes 0.3 — 1.5 cm long, sometimes stratified, concolorous with context or with dark regions around their mouths; context white or pale cream, 0.5 — 2 cm thick, tough-fibrous, concentrically zonate.

Fig. 24.— **Trametes suaveolens.** a - e. Structures from cultures: (a) nodose-septate hyphae from the advancing zone; (b) unbranched fibre hyphae; (c) fibre hyphae with tapering branches; (d) spear-shaped end of fibre hypha; (e) chlamydospores.
f - n. Structures from carpophores: (f) thin-walled, nodose-septate hypha; (g) unbranched fibre hypha; (h) fibre hyphae with one to three branches toward the tip; (k) fibre hyphae with numerous short, tortuous branches; (m) sub-solid, nodose-septate hypha with numerous short, tortuous branches; (n) basidia and basidiospores.

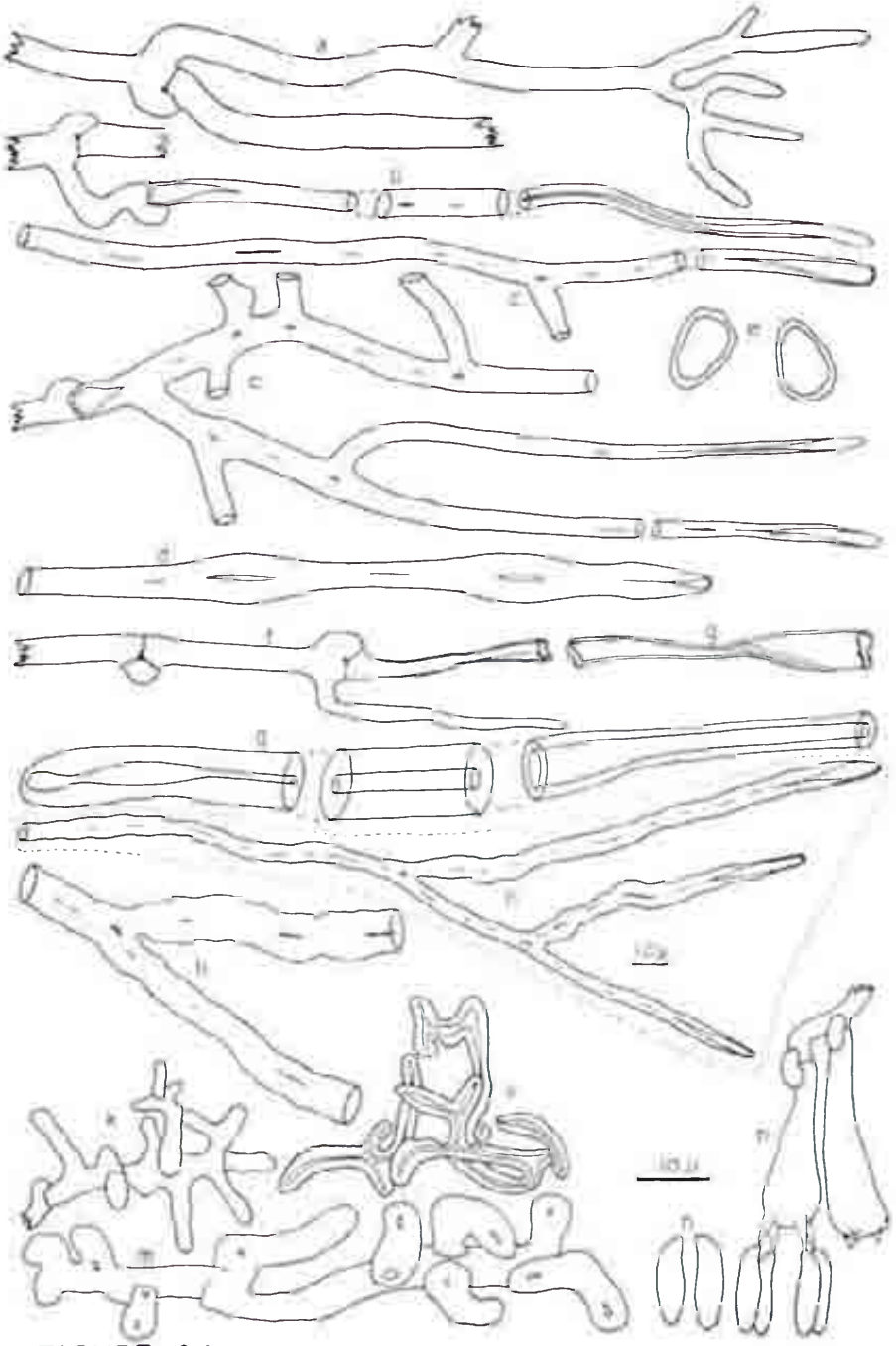

FIGURE 24.

Hyphal characters: (i) nodose-septate hyphae hyaline, branching, thin-walled, with deeply staining contents, 1.8 — 3.0μ in diameter (Fig. 24 f); (ii) fibre hyphae unbranched, long, more or less straight, hyaline, refractive, thick-walled, lumina narrow, aseptate often with staining contents, or reduced to a thin, interrupted line, but widening at the ends, 3.0 — 6.0μ in diameter (Fig. 24 g); (iii) fibre hyphae with one to three branches towards the tips, the branches long, tapering, irregularly beaded in outline, the walls thick, refractive, lumina reduced to an interrupted line, widening only at the tapering tips, 2.5 — 6μ in diameter (Fig. 24 h); (iv) fibre hyphae hyaline, repeatedly branched, the branches short, or very short, tortuous, lumina narrow or occluded, aseptate, 1.8 — 3.0μ in diameter, arising at clamped septa from lateral, thin-walled branches or thin-walled, nodose-septate hyphae (Fig. 24 k); (v) nodose-septate hyphae with numerous short, tortuous branches, thick-walled or solid with solid clamp connections, 3.0 — 4.0μ in diameter (Fig. 24 m).

Hymenium: basidia long clavate, hyaline 16.0 — 24.0 x 5.0 — 6.0μ bearing 4 thick sterigmata, 3.6 — 4.2μ long; basidiospores hyaline, long ellipsoidal to cylindrical, obliquely apiculate, thin-walled, smooth, 7.5 — 9.8 x 3.2 — 4.0μ (Fig. 24 n). *Construction.* The margin consists mainly of long, unbranched, hyaline, fibre hyphae mostly straight, arranged parallel to one another and intertwined to a small extent. Intertwined with the fibre hyphae are numerous thin-walled, branching, nodose-septate hyphae, from which the fibre hyphae arise. Behind the margin the fibre hyphae become sub-solid, or solid, and turn upward into the upper context or downward towards the pores. In the upper context the fibre hyphae are very loosely arranged, mostly parallel to each other with little intertwining, and with their thin-walled ends arranged at a common level and free to form the velutinous upper surface, or, agglutinated into tufts by brownish, resin-like material to form the villose-tomentose upper surface. Intertwined with the unbranched fibre hyphae are thin-walled, nodose-septate hyphae in small numbers as well as small numbers of fibre hyphae with irregularly beaded walls and two or three branches (Fig. 23 c, 24 h) the branches running diagonally across the unbranched fibre hyphae and interwoven with them. In the upper part of the context, aseptate fibre hyphae with numerous tortuous branches, (Fig. 24 k) intertwined with the other hyphae, are present in small numbers. In the lower context the tissues become much more dense and more compact. Small numbers of long, unbranched, fibre hyphae, turn downwards into the trama of the dissepiments; fibre hyphae with somewhat beaded walls and branches towards their ends, become more numerous, and their branches are extensively intertwined. Fibre hyphae with many short, contorted, sub-solid or solid branches (Fig. 23 d), intertwined with the other hyphae, and binding them into a compact tissue, are present in large numbers. Thin-walled, nodose-septate hyphae with deeply staining contents and branching frequently are intertwined and interwoven with the fibre hyphae. In the dissepiments, fibre hyphae with fairly long branches, tortuous and intertwined, and binding hyphae with numerous, short, tortuous branches, interwoven with the fibre hyphae and binding them across their direction of growth, constitute the bulk of the dense tissue. Thin-walled, nodose-septate hyphae, intertwined with the fibre hyphae, branch repeatedly and turn outwards towards the hymenial surfaces where their numerous, short, intertwined branches form a sub-hymenial layer of small isodiametrical cells about 5μ thick. From this layer the basidia are produced in a dense even stand. No accessory structures are present in the hymenium.

Decay and hosts

Trametes suaveolens causes a white, mottled rot of the heartwood of *Salix* spp. but is found occasionally on *Populus* and *Betula* spp.

Specimens examined

Herb. DAOM: F50, on *Salix* sp., Ottawa, Ont., Oct. 1929; F911, on *Salix* sp., Gaspé, Que., Sept. 1927; F948, on *Salix* sp., Ottawa, Ont., Sept. 1928; F994, on *Salix* sp., Ottawa, Ont., July 1929; F1297, on *Salix nigra,* Syracuse, N.Y., Nov. 1929; F1393, on *Salix* sp., Ottawa, Ont., Sept. 1930; F1633, on *Salix* sp., Woodpecker, B.C., Sept. 1927; F1954, Syracuse, N.Y., Aug. 1931; *F1964, on *Salix* sp., Hopewell, N.J., Sept. 1931; F2249, on living *Salix* sp., Winnipeg, Man., Apr. 1932; F2919, on living *Populus balsamifera,* Edmonton, Alta., Oct. 1932; F2994, on *Salix,* Greenwich, N.S., Sept. 1930; F3500, on *Salix* sp., Ottawa, Ont., Sept. 1933; *F3523, on *Salix* sp., Ottawa, Ont., Sept. 1933; F3669, on *Alnus incana,* Ste. Philomiene, P.Q., Apr. 1931; F3704, on dead *Populus balsamifera,* Edmonton, Alta., Nov. 1933; F5031, on *Salix* sp., Ottawa, Ont., Sept. 1934; F5032, on *Salix* sp., Ottawa, Ont., Sept. 1934; F5641, on *Salix* sp., Nov. 1941; *7654, on *Salix* sp., Matapedia, Que., Aug. 1937; F8043, on *Salix* sp., Ottawa, Ont., Oct. 1937; F8331, on living *Salix* sp., Matapedia, Que., Aug. 1938; 10812, on *Salix* sp., Kentville, N.S., Nov. 1941, 21570, on *Populus trichocarpa,* Quesnel, B.C., 1948; 30803, on living *Salix alba,* Leighton Buzzard, Gt. Brit., Jan. 1953; 31500, on *Salix* sp., Fredericton, N.B., Nov. 1954.

Herb. PRE: 21920, on *Salix alba,* Krieger, Schädliche Pilze, Apr. 1904; 10731, on *Populus trichocarpa,* Priest River, Idaho, July 1913.

Discussion

The description of the cultural characters, agrees well with those of Hirt (1932) and Nobles (1948). The cultures agree with those of other species in this group in many ways, but the fibre hyphae with short, tortuous branches or nodose-septate hyphae with solid, branching processes formed in some other species of this group as described below, were not present in cultures of *Trametes suaveolens.* The absence of these kinds of hyphae together with the soft, cottony-woolly texture of the mycelial mat and the fragrant, anise-like odour given off may serve to distinguish cultures of this species from the others with otherwise similar characters in this group.

The fruit-bodies of *Trametes suaveolens* are rather unusual in that their soft spongy feel belie their complex construction. From the descriptions it is clear that five kinds of hyphae could be distinguished in the carpophores. Besides thin-walled, nodose-septate hyphae or generative hyphae (Corner, 1932 a) two kinds of fibre hyphae of the skeletal system (Corner, 1932 a) are present while the binding system (Corner, 1932 a) consists of fibre hyphae with short tortuous branches and solid, nodose-septate hyphae with solid clamps and tortuous branches. These "binding hyphae" are very numerous only in the lower context above and among the tubes. Towards the upper context their numbers decrease rapidly so that their binding action is less pronounced and the upper context attains the soft texture so characteristic of the type species of *Trametes* Fr.

Bourdot & Galzin (1928) and Overholts (1953) reported that the hyphae of the carpophore of *Trametes suaveolens* are sparingly branched and thick-walled. Pinto-Lopes (1952) reported that the primary hyphae are thin-walled and nodose-septate while the secondary hyphae are thick-walled and aseptate. Donk (1933) described three types of hyphae from the carpophores of *Trametes suaveolens.* Teston (1953 b) after studies of species of Polyporaceae in the Bourdot herbarium in the Museum of Natural History in Paris, reported that the carpophores of *Trametes suaveolens* have a trimitic hyphal system, according to Corner's (1932 a) concepts, with branching, thin-walled, nodose-septate, generative hyphae and thick-walled or solid, branching, skeletal hyphae, staining in Giemsa, present in the context. In the tubes, extremely contorted, branching, binding hyphae, not staining with Giemsa, were present as well. The distribution of hyphae according to Teston (1953 a) however gives the impression that the context is dimitic, consisting of generative hyphae and branching and unbranched skeletal hyphae only whilst

the trama is trimitic with binding hyphae present as well. This trimitic hyphal system was later also reported by Kotlaba & Pouzar (1957) and O. Fidalgo (1957). These descriptions agree quite well with that given above, but do not distinguish clearly between the different kinds of hyphae in the different hyphal systems. As in the fruit-bodies of species of *Ganoderma* Karst. (Hansen, 1958), the fibre hyphae with branches towards the distal end contribute to the binding hyphal system in carpophores of *Trametes suaveolens*. The solid or thick-walled, nodose-septate hyphae, considered by Corner (1932 a) and Cunningham (1946, 1954) to be generative hyphae, similarly contribute to the binding system. In the fruit-body of *Trametes suaveolens* which has a trimitic hyphal system sensu Corner (1932 b), morphologically and ontogenically different hyphae thus contribute to the different hyphal systems. In this respect the fruit-bodies of *Trametes suaveolens* (L. ex Fr.) Fr. are similar to those of *Polyporus versicolor* L. ex Fr.

Comparison of the anatomy and hyphal characters of the fruit-bodies of *Trametes suaveolens* with those of *Polyporus versicolor*, shows great similarity in hyphal characters but a great difference in construction. Where the thin fruit-bodies of *Polyporus versicolor* abound with tortuous binding hyphae, the thick fruit-bodies of *Trametes suaveolens* have a poorly developed binding system with binding hyphae almost entirely absent from the upper context; but this difference appears to be one of degree of development of a particular hyphal system in a particular species and not a difference in the types of hyphae present which could indicate a phylogenetic difference in the carpophores of the two species. These two species thus appear to be related and in fact apparently represent two extremes of a series of species with similar hyphal, anatomical and micromorphological characters but varying in construction and texture. Other species described below, especially *Polyporus pubescens* Schum. ex Fr. and *Lenzites palisoti* (Fr.) Fr. appear to be intermediate between *Polyporus versicolor* and *Trametes suaveolens* in construction. This appears to be strong evidence in favour of the view held by Pilát (1936), and Kotlaba & Pouzar (1957) that the two species are congeneric; but it appears to be desirable that the hyphal characters and construction of the fruit-bodies of many more species in this complex of species be studied carefully before a final and satisfactory conclusion can be reached.

Comparison of the hyphal characters and carpophore construction of *Trametes suaveolens* (L. ex Fr.) Fr. with those of *Daedalea quercina* Fr. shows that the binding hyphae are not present in carpophores of the latter. The nodose-septate hyphae with irregularly thickened walls present in carpophores and cultures of *Daedalea quercina* are absent from those of *Trametes suaveolens*. This difference in the kinds of hyphae present in the carpophores indicates a phylogenetic difference between these two species so that *Daedalea quercina* and *Trametes suaveolens* cannot be regarded as being congeneric as suggested by O. Fidalgo (1957).

In *Trametes suaveolens* the structures formed in cultures are, with the exception of the chlamydospores, also present in the carpophores from which they were made. It is not unlikely that chlamydospores may be found in wood decayed by *Trametes suaveolens* as reported in other species by Cartwright & Findlay (1946).

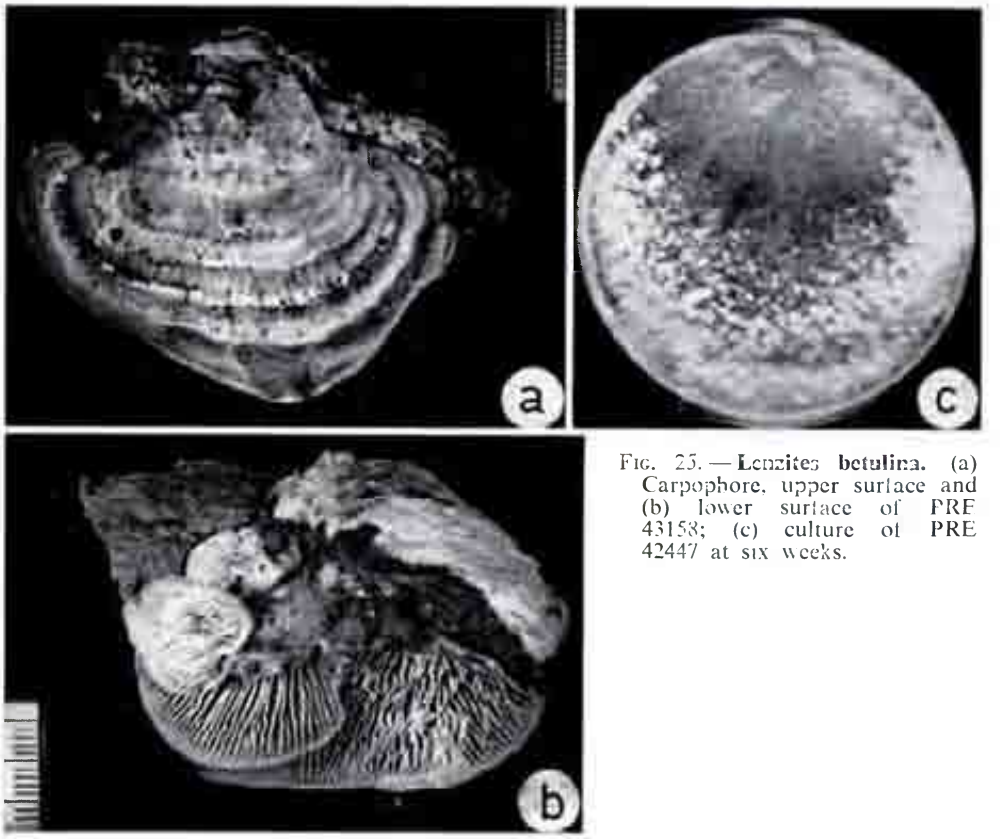

FIG. 23. — **Lenzites betulina.** (a) Carpophore, upper surface and (b) lower surface of PRE 43158; (c) culture of PRE 42447 at six weeks.

Lenzites betulina (L. ex Fr.) Fr., Epicr. Syst. Myc., 405, 1836 — 1838;
Daedalea betulina L. ex Fr., Syst. Myc. 1, 333, 1821;
Trametes betulina (L. ex Fr.) Pilat, Atl. Champ. Eur. III, 327, 1936.

Cultural characters

Growth is rapid to moderately rapid, the colony reaching a radiius of up to 30 mm in one week and covering the plate in 2 — 4 weeks. The margin is even, appressed, in some isolates over a narrow zone only, mycelium then raised, mostly cottony to woolly in a zone behind the advancing zone, then somewhat collapsed and more densely woolly with a pebble-like surface over the older part of the white mat. In time the mat gradually thickens developing raised areas of tough, felty or woolly-felty mycelium somewhat lacunose or developing a warty surface or rounded lumps of mycelium giving it a pebbly appearance, the intervening areas mostly thin appressed, sub-felty to felty. Mat very tough but separating easily from the agar. After about 4 weeks the pebbly mycelium may develop fruiting areas, at first warty, of pale "cream color" developing short, blunt, spines, rounded or somewhat flattened, glabrous or chamois. The reverse bleaches rapidly while a faint, pleasant, sweet, mushroomy odour is given off during the first two to four weeks. A strong positive reaction for extra-cellular oxidase results when alcoholic gum guaiac solution is applied to the mat.

Advancing mycelium: hyphae hyaline, thin-walled, nodose-septate, branching, often opposite the clamp connections, 2.0 — 6.0μ in diameter (Fig. 26 a).

Aerial mycelium: (a) nodose-septate hyphae hyaline, richly branched, narrow, 1.0 — 2.5μ in diameter (Fig. 26 b); (b) fibre hyphae long, straight, unbranched, hyaline, widest along the middle part, walls thickened and refractive, lumina narrow or reduced to a series of interrupted spaces, widening only towards the narrower, thin-walled ends, aseptate, 3.5 — 4.0μ in diameter at the widest parts (Fig. 26 c); (c) fibre hyphae with long tapering branches, hyaline, narrow, with prominent aseptate lumina with deeply staining contents, or lumina narrow or occluded, and hyphae solid, 1.5 — 3.0μ in diameter (Fig. 26 d); (d) nodose-septate hyphae with numerous short branches, walls thickened, lumina much reduced or hyphae solid, 1.5 — 3.0μ in diameter (Fig. 26 h).

Submerged mycelium: (a) nodose-septate hyphae as in the advancing zone.

Carpophore characters

Carpophore annual or perennial, lignicolous, solitary, sessile to effused-reflexed; pileus dimidiate, occasionally imbricate to laterally connate, coriaceous, up to 6.0 x 9.0 x 1.0 cm; surface tomentose or hirsute, concentrically zonate often multi-coloured, whitish or pale greenish grey or greyish brown; margin acute, entire, concolourous with upper surface, or lighter; pore surface white to "cream color" darkening somewhat on drying, usually lamellate, lamellae frequently branched or anastomising, occasionally poroid or labyrinthiform, about 1 mm apart, edges even or interrupted, decurrent behind; context white 0.5 — 3.0 mm thick, fibrous. *Hyphal characters:* (i) nodose-septate hyphae hyaline, branched, thin-walled, with conspicuous clamps, 1.2 — 3.0μ in diameter (Fig. 26 e); (ii) fibre hyphae long, more or less straight, unbranched or with an occasional short branch near the distal end, widest along the middle portion, thick-walled, refractive, lumina aseptate, narrow or reduced to an interrupted line, or hyphae solid except near the ends, 3.0 — 7.5μ in diameter (Fig. 26 f); (iii) fibre hyphae with numerous, short, tortuous branches, walls thickened, lumina narrow or occluded, aseptate 1.0 — 3.0μ in diameter (Fig. 26 g); (iv) nodose-septate hyphae with numerous flexuous branches, solid, occasionally sub-solid, 1.0 — 3.0μ in diameter (Fig. 26 h).

Hymenium: basidia hyaline, narrowly clavate, small, 20.0 — 26.0 x 4.0 — 5.0μ, with four, short, curved sterigmata, 2.5 — 3.0μ long (Fig. 26 k); basidiospores hyaline, cylindrical to slightly curved, smooth, thin-walled, with a small, oblique apiculus, 4.5 — 6.0 x 2.0 — 2.5μ (Fig. 26 m); tramal cystidia projecting 6.0 — 20.0μ above the hymenium, upper part broadly subulate, thick-walled, hyaline, lumina prominent, aseptate, mostly with brownish contents, and arising as lateral branches of fibre hyphae or directly from thin-walled, nodose-septate hyphae in the trama (Fig. 26 n).

Construction. At the margin the carpophore consists of long unbranched fibre hyphae, mostly with prominent lumina, more or less parallel in arrangement and

FIG. 26.— **Lenzites betulina.** a - d. Structures from cultures: (a) nodose-septate hyphae from advancing zone; (b) narrow, branched, nodose-septate hyphae from aerial mycelium; (c) unbranched fibre hyphae; (d) fibre hyphae with long, tapering branches.
e - n. Structures from carpophores: (e) thin-walled, nodose-septate hyphae; (f) unbranched, fibre hyphae; (g) fibre hyphae with numerous tortuous branches; (h) sub-solid or solid nodose-septate hyphae with numerous flexuous branches also found in cultures; (k) basidia; (m) basidiospores; (n) tramal cystidium with dark-coloured contents in sagittate terminal part.

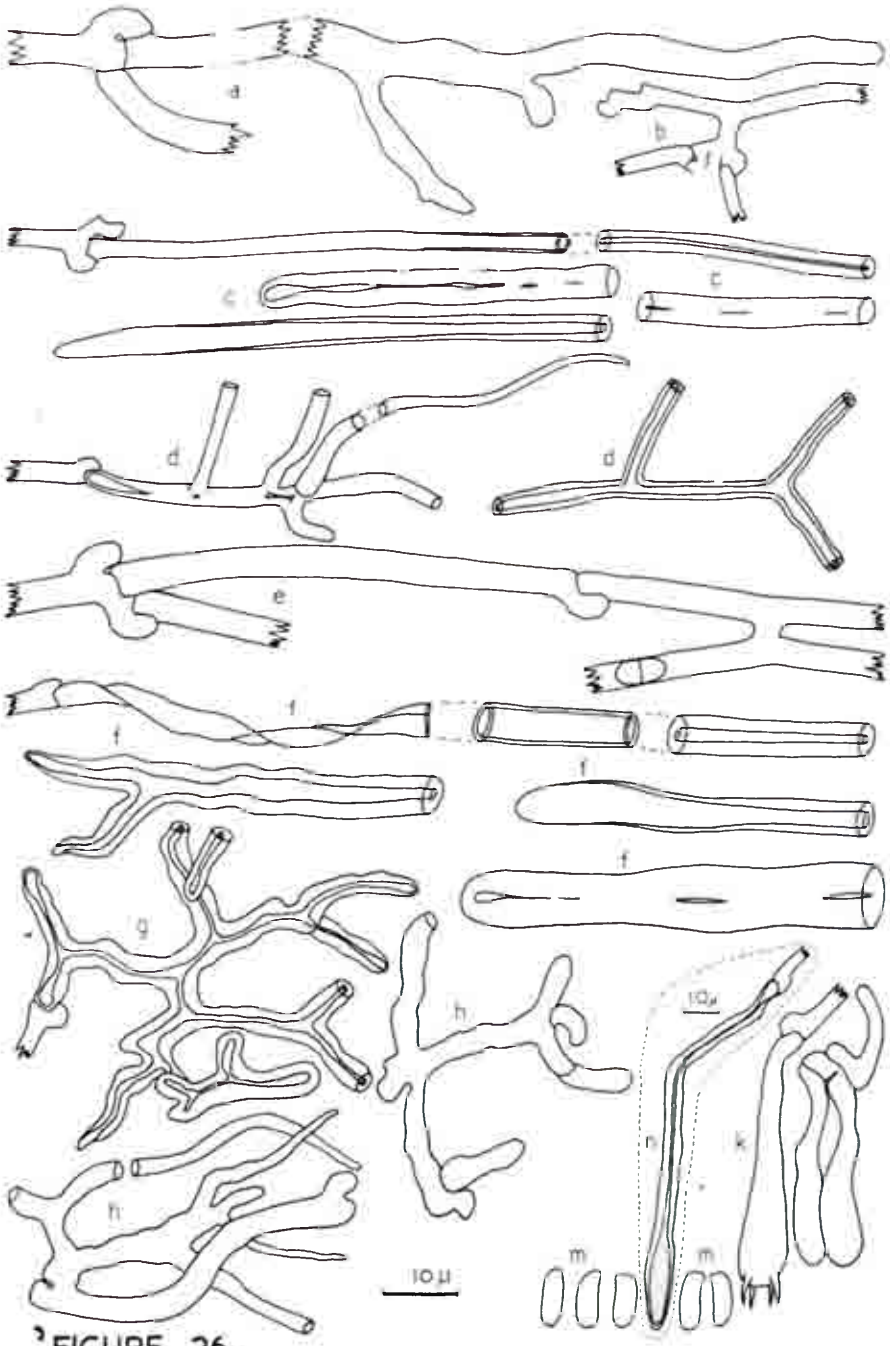

FIGURE 26.

interwoven with the numerous branching, thin-walled, nodose-septate hyphae from which they arise. In the context behind the margin the fibre hyphae are sub-solid and fibre hyphae with numerous, flexuous, lateral branches (binding hyphae) appear, with their branches interwoven with the unbranched hyphae across the direction of growth. The context consists mainly of long, unbranched, hyaline fibre hyphae, parallel to each other, slightly intertwined and small numbers of binding hyphae, tightly interwoven with the long fibre hyphae. In the upper context the long fibre hyphae turn upwards and the numbers of binding hyphae increase rapidly and thin-walled, nodose-septate hyphae, interwoven with the other hyphae, appear. This merges into a dense layer 100 — 200μ thick, at the upper surface which consists of numerous, branching, thin-walled, nodose-septate hyphae and binding hyphae all tightly interwoven with the long unbranched fibre hyphae which project beyond this layer to form the tomentose upper surface of the pileus (Fig. 26 f). These "hairs" of the upper surface may be sub-solid or solid, hyaline, or may have wide, aseptate, prominent lumina occasionally with brownish contents, and may be free or agglutinated into tufts. In the lower context the tissues are similar to the upper context but the numbers of binding hyphae increase rapidly towards the dissepiments and bind the straight fibre hyphae and thin-walled, nodose-septate hyphae into a dense, tough tissue from which individual elements can be dissected out only with difficulty. Many of these binding hyphae have solid or sub-solid clamps and appear to develop as a result of thickeneing of the walls of branched, nodose-septate hyphae (Fig. 26 h). Into the trama of the dissepiments, fibre hyphae from the lower context turn downwards where many may have one or more short, lateral branches near their tips (Fig. 26 f). The dissepiments consist mainly of binding hyphae with solid or sub-solid, aseptate, tortuous branches and nodose-septate hyphae with short, flexuous, sub-solid or solid branches, tightly interwoven with the unbranched fibre hyphae and branching, thin-walled, nodose-septate hyphae in a dense, tough tissue. In the dissepiments the thin-walled, nodose-septate hyphae branch frequently and turn towards the hymenial surfaces of the pores where the basidia are borne on their numerous, short, terminal branches. From the tramal tissues the ends of short, unbranched, fibre hyphae or lateral branches of fibre hyphae, project into and beyond the hymenium as tramal cystidia (Fig. 26 n).

Decay and hosts

Lenzites betulina causes a white rot of hardwoods.

Specimens examined

Herb. DAOM: F5115, on *Betula occidentalis,* Aleza Lake, B.C., July 1934; F5121, on *Betula* sp., Frankfurt am Main, Germany, Oct. 1934; F5229, on *Alnus incana,* Edmonton, Alta., Sept. 1931; F7205, on *Quercus* stump, Halifax, N.S., Jan. 1937; F7375, on *Populus tremuloides,* Oslo, Norway, Apr. 1937; F7462, on *Betula* sp. Ottawa, Ont., Aug. 1937; F8021, on *Fagus grandifolia,* Iberville, Que., Sept. 1938; F9071, on *Quercus acutissima,* Tokyo Science Museum No. 200645; F9156, Trinity Valley, B.C., Oct. 1938; F9909, on *Acer saccharum,* Petawawa, Ont., Sept. 1937; F9934, on *Acer saccharum,* Petawawa, Ont., Sept. 1939; *F10199, on *Betula* sp., dead branch, Montreal Is., Que., Aug. 1941; F10609, on *Betula* sp. dead branch, Montreal Is., Que., Aug. 1941; 10713, on *Betula* sp., Petawawa, Ont., Aug. 1941; 22291, on *Betula* sp. Quesnel, B.C., Aug. 1949; 22362, on *Eucalyptus* sp., Portugal, Herb. I. Pinto-Lopes No. 983; 22936, ex Herb. Hort. Bot. Reg., Kew; 30501, on *Betula papyrifera* pole, Parry Sound, Ont., Sept. 1951; 30504, *Acer rubrum* log, Horseshoe Lake, Ont., Aug. 1951; 30879, on *Acer rubrum,* Lake Rossignol, N.S., Sept. 1953; 30963, on *Betula pubescens,* Viljo Kujala, Fungi Fennici 663; 43109, Ithaca, N.Y., April 1953; 46598, on *Lithocarpus densiflorus,* Darlingtonia, Calif., Feb. 1944; 62359, on *Betula papyrifera,* Stone Creek, B.C., Aug. 1956; 52399, decaying trunk, Rio de Janeiro, Brazil, Sept. 1955; 53772, on *Betula* sp. stump, Flitwick, England, Oct. 1959; 69205, on *Betula papyrifera,* Naney, B.C., Aug. 1960; 69960, on *Betula papyrifera,* Dawson, Yukon, Terr. July 1959.

Herb. PRE: 2339, Knysna, C.P., June 1912; 3869, Rabenhorst-Winter, Fungi Europi No. 3529; 6616, on *Eucalyptus diversicolor,* Fort Cunynghame, C.P., May 1913; 13875, Herb.

J. R. Weir No. 654; 14833, Kirstenbosch, C.P., June 1921; 15485, on dead wood, George C.P., May 1922; 15576, on *Acacia mollisima*, Schwarzwald, Natal, May 1915; 17802, on *Podocarpus* sp., Knysna, C.P., May 1923; 20465, on *Podocarpus* sp., Knysna, C.P., Jan. 1925; 23478, on *Podocarpus* sp., Mount-aux-Sources, Natal, July 1928; 27277, on *Podocarpus* sp., Newlands, C.P., Aug. 1933; 27716, on *Podocarpus* sp., Donnybrook, Natal, Jan. 1935; 27967, Fungi Columbiani, E. Batholomeas No. 4935; 28604, on dead wood, Mooirivier, Natal, April 1936; 28878, on dead wood, Drakensberg, Natal, July 1937; 30189, on dead wood, Nkandhla Forest, Natal, March 1935; 30696, on dead wood, Deepwalls, Knysna, C.P., Apr. 1939; 31306, on *Quercus* sp., Kirstenbosch, C.P., Apr. 1939; 31333, on *Quercus* sp., Knysna, C.P., Apr. 1939; 31535, on living *Celtis kraussiana*, C.P., June 1921; 31558, on *Celtis kraussiana*, Katberg, C.P., Aug. 1915; 31879, *Eucalyptus* sp. logs, Knysna, C.P., Apr. 1917; 34926, on *Eucalyptus* sp., Melrose, Johannesburg, Apr. 1945; 34994, on *Acacia mearnsii* logs, Qudeni Forest, Natal, March 1935; 37481, on *Quercus* sp., Mycotheca generalis, Petrak, No. 574; 41526, on dead wood, Knysna, C.P., May 1956; 41527, on dead wood, Hogsback, C.P., May 1956; *42339, on dead wood, Dorset, Ont., Sept. 1962; *42363, on *Betula* sp., Dorset, Ont., Sept. 1962; *42434, on dead wood, Barberton, Tvl., June 1959; *42447, on *Acacia mearnsii* stumps, Kaapse Hoop, Tvl., Feb. 1961; 43158, on dead wood, George, C.P., March 1966.

Herb. STE: 352; 353, Eastern Cape Province; 422, Karkloof, Jan. 1922; 478, oak stump, Stellenbosch, Aug. 1921; 2156, oak stump Kirstenbosch, L. Bolus, July 1925; 2810, ou hout, Stellenbosch, A. J. le Roux, Oct. 1944; 43, ou hout, (as *Lenzites guineensis* Fr.); 474, old logs, Stellenbosch, Oct. 1921; 488, ou hout, J. P. Leslie, ('n vorm van *L. betulina*); 2212, *L. aspera*, on dead *Olea laurifolia*, Knysna, J. F. V. Phillips, Dec. 1923.

Discussion

The description of cultural characters of *Lenzites betulina* agrees well with earlier descriptions by Davidson, Campbell & Blaisdell (1938), Cartwright & Findlay (1946) and Nobles (1948, 1965). This species resembles *Trametes suaveolens* and *Polyporus versicolor* in cultural characters and the structures produced in culture. The characteristic pebble-like mounds of mycelium forming on top of the very tough mat, may serve to distinguish cultures of this species from other closely similar species in Group 45.

From the descriptions it is evident that four kinds of hyphae are present in the carpophores of *Lenzites betulina*. The fifth kind, the long fibre hyphae with branches near the tip (arboriform hyphae, Teixeira, 1962 b) which are present in carpophores of *Polyporus versicolor* and *Trametes suaveolens* are absent from those of *Lenzites betulina*. Although short branches were seen on some fibre hyphae, these branches were so short as to be almost inconspicuous and not comparable to those in the carpophores of *Trametes suaveolens* and *Polyporus versicolor* so that these hyphae do not merit special designation. In carpophores of *Lenzites betulina*, the binding hyphal system also consists of branched, aseptate fibre hyphae and branched, thick-walled, nodose-septate hyphae which are morphologically and ontogenically distinct as in the carpophores of *Polyporus versicolor* and *Trametes suaveolens;* but since nodose-septate hyphae are regarded as generative hyphae by Corner (1932 a, b), Cunningham (1946, 1954) and Teixeira (1962 b) the carpophores of *Lenzites betulina* must possess a trimitic hyphal system as reported by Cunningham (1948 h), Teston (1953 b), Kotlaba & Pouzar (1957) and Fidalgo (1957). None of these authors however reported the nodose-septate, thick-walled binding hyphae.

From the above it is clear that the structures formed in cultures are also present in the carpophores from which they were made. The branched fibre hyphae or binding hyphae in cultures were less sinuous than those from the carpophores but as these hyphae are interwoven with the unbranched fibre hyphae in both the cultures and also in the carpophores, they must be regarded as homologous structures.

Comparison of the hyphal characters and construction of *Lenzites betulina* (L. ex Fr.) Fr. with those of the "brown species of *Lenzites*" (Overholts, 1953)

now generally referred to *Gloeophyllum* Karst., and desscribed in Group 13, reveals important differences. Apart from the yellowish-brown pigment in the walls of the fibre hyphae of these brown species, aseptate binding hyphae, which are so numerous in the carpophores of *Lenzites betulina,* are completely absent from those of *Lenzites trabea* Pers. ex Fr. In the trama of *Lenzites sepiaria* (Wulff. ex Fr.) Fr. the aseptate binding hyphae are present in the older parts of the context and have pale umber-brown walls and longer, less tortuous branches than those of *Lenzites betulina.* In cultural characters *Lenzites betulina* also differs markedly in respect of its white mat, hyaline hyphae and positive oxidase reaction from cultures of *Lenzites trabea* and *Lenzites sepiaria* with their brown coloured mats, pale brown fibre hyphae and negative reaction when tested for extra-cellular oxidase. *Lenzites betulina* therefore cannot be regarded as congeneric with the two brown species, *Lenzites sepiaria* and *Lenzites trabea*

In a discussion of the nomenclatural status of the genus *Daedalea* Pers. ex Fr. and related genera, Fidalgo (1957) concluded that no real distinction could be found between the genera *Daedalea* Pers. ex Fr., *Lenzites* Fr. and *Trametes* Fr. other than in hymenial configuration as expounded by Fries (1838). He named *Lenzites palisoti* (Fr.) Fr. as an example in which these three types of hymenial surfaces may often be seen combined in one fruit-body thus illustrating the artificiality of even this distinction. He therefore regarded the genera *Lenzites* Fr. and *Trametes* Fr. as synonymous with *Daedalea* Pers. ex Fr., the oldest genus. A comparison of the descriptions of the type species of the genera *Lenzites, Trametes* and *Daedalea* given above, shows that the nodose-septate hyphae with irregularly thickened walls which are found in cultures and carpophores of *Daedalea quercina* L. ex Fr., the type of the genus *Daedalea* (Donk, 1960), are absent from the cultures and carpophores of *Lenzites betulina* (L. ex Fr.) Fr. and *Trametes suaveolens* Fr., the type species of the genus *Lenzites* Fr. and *Trametes* Fr. respectively (Donk, 1960). Furthermore, the binding hyphae which are characteristic of the carpophores of *Lenzites betulina* and *Trametes suaveolens* are absent from those of *Daedalea quercina.* The carpophores of *Daedalea quercina* thus have dimitic hyphal systems, in the sense of Corner (1932 a, b) while those of *Lenzites betulina* and *Trametes suaveolens* have trimitic hyphal systems. There are thus distinct and fundamental differences in the hyphal systems and construction of the carpophores of the type species of the genus *Daedalea* Pers. ex Fr. on the one hand and the genera *Lenzites* Fr. and *Trametes* Fr. on the other. Therefore, the latter two genera cannot possibly be regarded as being congeneric with *Daedalea quercina* despite similarities in gross morphological characters.

From the above descriptions it is evident that cultural characters, hyphal characters and the construction of the carpophores of *Polyporus versicolor, Trametes suaveolens* and *Lenzites betulina* are very similar in many respects. This similarity caused Donk (1933) to express the view that the genera *Coriolus* Quél., *Trametes* Fr. and *Lenzites* Fr., of which these three species are the respective types, (Cooke, 1959) may be congeneric. This was also the basis for Pilát's (1936) inclusion of the genera *Coriolus* Quél. and *Lenzites* Fr. in *Trametes* Fr. A careful comparison of the hyphal characters of the three species shows that the fibre hyphae with one or two long branches near their ends are absent from the carpophores of *Lenzites betulina* but are present in those of *Polyporus versicolor* and *Trametes suaveolens.* In carpophores of *Trametes suaveolens,* fewer binding hyphae are present than in those of the other two species. Carpophores of *Trametes suaveolens* thus differ from those of the other two species in the numbers of one kind of hypha present while carpophores of *Lenzites betulina* differ from those of *Polyporus versicolor* and *Trametes suaveolens* in the kinds of hyphae present. Since the kinds of hyphae present in carpophores are considered to be important at the

generic level (Bondartzeva, 1961; Teixeira, 1962 b), it appears that *Lenzites betulina* cannot be considered to be congeneric with *Polyporus versicolor* and *Trametes suaveolens*. The importance of the absence of these hyphae from carpophores of *Lenzites betulina* can however be confirmed only by examination of a large number of specimens and many different species with similar anatomical and micromorphological characters; but from the above descriptions and descriptions of the following species in this group, it appears as if this character, if considered in combination with the presence of a predominantly lamellate hymenium, may be the characters which distinguish the genus *Lenzites* Fr. from the closely related genus *Trametes* Fr.

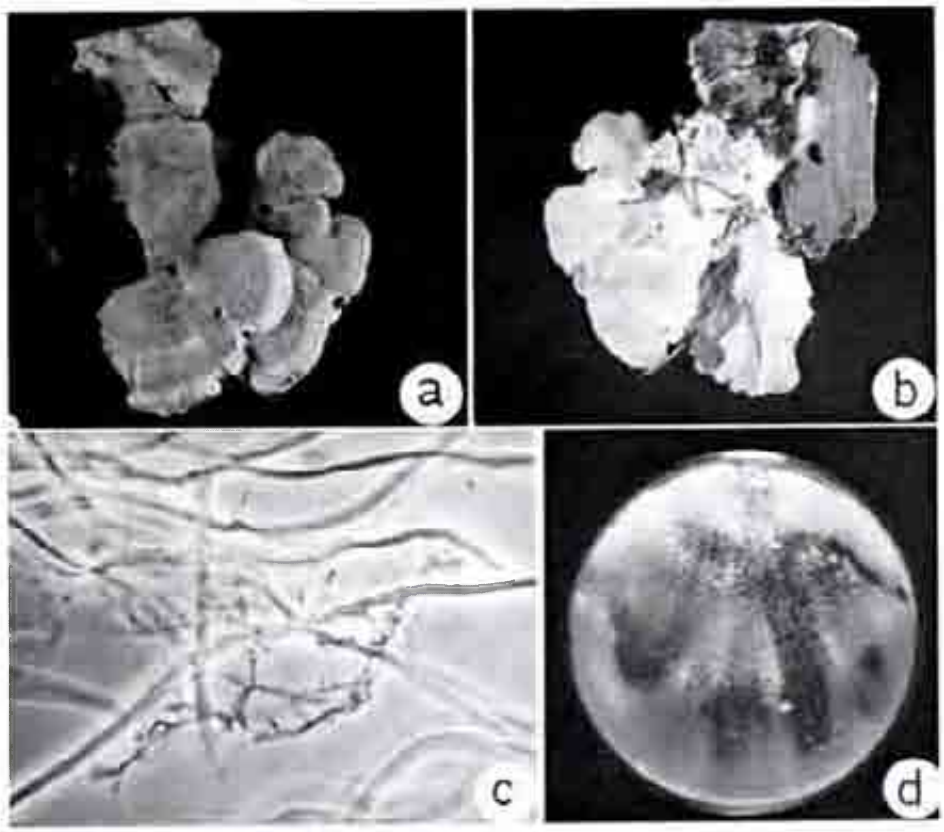

FIG. 27.— **Polyporus pubescens.** (a) Carpophores of DAOM 17530, upper surfaces and (b) hymenial surfaces; (c) narrow, dichotomously branched hyphae and unbranched fibre hyphae from culture, × 500; (d) culture of DAOM 17577 at six weeks.

Polyporus pubescens *Schum. ex Fries*, Syst. Myc. 1, 367, 1821;
Coriolus pubescens (Schum. ex Fr.) Quelet, Fl. Myc. Fr. p. 391, 1881;
Trametes pubescens (Schum. ex Fr.) Pilat, Atl. Champ. Eur. III, 268, 1939.

Cultural characters

Growth is moderately rapid, the mat reaching a radius of up to 35 mm after 1 week and covering the plate after 2 to 3 weeks. Margin even, raised, white, cottony to woolly; mat raised behind margin, becoming appressed, compact, woolly,

towards inoculum. Farinaceous areas appear and increase in size resulting in a finely pebbled appearance of the surface; or, mat felty with thin, pellicular areas appearing, which increase in size and coalesce to form irregular, pellicular areas occasionally involving the entire mat, the surface irregularly, radially grooved, or, smooth between the grooves, or, roughly lacunose with small raised, anastomosing ridges and wart-like protruberances in the older parts of the pure, white mat. Pale "cream color" irregular, raised, spongy areas may appear along the side of the dish, with similar warted surfaces, giving rise to minute, acicular spines, bearing basidia and basidiospores. The reverse bleaches after one to two weeks and a faint mushroomy odour is given off. A strong positive reaction for extra-cellular oxidase is given with gum guaiac solution. Strong diffusion zones are formed on gallic acid agar and tannic acid agar. No growth occurs on gallic acid agar but colonies up to 40 mm in diameter on tannic acid agar after one week.

Advancing mycelium: hyphae hyaline, branching, thin-walled, nodose-septate, 2.0 — 3.5μ in diameter and with deeply staining contents (Fig. 28 a).

Aerial mycelium: (a) thin-walled, nodose-septate hyphae as in the advancing zone; (b) fibre hyphae hyaline, long, unbranched, walls thick, refractive, sub-solid to solid, up to 4.5μ in diameter (Fig. 28 b); (c) fibre hyphae hyaline, branched, the branches long, flexuous, tapering gradually towards the tips, the lumina prominent, aseptate, 2.0 — 3.0μ in diameter (Fig. 28 c); (d) hyaline, much branched, solid, refractive processes, arising from nodose-septate hyphae, 1.5 — 4.0μ in diameter (Fig. 28 d); (e) hyaline, very narrow, reticulately branching hyphae, solid, 0.5μ in diameter (Fig. 27 c).

Fructification: basidia long, clavate, 10.0 — 17.0 x 3.6 — 4.5μ, with 4 straight sterigmata, 3.0 — 3.6μ long (Fig. 28 h); basidiospores hyaline, cylindrical, straight or slightly curved, apiculate, smooth, thin-walled, 4.5 — 5.0 x 1.5 — 2.0μ (Fig. 28 h).

Submerged mycelium: (a) nodose-septate hyphae as in the advancing zone; (b) hyaline, branched, nodose-septate hyphae with slightly thickened walls, empty, 1.0 — 3.0μ in diameter with short, much-branched processes either with thickened walls or solid and refractive (Fig. 28 f); (c) chlamydospores hyaline, ovoid to irregularly ellipsoid or fusoid, 6 — 14 x 4.5 — 9.0μ (Fig. 28 g).

Carpophore characters

Carpophores annual, lignicolous, grouped or compound, sessile, or in circular clusters attached at the centre, often imbricate and laterally connate; pileus applanate to conchate or flabellate; coriaceous and somewhat watery when fresh, drying to rigid 1 — 5 x 2 — 6 x 0.3 — 1.0 cm; surface villose-tomentose to almost hirsute at base, to finely tomentose or glabrescent, often radially striate towards the margin, creamy white to "cartridge buff" or "tilleul buff"; margin obtuse, entire to lobate, creamy white; pore surface poroid, white, drying to "cream buff" or

FIG. 28.—**Polyporus pubescens.** a - h. Structures from cultures: (a) thin-walled, nodose-septate hyphae from advancing zone; (b) unbranched fibre hyphae; (c) branched fibre hyphae; (d) hyaline, much-branched solid processes arising from nodose-septate hyphae; (f) nodose-septate, thick-walled hyphae with solid, refractive, branched processes; (g) chlamydospores; (h) basidia and basidiospores.
k - s. Structures from carpophores: (k) thin-walled, nodose-septate hyphae; (m) unbranched fibre hypha; (n) fibre hypha with branches towards the distal end; (p) fibre hypha with short, tortuous branches; (q) solid, contorted, branched, nodose-septate hyphae; (s) basidia and basidiospores.

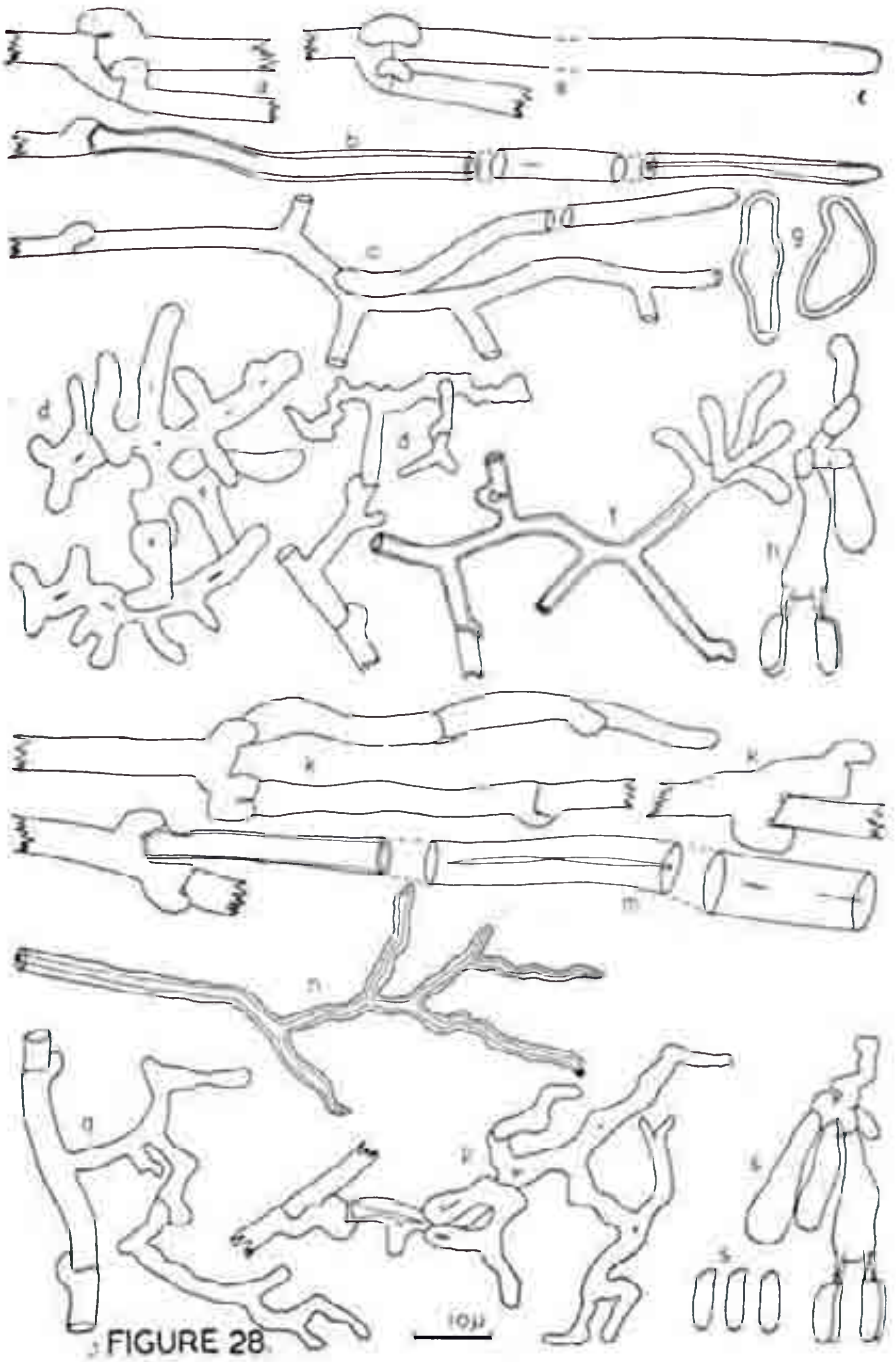

FIGURE 28

"warm buff"; pores angular, 3 — 4 mm; dissepiments thick at first, 1 — 4 mm deep; context white, zonate and with fine radiating fibres 1 — 6 mm thick.

Hyphal characters: (1) nodose-septate hyphae hyaline, branching at or between the septa, thin-walled, with deeply staining contents, 2.2 — 3.6μ in diameter (Fig. 28 k); (2) fibre hyphae long, unbranched, hyaline, walls somewhat thickened, lumina prominent, aseptate often collapsed towards the thin-walled extremities, 3.0 — 4.5μ in greatest diameter, or, walls much thickened, lumina very narrow, aseptate or occluded and hyphae sub-solid to solid with lumina visible at the extremities only, 4.0 — 6.0μ in diameter (Fig. 28 m); (3) fibre hyphae with thick hyaline walls and aseptate lumina, branching repeatedly over a short distance towards their tips the branches long, somewhat beaded in appearance and 3.5 — 6.0μ in diameter (Fig. 28 n); (4) contorted fibre hyphae with many short thick, solid branches, 3.0 — 6.0μ in diameter (Fig. 28 p); (5) thick-walled solid nodose-septate hyphae twisted and contorted and resembling (4) above but with solid clamps, 2.5 — 5.0μ in diameter (Fig. 28 q).

Hymenium: basidia clavate, 11.0 — 16.0 x 3.6 — 4.5μ, bearing four straight sterigmata, 3.0 — 3.5μ long; basidiospores hyaline, long cylindrical, occasionally somewhat curved, obliquely apiculate, smooth, thin-walled, 4.2 — 7.2 x 1.8 — 2.4μ (Fig. 28 s). Hyphal pegs broadly conical rising up to 50μ above level of hymenium.

Construction. At the margin the carpophore consists mainly of long, straight, unbranched fibre hyphae with relatively thick walls and tips often collapsed, the hyphae slightly interwoven and orientated parallel to the direction of growth of the pileus. Immediately behind the foremost marginal fibre hyphae and intertwined with other fibre hyphae, are numerous branching, thin-walled, nodose-septate hyphae from which the fibre hyphae arise. Intertwined and interwoven with these hyphae are the numerous short, contorted branches of thick-walled or solid, branched fibre hyphae which bind these other hyphal elements into a tough tissue. Behind the margin and towards the upper part of the context the fibre hyphae bend upwards towards the upper surface. In the upper context the unbranched fibre hyphae are orientated upwards and lightly intertwined. Interwoven with these hyphae are binding hyphae which are either short, tortuous branches of long fibre hyphae or short, much-branched, fibre hyphae with sub-solid or solid branches, or, thick-walled or solid much-branched, nodose-septate hyphae. These hyphae bind the tissues into a tough, homogeneous mass. Thin-walled, nodose-septate hyphae with deeply staining contents are numerous in the upper context especially just below the upper surface. The upper surface is acuticulate and consists of the ends of long fibre hyphae, mostly solid and projecting somewhat above the level of the tissues, bound together by the binding hyphae to form the tomentose upper surface of the younger part of the pileus. In the older parts nodose-septate hyphae with deeply staining contents grow upwards beyond this layer and become closely associated and agglutinated with the ends of fibre hyphae to form the hirsute to fibrillar trichoderm of the older parts of the context. In the lower context the long fibre hyphae turn downwards into the tramal tissues. Here the fibre hyphae with terminal branches become more numerous and the short, much-branched fibre hyphae with solid branches and thick-walled nodose-septate branched hyphae become very numerous to form a denser and tougher tissue than the upper context. All hyphae are more flexuous and narrower than in the upper context and are tightly interwoven to form the tramal tissues. Here, the thin-walled, nodose-septate hyphae with deeply staining contents are inextricably interwoven with the other hyphae, branching profusely, the branches short and emerging on the surfaces of the pores where they bear fasicles of basidia. On the pore surfaces are conical hyphal pegs consisting of small bundles of fibre hyphae of which the ends project beyond the hymenial surfaces.

Decay and hosts

Polyporus pubescens causes a white rot of hardwood logs (Nobles, 1948).

Specimens examined

Herb. DAOM: *17530, on *Quercus macrocarpa*, Carberry, Man., Sept. 1947; *17542, on *Betula papyrifera*, Blue Lake, Duck Mt. For. Res., Sept. 1947; 17561, on dead *B. papyrifera*, Buffalo Narrows, Sask., Sept. 1947; *17577, on *Fagus grandifolia* log, Chelsea, Que., Oct. 1947; *17578, on *Acer* sp., Gatineau Park, Que., Oct. 1947; *52833, on *Populus* sp., Belfast, New York, Oct. 1956; 53503, Pack Forest, Warrensburg, N.Y., Oct. 1959; *73309, on dead *Alnus* stump, Deux Rivieres, Ont., Sept. 1955; *94017, on dead *Acer* sp., Dorset, Ont., Sept. 1962; *94026, on dead *Acer* sp., Moose Lake, Ont., Sept. 1962; *94039, on yellow birch, Dorset, Ont., Sept. 1962.

Interfertility studies

Nobles (1965) reported that this species has the tetrapolar type of interfertility. It was attempted to establish the conspecificity of some new collections of *Polyporus pubescens* with older collections by means of the "Buller phenomenon." For this purpose, two mycelia, each obtained from a single basidiospore of collection DAOM 94039, were used as the haploid mycelium. The dikaryotic mycelia of the collections to be examined were inoculated on the plates four days after the plates had been inoculated with the haploid mycelia. Two days later the mycelia from the two inocula met and after three more days the haploid mycelia were examined at their peripheries for clamp connections. None were found. After 7 more days' incubation the colonies were again examined and again after a further 7 days, i.e. up to 14 days after the mycelia met on the plates. No clamp connections were ever observed on these haploid mycelia It is thus not possible to use the "Buller phenomenon" to test conspecificity among isolates of *Polyporus pubescens*. The cause for the failure of clamps to form on these mycelia, is not known but was not due to the disintegration of hyphae as a result of oidium formation by the haploid mycelium as found in *Merulius americanus* by Hwang (1955). A similar failure of dikaryotic mycelia to dikaryotise a haploid mycelium of the same species was reported by Nobles (1967) in *Basidioradulum radula* [(Fr.) Fr.] Nobles.

The collections examined in this way are listed in TABLE 5.

Discussion

The cultural characters as described above, agree well with those of other species in Group 45. In an earlier description Nobles (1948) described the fibre hyphae formed in cultures as having branches "ending in whiplash-like ends." This description, as well as a later one (Nobles, 1965) in which she mentioned the "network of narrow hyphae" formed in cultures, agree well with the above description. The mat formed by *Polyporus pubescens* in culture resembles those of *Polypores versicolor* and *Lenzites betulina* in many respects but may be distinguished from these two species by careful observation and comparison of all characters.

In the carpophore five kinds of hyphae could be distinguished. It was found that three types of hyphae, viz. nodose-septate hyphae with thickened walls, lateral branches of long fibre hyphae and fibre hyphae with numerous short, aseptate branches together constitute the hyphae of the binding system. These hyphae arise in different ways and are morphologically and ontogenically different; but since the thick-walled, nodose-septate hyphae are regarded as homologous with thin-walled, nodose-septate hyphae by Corner (1932 a), Cunningham (1946) and Teixeira (1962 b) and since branched fibre hyphae are regarded as hyphae of the skeletal system like unbranched fibre hyphae by Teixeira (1962 b), the carpophores of *Polyporus pubescens* have a trimitic hyphal system consisting of nodose-septate generative hyphae, skeletal hyphae and binding hyphae as reported by Teston (1953 b).

From the above description it is evident that the structures formed in cultures are also present in the carpophores from which they were made with the exception of the narrow, reticulately branching hyphae. These hyphae could not be located in the carpophores. The hyphae with solid, branched processes formed in culture, do not form pseudo-parenchymatous areas over the cultures in the manner of hyphae with interlocking projections found in cultures of Group 53. Instead, these processes are interwoven with fibre hyphae in the mat, which they bind into tough, felty parts which are teased out only with great difficulty. These hyphae thus appear to be binding hyphae which are also found in such large numbers in the carpophores, interwoven with long, unbranched, fibre hyphae.

Carpophores of *Polyporus pubescens* resemble those of *Polyporus versicolor* and *Trametes suaveolens* in hyphal characters and, to a lesser extent, in construction. The same types of hyphae present in the carpophores of *Polyporus pubescens* are also present in carpophores of the other two species but in apparently different numbers, so that the carpophores differ in construction and texture. Although carpophores of *Polyporus pubescens* have relatively fewer binding hyphae than those of *Polyporus versicolor*, especially in the middle context, and are consequently somewhat softer and less leathery, the binding hyphae are concentrated in the trama and at the upper surface. In this respect the carpophores of *Polyporus pubescens* differ somewhat in construction from those of *Polyporus versicolor;* but they differ even more from those of *Trametes suaveolens* in which binding hyphae are almost absent from the upper context. Therefore *Polyporus pubescens* seems to be more closely related to *Polyporus versicolor* than to *Trametes suaveolens* a fact recognized by Quélet (loc. cit.) when he included *Polyporus pubescens* in his new genus *Coriolus*.

Trametes meyenii *(Klotzsch) Lloyd*, Myc. Writ. 5, Lett. No. 67, 14, 1918;

Polyporus meyenii Klotzsch, Nova Acta Acad. Leop. — Carol. 19, Suppl. 236, 1843;

Polystictus meyenii Klotzsch in Fungi Orb. terv. circ. a Meyen. Coll. p. 236, 1843;

Coriolus meyenii (Klotzsch) G. H. Cunningham, Proc. Linn. Soc. N.S.W., 75, 214 — 249, 1950;

Cerrena meyenii (Klotzsch) Hansen, Na. Hist. Rennell Isl., Brit. Sol. Isl. 3, 129, 1960.

Cultural characters

Growth is rapid the mat reaching a radius of 60 — 70 mm in 7 days and covering the plate in 10 — 12 days. Advancing zone even, thin, appressed for 1 — 2 mm behind the margin, then raised, the young mycelium hyaline and evenly thin, woolly, the mat increasing in thickness towards the inoculum. The thickest parts develop faint tints of "cream color" after two weeks Surface at first smooth, even or faintly, radially sulcate and remaining so with the mat gradually thickening to an extremely tough, sub-felty texture, or, later becoming roughened or irregularly lacunate or granular over the thickest part and around the inoculum. The mat remains white except over the thickest parts where colours gradually deepen to "light buff" or "pale ochraceous buff". Occasionally thin, short, erect, "light buff" spines, up to 1.0 mm in height and bearing basidia and basidiospores, develop in small depressions in lacunose areas over the thickest part. The reverse is bleached after 2 weeks and a faint, fragrant, mushroomy odour is given off up to the fourth week. On gallic acid and tannic acid media colonies of up to 40

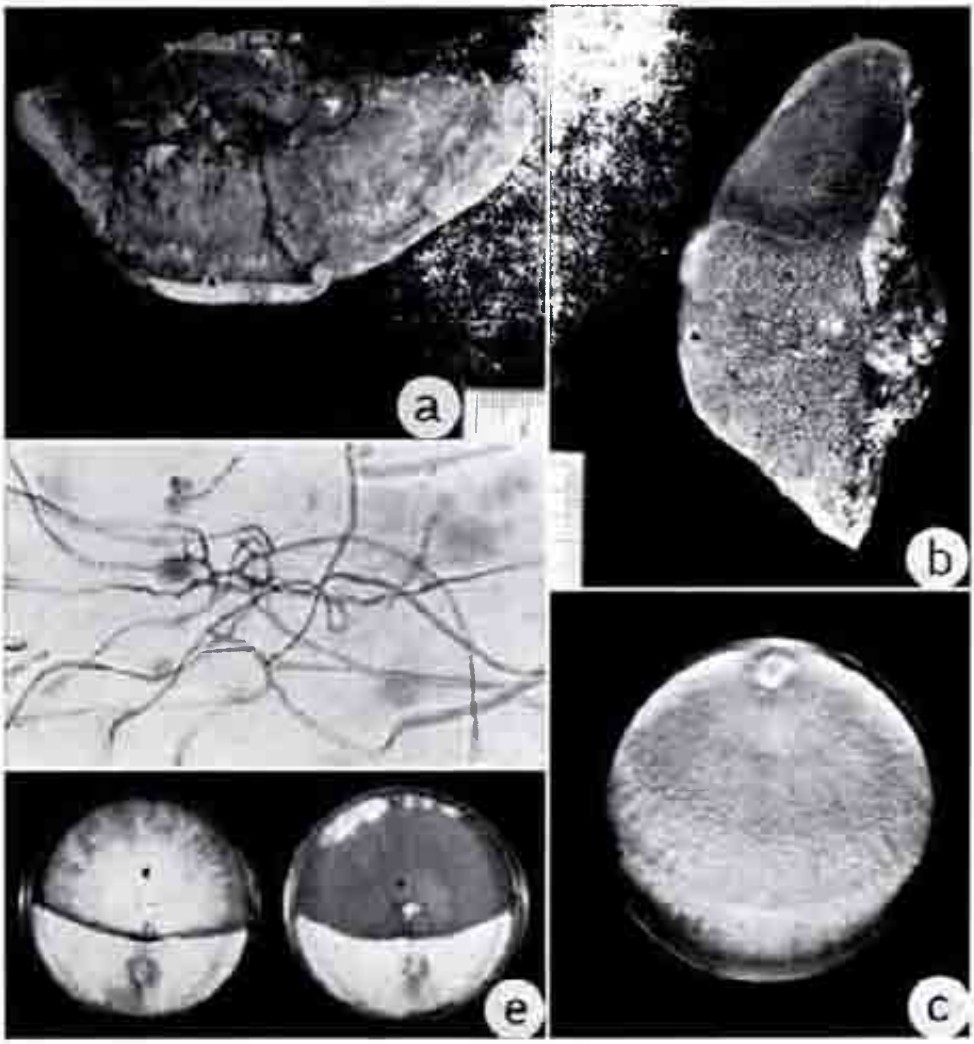

FIG. 29.— **Trametes meyenii.** (a) Carpophore of PRE 42446, upper surface and (b) hymenial surface; (c) culture of PRE 42446 at six weeks; (d) fibre hypha with numerous long, tapering branches from fruit-body, × 250; (e) "Buller phenomenon" plates of PRE 42459, bottom, diploid, with PRE 42446 — 14 and PRE 42446 — 16, top, haploid.

mm and 60 mm respectively and strong diffusion zones, are formed in seven days. A strong positive reaction results when cultures are tested for extra-cellular oxidase by means of gum guaiac solution.

Advancing mycelium: hyphae hyaline, thin-walled, with simple clamp connections at the septa, branching near the septa, 2.5 — 4.0μ in diameter (Fig. 30 a).

Aerial mycelium: (a) hyphae as in the advancing zone; (b) fibre hyphae hyaline, long, unbranched, narrow towards the ends, widening to up to 6μ in diameter near the middle part, walls thick, refractive, lumina aseptate, narrow or occluded, widening towards the ends (Fig. 30 b); (c) fibre hyphae narrow, 1.5 — 3.0μ in diameter branching repeatedly over a short distance of main stem, the branches sub-solid to solid, flexuous, tapering gradually towards the tips (Fig. 30 c); (d) oidia numerous in some isolates, hyaline, ovoid to cylindrical with rounded ends, 2.0 — 3.0 x 3.0 — 6.0μ (Fig. 30 d).

Fructifications: basidia short, broadly clavate, 10.0 — 15.0 x 4.5 — 6.0μ, with four slender, straight, sterigmata 3.0μ long (Fig. 30 e); basidiospores hyaline, smooth, ellipsoid-cylindrical to cylindrical with rounded ends, obliquely apiculate, thin-walled, 4.5 — 6.0 x 2.0 — 2.5μ (Fig. 30 f).

Submerged mycelium: (a) nodose-septate hyphae as in the advancing zone, often without contents and walls thickened; (b) oidia as in the aerial mycelium.

Carpophore characters

Carpophores annual or reviving a second season, lignicolous, solitary; pileus sessile, dimidiate, occasionally imbricate, to effused-reflexed, often concave above, woody or corky up to 30 x 12 x 6 cm; upper surface yellowish buff to brownish grey or grey, velvety to tomentose often glabrous with age or rimose, often tuberculate and concentrically sulcate, zonate or azonate, mostly with a hard, bay-brown layer under the tomentum in the older part; margin obtuse, rounded, entire or lobed, finely velvety, creamy white, drying yellowish; pore surface creamy white when fresh, drying to pale buff or creamy buff; pores usually elongate, sinuous to labyrinthiform 1 — 3/mm, dissepiments thin; tubes 0.5 — 2.0 mm deep, concolourous with surface, occasionally indistinctly stratified, becoming bleached in age. Context creamy white to pale creamy or buff, fibrous, zonate, 5.0 — 40.0 mm thick, often with a dark, hard zone under the tomentum in older part.

Hyphal characters: (1) thin-walled, nodose-septate hyphae with simple clamp connections, frequently branched, 2.0 — 3.0μ in diameter (Fig. 30 g); (2) fibre hyphae hyaline, long, unbranched, narrow, thin-walled, 1.5 — 2.0μ in diameter near their origin, widening to 6μ maximum diameter with narrow or occluded, aseptate lumina (Fig. 30 h); (3) fibre hyphae as above but with two or three branches towards the distal ends, branches long, tortuous and tapering towards the ends, 1.5 — 3.5μ in diameter (Fig. 30 k); (4) fibre hyphae unbranched as above but with short, barblike, lateral projections or branches towards the distal ends, 4.0 — 6.0μ in diameter (Fig. 30 m); (5) hyaline fibre hyphae usually solid, without clamp connections or septa, with numerous branches, the branches short and tortuous or long, flexuous and tapering towards their ends, 0.7 — 3.0 in diameter (Fig. 30 n); (6) nodose-septate hyphae with numerous short, tortuous, sub-solid to solid branches, 1.2 — 3.0μ in diameter (Fig 30 p).

Hymenium: basidia short, broadly clavate, 10.0 — 15.0 x 4.5 — 6.0μ, with four sterigmata, 3.0μ long (Fig. 30 p); basidiospores hyaline, smooth, ellipsoid-cylindrical or short cylindrical with rounded ends, obliquely apiculate, thin-walled, 4.5 — 6.0 x 2.0 — 2.5μ (Fig. 30 q). Hyphal pegs small, conical, projecting up to 60μ beyond the hymenium.

Construction. The margin of the carpophore consists mainly of long unbranched fibre hyphae with narrow lumina and arranged parallel to one another. Intertwined with these are numerous thin-walled, nodose-septate, frequently branching hyphae, from which they arise. Behind the margin the fibre hyphae are mostly solid. Hyaline, solid or sub-solid, aseptate binding hyphae with their branches interwoven with the other hyphae, appear in the context tissue. The middle and upper context consist mainly of more or less parallel, intertwining fibre hyphae, unbranched or with one to three branches towards the tips, which turn upwards towards the upper surface. Intertwined with these are thin-walled, nodose-septate hyphae just below the upper surface, and numerous narrow, solid, branching fibre hyphae, binding the tissues together, in the middle part of the context. At the upper surface numerous branched fibre hyphae, mostly with the upper parts of their lumina fairly wide, project beyond the context tissues to form the hairy upper surface present in many specimens. In the older parts of the specimen, these fibre hyphae often become agglutinated by a hard, lacquer-like substance into a hard, rimose crust up to 1.5 mm thick. In the younger parts, the fibre hyphae project very little beyond the upper level of tissue composed of nodose-septate hyphae, fibre hyphae and binding hyphae to form the smooth, finely pubescent, upper surface. In the lower context and towards the tubes, the tissues become increasingly dense and consist of solid, unbranched, fibre hyphae and fibre hyphae with one to three long branches near their ends, often somewhat flexuous, and turning downwards towards the dissepiments. Intertwined with these are occasional fibre hyphae with short lateral projections. Numerous "binding hyphae", some with solid clamp connections, tightly interwoven with the other fibre hyphae, bind them into a tough, woody tissue. In the dissepiments the fibre hyphae are indistinguishable from each other, are very tortuous and tightly interwoven but orientated in a downward direction. Here they have slightly wider lumina and are narrower in diameter. Intertwined with the fibre hyphae are numerous, thin-walled, nodose-septate hyphae which branch profusely towards the surfaces of the dissepiments where they bear clusters of basidia on numerous, short, lateral branches. On the hymenial surfaces, conical hyphal pegs,consisting of bundles of parallel ends of fibre hyphae, project beyond the hymenium.

Decay and hosts

This fungus causes a white rot of hardwoods. It is common in subtropical regions where it grows on dead wood but is frequently found fruiting on the trunks of living *Acacia* species in South Africa.

Specimens examined

Herb. DAOM: 30792, on *Cassia siamea,* Njala, Sierra Leone, Aug. 1953; 69924, on *Cassia siamea* Rennell Island, Brit. Solomon Isl., Oct. 1954.

Herb. PRE: 1873, on *Citrus sinensis,* Pretoria, Tvl., July 1911; 2114, on dead hardwood, Pretoria, Tvl., Feb. 1912; 5184, on *Acacia decurrens,* Ixopo, Natal, Sept. 1912; 6917, on *Acacia decumens,* Ixopo, Natal, July 1913; 8859, on *Acacia horrida,* Pretoria, Tvl., March 1915; 8877, on *Acacia horrida,* Pretoria, Tvl., March 1915; 9545, on dead *Celtis thamnifolia,* Ngadu Forest, C.P., Jan. 1916; 11437, in Fungi Malayana, Mt. Maquiling, Philippines, July 1916; 12183, on dead *Acacia* sp. stumps, Adelaide, C.P., May 1919; 13040, on stumps, Mulanga For., Uganda, July 1919; 13943, as *Daedalea hobbsii* v.d. Bijl, Howick, Natal; 14651, on dead tree, Pretoria, April 1921; 14840, on dead tree, Kirstenbosch, Cape Prov., June 1921; 14904, on dead tree, Entebbe, Uganda; 15569, on dead tree, Ginginhlovu, Natal, July 1915; 24874, on dead tree, Pretoria, March 1915; 26402, on dead tree, Pietermaritzburg, Natal, Aug. 1932; 27564, dead stump, Pretoria, Tvl., April 1934; 27705, dead stump, Donnybrook, Natal, Jan. 1935; 28563, as *Daedalea hobbsii,* Winters Kloof, Pietermaritzburg, Sept. 1934; 28875, on *Acacia* sp., Louis Trichardt, Tvl., Aug. 1937; 30267, on dead wood, Donnybrook, Natal, Feb. 1936; 30725, on dead wood, Rustenburg, Tvl., March 1939; 30804, on dead wood, Xumeni Forest, Natal, Dec. 1936; 31311, on dead wood, Knysna, C.P., Dec. 1936; 31543, on dead wood, Pretoria, Tvl., July 1915; 31548, on dead wood, Grahamstown, C.P.,

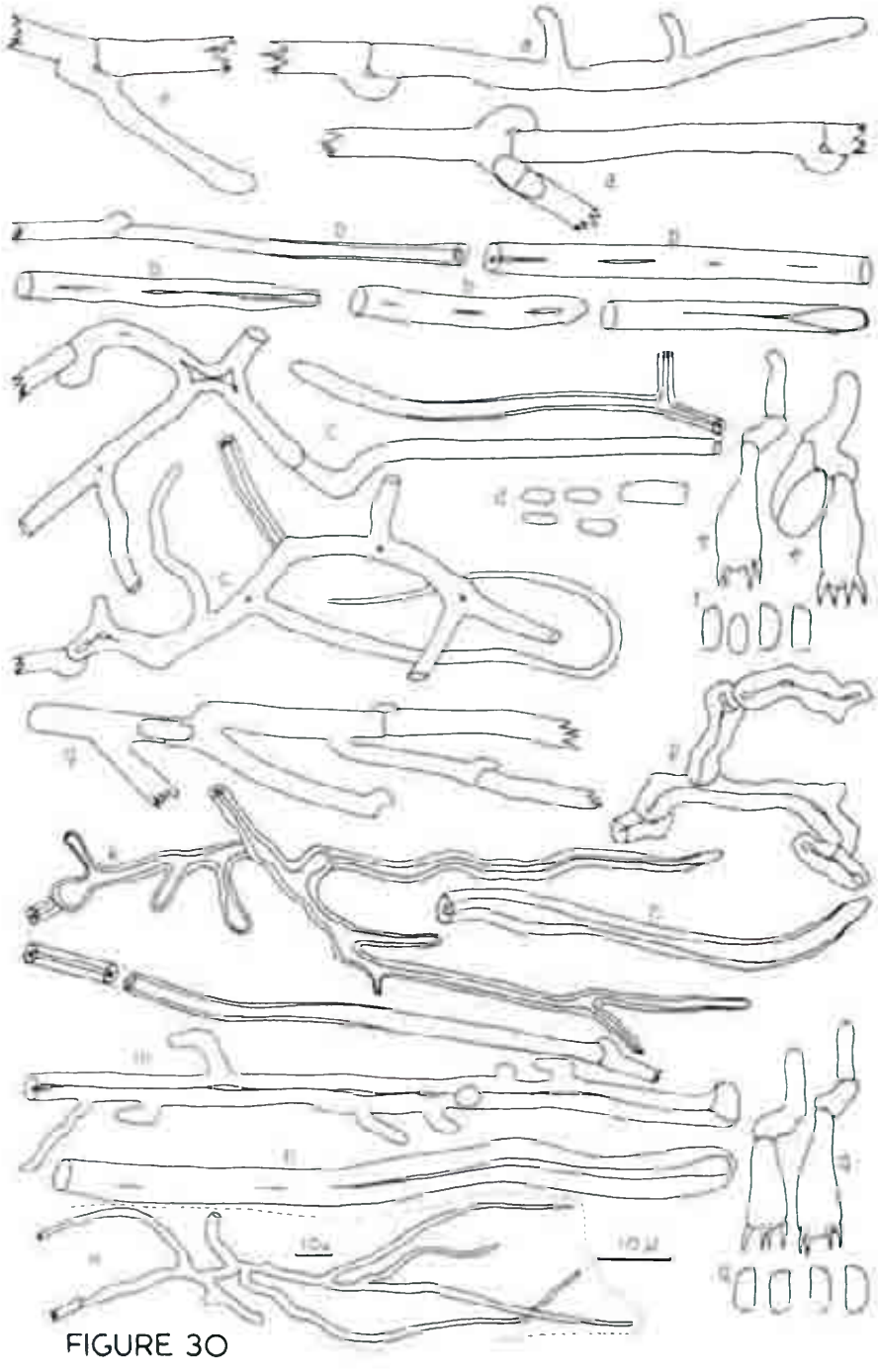

FIGURE 30

Aug. 1915; 31586, on dead wood, Pretoria, Tvl. 1915; 31623, on rotten logs, Knysna, C.P., Jan. 1916; 31685, on rotten logs Pietermaritzburg, Natal, Aug. 1916; 31712, on rotten logs, Pietermaritzburg, Natal, Dec. 1916; 31729, on rotten logs, Pietermaritzburg, Natal, Dec. 1916; 31820, on rotten logs, Umgeni, Natal, April 1917; 31974, on living *Trema* sp., Durban, Nov. 1917; 32030, on *Celtis kraussiana*, Durban, Nov. 1917; 33072, on *Acacia mollissima*, Donnybrook, Natal, June 1940; 33905, on dead wood, Scottburgh, Natal, Feb. 1943; *42446, on *Acacia mearnsii* stump, Graskop, E. Tvl., Feb. 1961; *42449, on *Acacia mearnsii* stump, Kaapse Hoop, Tvl., Feb. 1961; *42459, decaying hardwood log, Blouberg, Tvl., Apr. 1961; *42723, on living *Acacia* sp., Rustenburg, Tvl., Aug. 1953.

Herb. STE: 262, at base of *Acacia* tree, Pretoria; 575, at base of *Acacia* tree, Howick Natal; 2267, at base of *Acacia* tree, Pietermaritzburg, March 1930; 2755, at base of *Acacia* tree, Maclear, C.P.

Interfertility studies

In order to determine the type of interfertility of this species, a set of 16 cultures, each grown from a single basidiospore, was made from spores collected from a fructification formed in a culture of PRE 42446. By pairing these cultures in all possible combinations, it was found that *Trametes meyenii* has the tetrapolar type of interfertility with allelomorphs for heterothallism at two loci. The results showing the distribution of mating types among the single spore mycelia are presented below in TABLE 6.

The conspecificity of other collections of *Trametes meyenii* of which cultures were available, was tested by means of the "Buller phenomenon". Two mycelia of single spores of opposing mating types, PRE 42446 — 3 and PRE 42446 — 14, were used. Seven days after placing the dikaryotic mycelia on the plates on which the above haploid mycelia were growing, the haploid mycelia were examined for clamp connections at three different positions along their periphery. Clamp connections, indicating dikaryotization of the single spore mycelium by the added dikaryotic mycelia, were found in very position. Collections of *Trametes meyenii* numbered PRE 42449, PRE 42459 and PRE 42732 were demonstrated to be conspecific with PRE 42446 (Fig. 29 e)

Discussion

As described above, the cultural characters agree with an earlier description (Van der Westhuizen, 1958) but the hyphae are described in greater detail. Besides the thin-walled, nodose-septate hyphae, two types of fibre hyphae, one unbranched, and resembling the "vermiculiform skeletal hyphae" figured by Teixeira (1962 b), the other branched and resembling the "branched fibre hyphae with whiplash-like ends" described by Nobles & Frew (1962) from *Pycnoporus* spp., are present. These characters, as well as the strong positive oxidase reaction of the culture, agree well with the characters of other species in this group, especially with those of *Polyporus versicolor* and *Lenzites betulina;* but the cultures of *Trametes meyenii* form a thicker, smoother and more woolly mat, than those of *Polyporus versicolor* and *Lenzites betulina,* and develop colours not found on the other species. This combination of characters may serve to distinguish cultures of this species from cultures of other species in this group which are otherwise very similar.

FIG. 30.— **Trametes meyenii.** a - f. Structures from cultures: (a) thin-walled nodose-septate hyphae from advancing zone; (b) unbranched fibre hyphae; (c) fibre hyphae with long tapering branches; (d) oidia; (e) basidia; (f) basidiospores.
g - q. Structures from carpophores: (g) thin-walled, nodose-septate hyphae; (h) unbranched fibre hyphae; (k) fibre hypha with branches toward the distal end; (m) fibre hypha with lateral projections; (n) fibre hypha with numerous long, flexuous branches; (p) nodose-septate hypha with thickened walls and numerous short, tortuous branches; (q) basidia and basidiospores.

The presence of the tetrapolar type of interfertility in *Trametes meyenii*, which causes a white rot of hardwood and produces extra-cellular oxidase enzymes in culture, is in full agreement with Nobles' (1958 b) thesis that tetrapolarity is correllated with the production of extra-cellular oxidase in a large group of polypores with simple clamp connections on their thin-walled hyphae.

In the carpophores of *Trametes meyenii* five kinds of hyphae could be distinguished, viz.: thin-walled and thick-walled nodose-septate hyphae, unbranched fibre hyphae, fibre hyphae with one or two branches towards the tip and fibre hyphae with many short, flexuous branches. These latter are the binding hyphae in Corner's (1932 a) terminology but the thick-walled, nodose-septate hyphae as well as the branches of some of the long fibre hyphae also act as binding hyphae. Hyphae which are morphologically and ontogenically different thus contribute to the binding hyphal system. Since the nodose-septate hyphae are regarded as generative hyphae and the unbranched or sparingly branched hyphae as skeletal hyphae (Corner, 1932 a, b; Cunningham, 1946; Teixeira, 1962 b) carpophores of *Trametes meyenii* have a trimitic hyphal system in the terminology of Corner (1932 a, b) and Cunningham (1954).

From the above descriptions it is evident that the structures formed in culture are also present in the carpophores from which they were made. A greater variety of structures are present in the carpophores than in the cultures, a phenomenon also observed in most other species studied. The branched fibre hyphae or binding hyphae from cultures develop longer, less flexuous branches but in morphology approach the binding hyphae of the carpophores more closely than the branched skeletal hyphae.

The characters of the hyphae and construction of the carpophores of *Trametes meyenii* resemble those of *Polyporus versicolor* and *Trametes suaveolens* very closely. In construction the thin forms of *Trametes meyenii* resemble the carpophores of *Polyporus versicolor* by having large numbers of binding hyphae in the upper and lower context. The thick forms, some of which were found to be conspecific with a thin form by means of the "Buller phenomenon" technique, on the other hand have relatively fewer binding hyphae in the upper context and resemble carpophores of *Trametes suaveolens* more nearly. Such thick carpophores approach the softer upper surface and feel of those of *Trametes suaveolens* but are never as soft or have so few binding hyphae in the upper context as to be closely similar to the carpophores of *Trametes suaveolens*. *Trametes meyenii* thus appears to be a transitional species between *Polyporus versicolor* L. ex Fr., the type species of the genus *Coriolus* Quél., on the one hand and *Trametes suaveolens* (L. ex Fr.) Fr., the type species of the genus *Trametes* Fr., on the other. This indicates a close relationship between the two generic type species and is evidence in support of Pilát's (1936) and Kotlaba & Pouzar's (1957) inclusion of the genus *Coriolus* in the genus *Trametes* Fr.

Carpophores of *Trametes meyenii* also resemble those of *Lenzites betulina* in the usually lamellate hymenium and to a large extent in hyphal characters and construction, but the carpophores of *Lenzites betulina* do not have fibre hyphae with one or two branches near the tips which are present in the carpophores of *Trametes meyenii*, *Polyporus versicolor* and *Trametes suaveolens*. In respect of the characters of the other hyphae and in construction of their carpophores there are close similarities between *Trametes meyenii* and *Lenzites betulina*. It thus appears that *Trametes meyenii* has characters of all three genera, *Coriolus* Quél., *Lenzites* Fr. and *Trametes Fr.*, combined in its carpophores. This supports the view expressed by O. Fidalgo (1957) that the genera *Trametes* and *Lenzites* are congeneric but until the importance of the absence of these fibre hyphae with one or two branches can be determined, it appears desirable to regard them as distinct genera.

The relationship of *Trametes meyenii* to the genus *Coriolus* Quel., was recognized by Cunningham (1950 b) and Imazeki (1952) who independently transferred this species to the genus. Hansen (1960) transferred this species to the genus *Cerrena* Mich. ex S. F. Gray but the carpophores of the type species of this genus, *Cerrena unicolor* (Bull. ex Fr.) Murr. was shown to consist entirely of nodose-septate hyphae, mostly thick-walled, while nodose-septate, thick walled hyphae were formed in its cultures (Van der Westhuizen, 1963). *Trametes meyenii* thus has no affinities with the genus *Cerrena* Mich. ex S. F Gray.

Murrill (1907 b) cited *Polyporus meyenii* Klotzsch as a synonym of *Coriolus maximus* (Mont.) Murrill based on *Irpex maximus* Montagne of which the description antedates that of *Polyporus meyenii* by about six years. Overholts (1953) accepted Murrill's synonymy but made the combination *Polyporus maximus* (Mont.) Overholts which was later accepted by Lowe & Gilbertson (1961 b). Lloyd (1918), Imazeki (1952) and Hansen (1960) however regard *Irpex maximus* and *T. meyenii* as distinct species because of differences in the shape of their pores. This matter could not be investigated as the type specimens of these two species were not available for study. For this reason the name *Trametes meyenii* (Klotzsch) Lloyd which is well established in South Africa for the specimens studied, is used here.

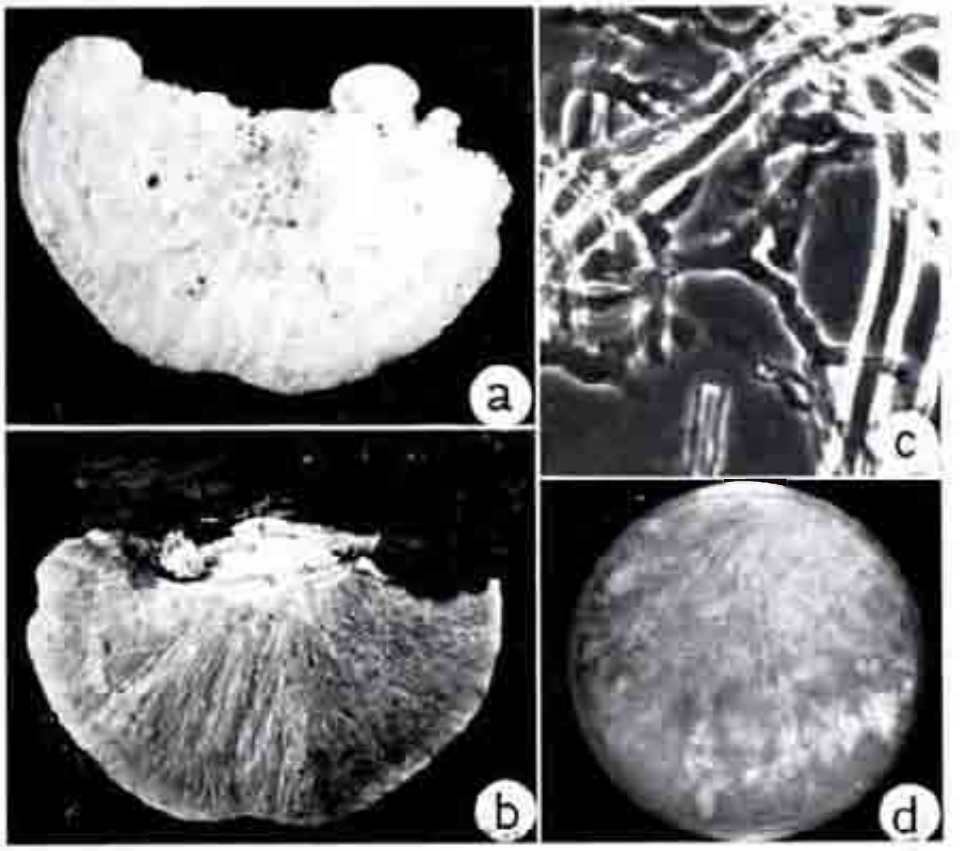

FIG. 31.— **Lenzites palisoti.** (a) Carpophore of PRE 42442, upper surface and (b) hymenial surface; (c) fibre hypha with numerous short branches and unbranched fibre hyphae from context of fruit-body, × 1000 phase contrast; (d) culture of PRE 42442 at six weeks.

Lenzites palisoti *(Fr.) Fries*, Epic. Syst. Mycol. 404, 1838;

Daedalea palisoti Fr., Syst. Mycol. 1, 335, 1821;

Trametes palisoti (Fr.) Imazeki, Bull. Tokyo Sci. Mus. 6, 73, 1943;

Coriolus ambiguus (Berk.) G. H. Cunn., Proc. Linn Soc. N. S. Wales 75, 216, 1950.

Cultural characters

Growth is moderately fast to slow the mat reaching a radius of 22 mm after one week and covering the plate after three to five weeks. The advancing zone is even at first but becomes uneven due to irregular growth of parts of the margin which result in radially elongate patches projecting beyond the margin. Mycelium mostly submerged, forming irregular milky patches in the agar. Aerial mycelium scanty, at first thin, downy, white becoming submerged but having irregular, radially elongated "islands" of white, farinaceous, downy mycelium which may gradually become tough, sub-felty or coalesce to form irregular, tough, white, sub-felty areas especially in the older parts of the colony. Fertile areas form occasionally on some of these "islands" but are not visibly differentiated. The reverse bleaches slowly and the cultures emit a strong, penetrating, sweetly fragrant odour. On gallic acid and tannic acid media strong diffusion zones are formed and colonies grow to diameters of 32 mm on gallic and 10 mm on tannic acid media in seven days. A strong blue colour is quickly formed when cultures are tested for the presence of extra-cellular oxidase by means of alcoholic gum guaiac solution.

Advancing mycelium: hyphae hyaline, branching, thin-walled, nodose-septate with simple clamp connections, 2.5 — 3.5μ in diameter (Fig. 32 a).

Aerial mycelium: (a) hyphae as in the advancing zone; (b) fibre hyphae hyaline, long, unbranched, refractive, mostly solid or with lumina reduced to an interrupted line, and suddenly expanding at the apex, 2.5 — 4.6μ in diameter (Fig. 32 b); (c) fibre hyphae hyaline, refractive, mostly solid, with a number of long branches, 2.5 — 4.0μ in diameter (Fig. 32 c); (d) fibre hyphae hyaline, mostly solid, tortuous with numerous short, solid, tortuous branches, 2.0 — 3.5μ in diameter intertwined with the long fibre hyphae and binding them into a tough tissue (Fig. 32 d); (e) nodose-septate hyphae with walls thickened or solid, empty or with staining contents and numerous short, tortuous, sub-solid or solid branches, 1.5 — 2.5μ in diameter, often inflated terminally up to 8μ in diameter or with clusters of short lateral projections, mostly solid, at the apex (Fig. 32 e).

Fructifications: basidia long, clavate almost cylindrical 10.0 — 15.0 x 3.5 — 4.0μ with four slender sterigmata 2.5 — 3.0μ long (Fig. 32 f); basidiospores ellipsoid-cylindrical to cylindrical, obliquely apiculate, hyaline, smooth, thin-walled, 3.5 — 6.5 x 2.0 — 2.5μ (Fig. 32 g).

Submerged mycelium: (a) hyphae as in the advancing zone; (b) chlamydospores thick-walled, fusiform, ovoid to sub-globose, 3.5 — 10.0 x 5.0 — 12.0μ.

Carpophore characters

Carpophore annual or reviving, lignicolous, solitary, sessile or sub-stipitate or with reduced, peltate base; pileus reniform to flabelliform or orbicular, variable, tough coriaceous to firm, rigid or woody, up to 20 x 35 x 3 cm; upper surface minutely velutinate or glabrous, tubercular or smooth or radially and concentrically sulcate, white when fresh drying to cream coloured, occasionally dark brown to blackish near the base; margin thin, acute, rounded, undulate or entire, white to cream coloured, sterile underneath; pore surface white to cream coloured poroid

to daedaloid or lenzitoid, 2 — 3 per mm, entire; tubes 2 — 4 mm deep, concolourous; context pure white or creamy white, even-textured, floccose, punky or corky.

Hyphal characters: (1) thin-walled hyphae nodose-septate with simple clamp connections, branching frequently, 1.8 — 3.0μ in diameter (Fig. 32 k); (ii) fibre hyphae hyaline unbranched, narrow near origins, with wide lumina, widening towards middlepart and simultaneously thickening of walls and narrowing of lumina, the latter widening towards the thinner-walled distal ends, aseptate, 3.0 — 6.0μ in diameter, or mostly solid with luminalacking or reduced to a narrow interrupted line which widens suddenly toward the tips (Fig. 32 m); (iii) fibre hyphae with numerous branches, the branches short, very tortuous or longer and tapering somewhat, hyaline, with thickened walls and conspicuous lumina or sub-solid with lumina lacking, aseptate, 1.5 — 3.5μ in diameter (Fig. 32 n); (iv) nodose-septate hyphae sub-solid or solid with short, tortuous branches, 1.5 — 3.5μ in diameter (Fig. 32 p); (v) fibre hyphae sub-solid or solid with two or three long branches arising over a short distance of main stem, 3.0 — 6.0μ in diameter (Fig. 32 q); (vi) short fibre hyphae with terminal clusters of branches with prominent lumina projecting into the hymenium, 1.0 — 3.0μ in diameter (Fig. 32 s).

Hymenium: basidia narrowly clavate, 18.0 — 24.0 x 4.5 — 6.0μ with four slender sterigmata up to 3.0μ long (Fig. 32 t); basidiospores cylindrical, smooth, hyaline, thin-walled, 5.0 — 7.0 x 2.0 — 2.4μ (Fig. 32 x); cystidioles occasional, narrowly cylindrical, hyaline, thin-walled, with deeply staining contents, 20.0 — 30.0 x 1.0 — 2.0μ and arising from the basidial fascicles (Fig. 32 y).

Construction. At the margin the carpophore consists of long, hyaline, unbranched, fibre hyphae more or less parallel to each other and slightly intertwined. Numerous branching and anastomosing, thin-walled, nodose-septate hyphae from which the fibre hyphae arise are intertwined and interwoven with them deeper in the tissues. Behind the margin in the upper context, the unbranched fibre hyphae turn towards the upper surface. Branched fibre hyphae (binding hyphae) with fairly wide lumina and the branches fairly long and interwoven with the fibre hyphae across their direction of growth, become increasingly numerous towards the upper surface. In the upper context the long, unbranched, fibre hyphae are mostly solid and run parallel to each other towards the upper surface where their ends are packed at a common level to form the finely pubescent surface of the younger part of the carpophore. At the upper surface, thin-walled, hyaline branching and anastomosing, nodose-septate hyphae become very numerous. They are tightly intertwined and interwoven with the fibre hyphae to form the smooth, glabrous, upper surface which becomes covered with a very thin, hyaline layer of lacquer-like material over the older parts of the carpophore The dark patches on the upper surface of some specimens, consist of the ends of fibre hyphae with their lumina dilated at the apex and the luminal contents discoloured to reddish brown or dark grey brown. The ends are embedded in a dark-coloured, resin-like substance.

In the lower context the unbranched fibre hyphae are arranged parallel to the direction of growth of the fruit-body while some turn downward toward the dissepiments. Fibre hyphae with long or short, tortuous branches and sub-solid or solid, nodose-septate hyphae with tortuous branches are interwoven with the unbranched fibre hyphae forming a tough dense tissue. In the lower parts of these tissues and in the dissepiments, thin-walled, nodose-septate hyphae become increasingly numerous, branching and anastomising and bearing basidia in fascicles on the surfaces of the dissepiments. In the dissepiments short fibre hyphae arise, bearing numerous, short, terminal branches which project into the hymenium as pseudocystidia or paraphyses as described by Overholts (1953) (Fig. 32 s).

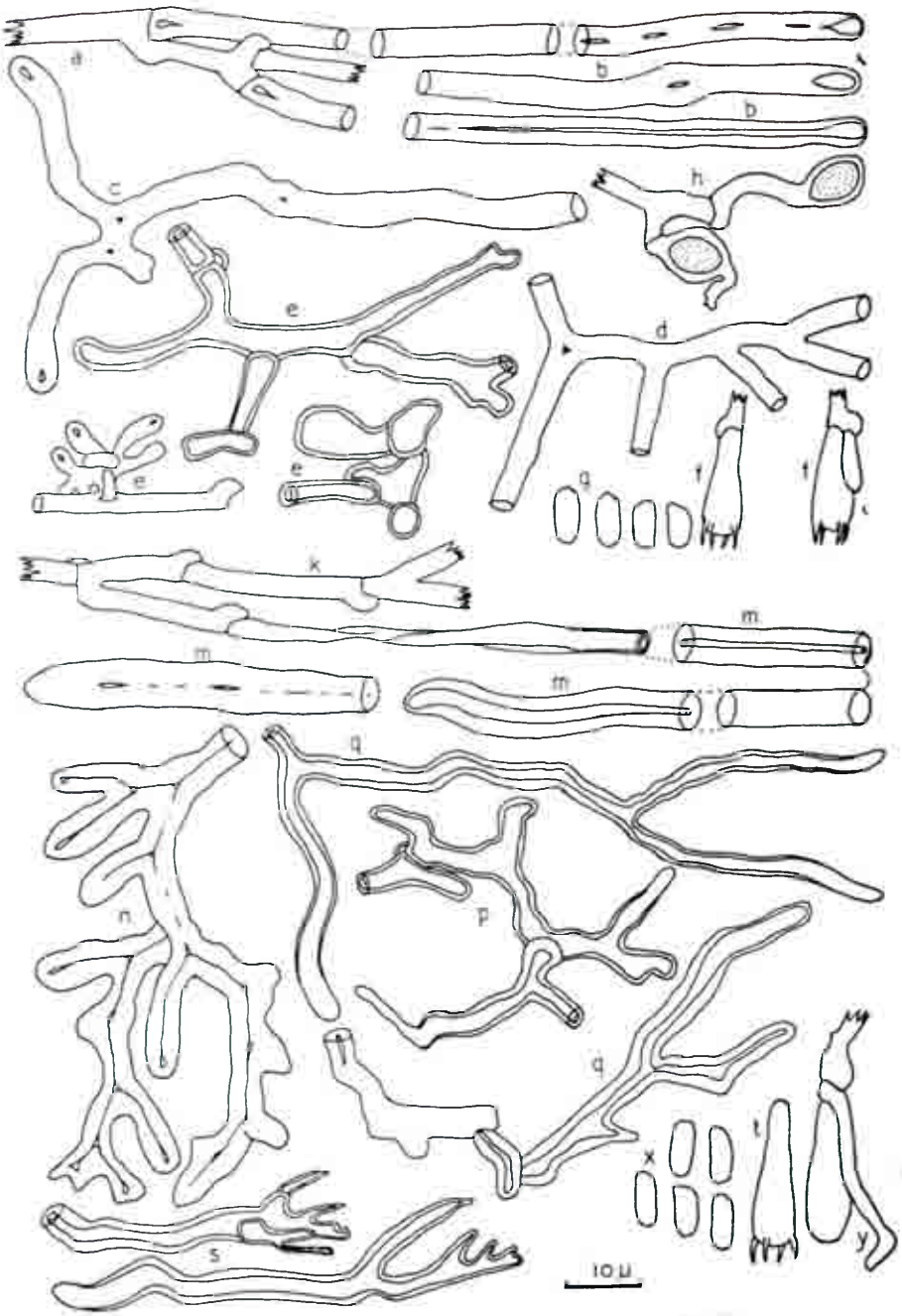

FIGURE 32.

Decay and hosts

This species causes a white rot of the sapwood of hardwood logs. It is widely distributed throughout the warmer regions of the world.

Specimens examined

Herb. DAOM: F5255, on *Quercus* log, Endora, Arkansas, Aug. 1931; F2093, on *Quercus* sp., Buzzards Roost, Alachua Co., Florida, Sept. 1954; *69696, on dead wood, Walker, Louisiana, Aug. 1960.

Herb. Berkeley in Herb. K: *Daedalea ambigua* Berk., from Ohio, (Holotype).

Herb. NY: *Lenzites repanda* Fr., Sierra Leone, Africa, 1889, North Am. Fl. 6003; *Lenzites palisoti* Fr., Somerset East, C.P., Feb. 1876, North Am. Fl. 804; *Lenzites deplanata* Fr., Plants of New Guinea No. 208, Crane Expedition, May 1929; *Lenzites palisoti* Fr., Sydow, Fungi exotica exsicati, 304, Luzon, Mt. Isarog, Dec. 1913; *Daedalea amanitoides* Beauv. 23714, Hulgra, Ecuador, Aug. 1918; *Daedalea amanitoides* Beauv. Dutch Guiana, Herb. NYBG 12; *Daedalea amanitoides*, British Guiana, 13529; *Lenzites applanatus* Fr., Novo Petropolis, Rio Grande du Sul, Brazil, 1924; *Lenzites applanata* Fr., Porto Novo, Sta. Catharine, Brazil, 1928; *Lenzites palisoti* Fr., Baker, Fungi Malayana 242; *Daedalea aesculi*, ex Herb. A.P. L. V. Morgan, No. Am. Fl.; *Daedalea ambigua* Berk. on dead, standing oak trees, Perryville, Mo., Aug. 1885; *Trametes lactea*, Florida, N. W. Calkins 185, Feb. 1886; *Trametes ambigua*, Fern, Putnam Co., Ind., Sept. 1891, L.M. Underwood Coll.; *Daedalea aesculi*, near New Orleans, L.A., F. S. Earle, Aug. 1908, NYBG 113; *Daedalea aesculi*, Batesville, Arkansas, Oct. 1908, 2829; *Daedalea ambigua* Berk., Middlebrove Ill., Sept. 1907, 2518; *Daedalea amanitoides*, Panama Canal Zone, S. L. Meyer, Jan. 1945, 17303.

Herb. PRE: *41, Lenzites repanda*, Zululand; 156, dooie hout, Salisbury, S. Rhodesia; 354, *Lenzites repanda*, dead logs, Zululand; 372, *Lenzites applanata*, Knysna, Jan. 1922; 757, *Lenzites repanda*, ou hout, Knysna; 911 *Lenzites applanata* on dead *Acacia melanoxylon*, Grootvadersbosch, Swellendam; 1235, Hectorspruit, Tvl., July 1916; 1318, Zoutpansberg, Transvaal; 1322, on *Acacia decurrens*, Harden Heights, Natal, April 1911; 1323, on wattle stumps, Cramond, Natal, April 1911; 1648 *Lenzites applanata*, on *Eucalyptus* poles, Tzaneen, July 1924; 1878, on dead tree stump, S. Rhodesia, Aug. 1923; 2370, *Lenzites repanda*, dead stump, Salisbury, S. Rhodesia, Dec. 1924; 2444, *Lenzites repanda*, on old stump, Zimbabwe, Rhodesia, July 1927; 2532, *Lenzites repanda*, Mycological Herbarium, Dept. of Agriculture, S. Rhodesia per J. C. Hopkins, May 1928; 6749, Sydow, Fungi exotica exsiccati No. 101; 8819, Pietermartizburg, Natal, Feb. 1915; 8877, on dead *Acacia karroo*, Pretoria, Tvl., March 1915; 9750, Hectorspruit, Tvl., July 1916; 9957, Fungi Malayana, No. 242; 11550, Buccleugh, Natal, July 1918; 11917, Kyiwaga, Uganda, Aug. 1915; 13155, Flora of the Philippines No. 45; 14932, Victoria Nyanza, Uganda; 15050, on dead *Ocotea bullata*, Hankey, C.P., Nov. 1921; 15488, on dead wood, George, C.P., May 1922; 17805, on *Olea laurifolia*, Knysna, C.P., June 1923; 22055, Somerset East, C.P., 1875; 23350, Alexandra Forest, C.P., July 1927; 27269, Donnybrook, Natal, Aug. 1933; 27707, Donnybrook, Natal, Jan. 1935; 28941, Xumeni Forest, Natal, July 1935; 30101, on *Acacia mollisima*, Butterworth, C.P., Aug. 1937; 30733, Knysna, C.P., Apr. 1949; 31624, Knysna, Cape Province, Jan. 1916; 31671, Ginginhlovu, Natal, May 1916; 33378, on dead wood, Grahamstown, C.P., Sept. 1941; 33923, Mufulira Copper Mines, Zambia, Feb. 1943; 34578, Lothair, E. Tvl., Apr. 1945; 34993, on *Olea laurifolia*, Qudeni Forest, Natal, Feb. 1945; 38738 Petrak, Mycotheca generalis No. 1831; *41534, Hogsback, C.P., May 1956; *42094, on wood, Potgietersrus, Tvl., March 1960; 42432, on dead hardwood, Graskop, E. Tvl., March 1957; *42442, on *Acacia* sp. log, Bushbuckridge, E. Tvl., Feb. 1961; *42531, on hardwood log, Louis Trichardt, N. Tvl., April 1964; *42748, on *Olea laurifolia*, Knysna, C.P., Oct. 1955; 43157, on dead wood, George, C.P., March 1966.

FIG. 32.— **Lenzites palisoti** a - h. Structures from cultures: (a) thin-walled, nodose-septate hyphae; (b) unbranched fibre hyphae; (c) solid fibre hypha with long branches; (d) fibre hyphae with short branches; (e) thick-walled, nodose-septate hyphae with short, tortuous branches; (f) basidia; (g) basidiospores; (h) chlamydospores.

k - y. Structures from carpophores: (k) thin-walled, nodose-septate hyphae; (m) unbranched fibre hyphae; (n) fibre hyphae with numerous, tortuous, short branches; (p) thick-walled, nodose-septate hyphae with tortuous branches; (q) fibre hyphae with branches toward the distal end; (s) short fibre hyphae with terminal clusters of branches; (t) basidium; (x) basidiospores; (y) cystidiole.

Interfertility studies

Spores were obtained from a fruiting area of the culture of PRE 42442. In order to determine the type of interfertility of this species, 16 cultures, each grown from a single basidiospore, were paired in all possible combinations. The results indicate that *Lenzites palisoti* possesses the tetrapolar type of interfertility with allelomorphs for heterothallism at two loci. The mycelia from five single spores did not mate with any one of the other mycelia. Where they were used in pairings, the two mycelia never met even after prolonged incubation but showed signs of mutual aversion and inhibition. The results, showing the distribution of mating types among the single spore mycelia are presented below in TABLE 7.

The cause of the failure of these five monospore cultures to mate with the others is not known and no attempt was made to determine it. It may be due to the "barrage phenomenon" as described by Vandendries and Brodie (1933) and Brodie (1935, 1936) or to staling effects since it was noticed that these monospore mycelia grew rather poorly in culture and always formed restricted colonies.

Discussion

The presence of nodose-septate hyphae, fibre hyphae and extra-cellular oxidase in its cultures and cylindrical basidiospores in the carpophores, places *Lenzites palisoti* in Group 45. In most respects it agrees in cultural characters with other trametoid species in this group but the rather penetrating fragrant odour given off by the ragged cultures, which produce so much submerged mycelium, serve to distinguish this species from others in this group.

Nobles (1958 b) placed *Lenzites repanda* (Pers.) Fr., (synonymous with *Lenzites palisoti*, Fidalgo & Fidalgo, 1966) in Group 27, among species with simple septate hyphae and a negative oxidase reaction in culture, but she placed *Daedalea ambigua* Berk. (synonymous with *Lenzites palisoti*, Fidalgo & Fidalgo, 1966) in Group 45. Davidson *et al.* (1938) reported the formation of strong diffusion zones by cultures of *Daedalea ambigua* on gallic acid and tannic acid media and the formation of a white rot by the fungus on wood. Van der Westhuizen (1958) also reported a strong, positive, oxidase reaction in cultures of *Lenzites palisoti* and a white rot of wood decayed by this common and widely distributed species.

Carpophores of *Lenzites palisoti* agree in anatomical characters with other species of this group as described above. The nodose-septate hyphae may be thin-walled generative hyphae or may be thick-walled "sclerified generative hyphae" with tortuous branches which form part of the binding system. The fibre hyphae may be unbranched, solid, or have a number of long, flexuous branches which contribute to the binding system or they may be short binding hyphae with numerous, short, tortuous branches. Hyphae which are morphologically and ontogenically distinct thus comprise the binding hyphal system. Because nodose-septate hyphae are regarded as generative hyphae, and because aseptate binding hyphae are present in the carpophores, the fruit bodies of *Lenzites palisoti* have a trimitic hyphal system in Corner's (1932 a, b) terminology.

From the above descriptions it is clear that the structures formed in cultures are also present in the carpophores of *Lenzites palisoti* from which they were made. The chlamydospores are however again the exception but this appears to be the general condition. It is possible that chlamydospores may be formed in the wood decayed by this fungus, which was not available for examination.

Despite its wide distribution, little was known about the anatomical characters of *Lenzites palisoti*. Cunningham (1950 b) placed this species in the genus *Coriolus* Quél, which he had characterized earlier (Cunningham, 1948 c) as having a trimitic hyphal system with nodose-septate generative hyphae, unbranched, aseptate, skeletal hyphae and aseptate, branched, binding hyphae of the bovista type. Overholts (1953) stated that the hyphae in the carpophore of *Daedalea ambigua* Berk. (= *Lenzites palisoti* (Fr.) Fr.) are "mostly simple, thick-walled with no cross-walls or clamps, 3 — 7μ in diameter; sometimes much branched hyphal complexes present."

Fidalgo & Fidalgo (1966) reported this species to possess a trimitic hyphal system with "generative hyphae thin-walled, hyaline . . . with clamp connections", "skeletal hyphae thick-walled, . . . unbranched, straight or wavy, never twisted . . . with no clamps or simple septa; binding hyphae thick-walled to solid, . . . much branched, very tortuous, curled, with no clamps or simple septa". These reports agree in most respects with the descriptions given above but these authors do not mention the presence of either the branched, thick-walled nodose-septate "binding hyphae," which are numerous in the lower context and trama of the fruit-bodies, or the branched fibre hyphae which are present in the lower parts of the carpophores.

Fidalgo & Fidalgo (1966) cited the full synonymy of this widely distributed species. From this list it is clear that the numerous specific epithets have been combined with the genera *Daedalea* Fr., *Trametes* Fr. or *Lenzites* Fr. by most authors. Fidalgo & Fidalgo (1966) regard *Daedalea elegans* Spreng. ex Fr. as the correct name for this fungus in view of O. Fidalgo's (1957) earlier argumentation that the genera *Lenzites* Fr. and *Trametes* Fr. are synonymous with *Daedalea* Fr. In that argumentation *Lenzites palisoti* was quoted as the species in which the morphological characters of all three genera were combined. Comparison of the cultural characters and hyphal characters of *Lenzites palisoti* with those of the type species of *Daedalea* Fr., *Daedalea quercina*, however reveal many differences. Cultures of *Daedalea quercina* do not produce extra-cellular oxidase like those of *Lenzites palisoti*, and form nodose-septate hyphae with irregularly thickened walls which are absent from the cultures of *Lenzites palisoti*. These nodose-septate hyphae with irregularly thickened walls are also present in the carpophores of *Daedalea quercina* but absent from those of *Lenzites palisoti*. In carpophores of the latter species, fibre hyphae with numerous tortuous branches (or binding hyphae) are present in large numbers but are absent from those of *Daedalea quercina*. Since such differences in the kinds of hyphae present in carpophores indicate phylogenetic dissimilarities and are regarded by Corner (1953), Cunningham (1954), Bondartzeva (1961) and Teixeira (1926 b) as of generic importance, *Lenzites palisoti* cannot be regarded as being congeneric with *Daedalea quercina*. On the other hand, it is evident from the descriptions given above that *Lenzites palisoti* resembles the type species of the genera *Coriolus* Quél., *Lenzites* Fr. and *Trametes* Fr. very closely in respect of cultural and micromorphological characters and construction of their carpophores. Not only are the same types of hyphae present in the carpophores of their respective type species [with the exception of the absence of long fibre hyphae with one or two branches near the distal ends from carpophores of *Lenzites betulina* (L. ex Fr.) Fr.] but the hyphae as well as the basidia and basidiospores show strong similarities in morphology. It is thus evident that *Lenzites palisoti* Fr. has close phylogenetic relationships with these three genera.

In order to determine the taxonomic position of *Lenzites palisoti* the construction of its carpophores and their variability in texture should be considered in relation to these characters of the carpophores of the type species of these

three genera. Different specimens of *Lenzites palisoti* may vary considerably in thickness and texture. In thin, leathery carpophores of *Lenzites palisoti*, the construction may resemble that of typical, thin, leathery specimens of *Polyporus versicolor* with very numerous binding hyphae in the tissues. In the thicker specimens the construction approaches that of carpophores of *Lenzites betulina* where binding hyphae are relatively less numerous in the middle context, or even *Trametes suaveolens* where binding hyphae are absent from the upper context. In view of this variability in construction together with the well known variability in the configuration of its hymenial surface, it appears that *Lenzites palisoti* is an intermediate form between *Lenzites betulina*, *Polyporus versicolor* and *Trametes suaveolens*. This is further evidence in support of the view that these latter three species are congeneric and that the genera of which they are the type species, are synonymous with *Trametes* Fr. If this view is accepted, then *Lenzites palisoti* should be included in the genus *Trametes* Fr. as *Trametes elegans* (Spreng. ex Fr.) Fr., (cf. Fidalgo & Fidalgo, 1966).

Polyporus occidentalis *Klotzsch*, Linnaea 8, 486, 1833;

Trametes occidentalis (Klotzsch) Fr., Epicrisis, p. 491, 1838;

Coriolopsis occidentalis (Kl.) Murr., Bull. Torrey Bot. Club, 32, 358, 1905;

Coriolus occidentalis (Kl.) G. H. Cunn., Proc. Linn. Soc. N.S. Wales, 75, 233, 1950.

Cultural characters

Growth is rapid, the mat reaching a radius of about 40 mm in one week and covering the plates in two weeks. The advancing zone is even or slightly bayed with the mycelium appressed for about 1 mm behind the extreme margin, then raised to form a woolly ridge about 1 cm wide across the plate, but becoming somewhat more felty and less raised behind this ridge towards the inoculum. A second and third woolly ridge may be formed across the mat between the first ridge and the edge of the plate. The mat is white at first but the ridges turn "light buff" to "cream color" within a week. As the mat ages, the raised ridges become more compact and tough, felty and darken in colour to "naples yellow" or almost "mustard yellow" after four weeks, becoming lacunose and uneven or, may develop irregular, raised lumps of tough, compact mycelium. Thinner areas of the mat become more farinaceous woolly to somewhat felty and remain white but eventually develop the "cream colour" to 'light buff" colour of the raised ridges. At six weeks the mat around the inoculum is mostly farinaceous felty, white or with patches of "maize yellow" and traversed by thick, raised, felty ridges, lacunose or roughened, mostly "cream buff" or "ochraceous buff" in colour and with irregular, smooth, velvety lumps of the same colour on them or at the sides of the dish. Occasionally depressions develop on these lumps from which acicular spines, up to 2 mm high, arise, bearing basidia and spores. The reverse of the colony bleaches quickly and remains so; a faintly fragrant odour is given off. A strong blue colour is quickly produced when the culture is tested for the presence of extra-cellular oxidase enzymes by means of alcoholic gum guaiac solution.

Advancing mycelium: hyphae hyaline, simple or branching, nodose-septate with simple clamp connections, thin-walled, with deeply staining contends, 2.5 — 5.0μ in diameter (Fig. 34 a).

Aerial mycelium: (a) hyphae as in the advancing zone; (b) fibre hyphae long, unbranched, thin-walled and narrow at the origins, widening towards the middle

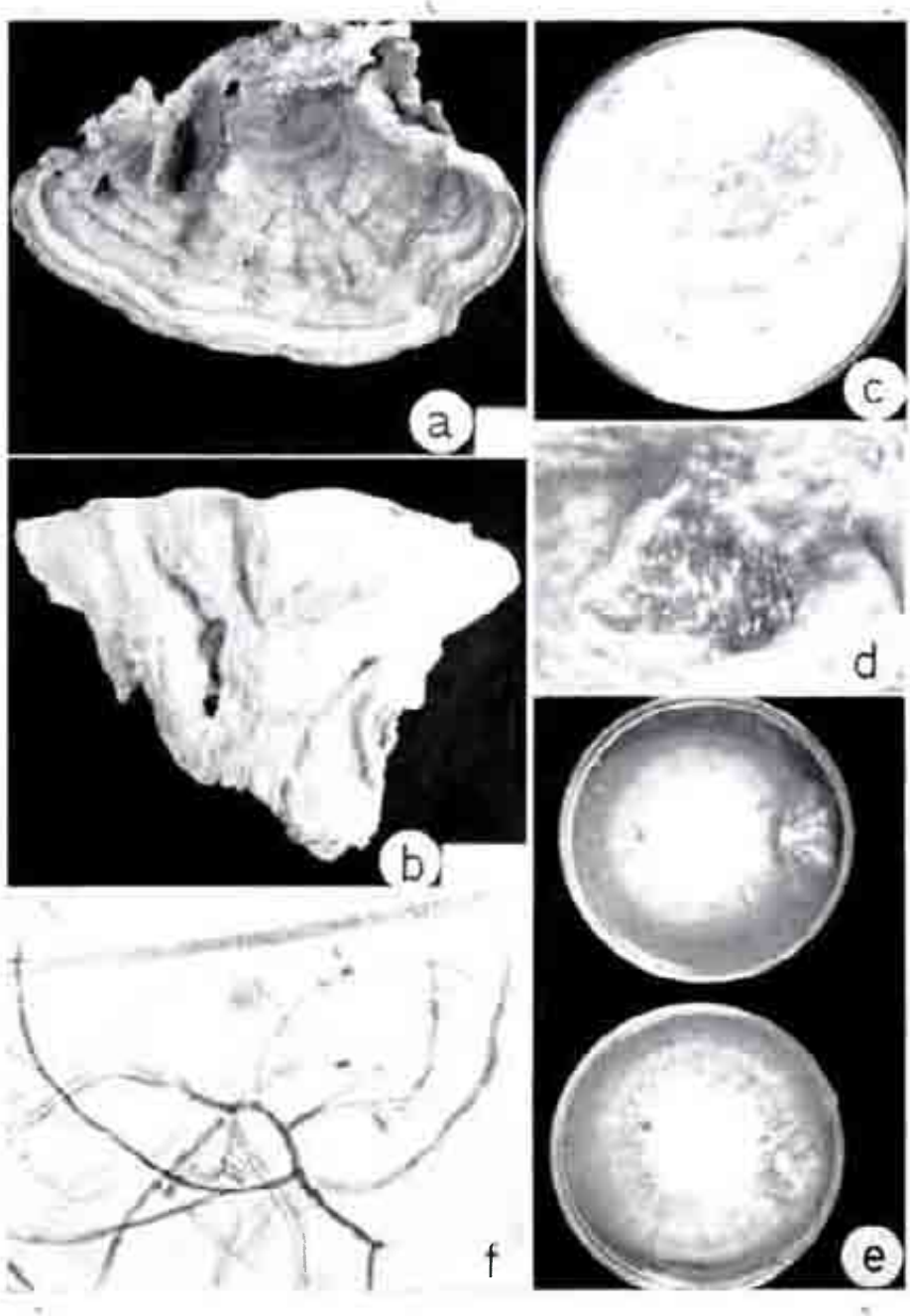

FIG. 33.— **Polyporus occidentalis.** (a) Upper surface and (b) hymenial surface of PRE 42450; (c) culture of PRE 42450 at six weeks; (d) fructification in culture; (e) "Buller phenomenon" plates of PRE 42863 × PRE 42445; (f) branched and unbranched fibre hyphae from culture of PRE 42863.

part with simultaneous increase in thickness of the walls which become faintly yellowish brown and narrowing of the aseptate lumina, often with contents staining in phloxine, but widening toward the thinner walled tips, 4.5 — 6.5μ in diameter at widest part (Fig. 34 b); (c) fibre hyphae hyaline, narrow, branching, the branches long, flexuous, of even diameter, walls thick, lumina prominent or reduced to interrupted lines, 0.7 — 1.5μ in diameter (Fig. 34 c); (d) oidia hyaline, cylindrical, ends rounded, 2.5 — 7.5 x 1.5 — 4.0μ (Fig. 34 d).

Fructification: basidia hyaline, narrowly clavate, 14.5 — 20.0 x 3.6 — 5.5μ and bearing four, straight, sterigmata, 3.0 — 3.6μ long (Fig. 34 e); basidiospores hyaline, cylindrical, smooth, thin-walled, 4.5 — 7.0 x 2.0 — 2.5μ (Fig. 34 f).

Submerged mycelium: (a) nodose-septate hyphae as in the advancing zone; (b) oidia as in the aerial mycelium.

Carpophore characters

Carpophore annual, lignicolous, solitary or grouped; pileus sessile to effused-reflexed, applanate or dimidiate frequently concave above and imbricate, tough coriaceous to firm and rigid, 6 — 13 x 1.5 — 8 x 0.1 — 1.0 cm; surface tomentose or hirsute, strongly concentrically sulcate, occasionally tuberculate, "olive brown", "buffy brown", "tawny olive" or "chamois" with zones of "ochraceous buff", "cinnamon buff" and "verona brown"; margin acute, undulate concolourous with upper surface or darker; pore surface "light ochraceous buff" drying to "cinnamon buff", or "ochraceous buff", pores rounded at first but later angular to elongate in older parts, 1 — 3 per mm; dissepiments mostly even, thick or thin; tubes "ochraceous buff", 1 — 2 mm deep, decurrent on the bases of the pileus, sometimes stuffed; context "pale ochraceous buff" to "ochraceous buff", zonate, fibrous corky to sub-woody, 0.5 — 8 mm thick.

Hyphal characters: carpophores consist of: (i) nodose-septate hyphae hyaline, branching, thin-walled, 2.2 — 3.0μ in diameter (Fig. 34 g); (ii) fibre hyphae long, unbranched straight or somewhat flexuous, sub-hyaline to pale yellowish-brown, thick-walled, the lumina aseptate, wide at the extremities but narrow or partly occluded near the middle portion, with or without staining contents, 3.0 — 7.5μ in diameter and arising from thin-walled, nodose-septate hyphae (Fig. 34 h); (iii) fibre hyphae long, straight or flexuous with one to three branches towards the distal end, the branches flexuous, thick-walled, sub-hyaline to pale yellowish brown, lumina prominent, aseptate, 2.0 — 5.2μ in diameter (Fig. 34 k); (iv) fibre hyphae hyaline with numerous long, tortuous, tapering branches mostly solid or lumina much reduced, arising from a short length of main stem, the branches interwoven with other hyphae, 1.0 — 4.0μ in diameter (Fig. 34 m).

Hymenium: basidia hyaline, long clavate almost cylindrical with four sterigmata, 14.5 — 18.0 x 3.6 — 4.5μ; sterigmata 3.0 — 3.6μ (Fig. 34 n); basidiospores cylindrical, hyaline, smooth, thin-walled, 4.5 — 7.0 x 2.0 — 2.5μ (Fig. 34 p); hyphal pegs conical, projecting 40 — 50μ beyond the level of the basidia.

Construction. The margin consists of long, unbranched fibre hyphae with thickened walls and prominent lumina, and arranged more or less parallel or slightly intertwined. Also intertwined with the fibre hyphae are numerous deeply staining, branching, nodose-septate, thin-walled hyphae from which they arise. Behind the margin the context consists mainly of fibre hyphae. In the upper context the fibre hyphae are mostly straight with partly thickened, pale yellowish-brown walls and prominent lumina. They are parallel in arrangement and loosely intertwined. Occasional thin-walled, nodose-septate hyphae are present among them. At the upper surface a somewhat denser layer of tissue is present which consists of branching, thin-walled, nodose-septate hyphae and hyaline, fibre hyphae with

many thick-walled or solid branches, intertwined with the unbranched fibre hyphae. The unbranched fibre hyphae project beyond this layer to form the dense, tomentose upper surface of the carpophore. In the lower context the construction of the tissues is similar but the tissues become more dense towards the pores. Long unbranched fibre hyphae, 3.5 — 4.5μ in diameter, with the lumina narrow or partly occluded, turn downwards into the trama of the dissepiments where they become interwoven with hyaline much-branched fibre hyphae with solid or sub-solid branches, and branched, thin-walled, nodose-septate hyphae to form a dense, tough, homogeneous tissue. In the dissepiments, thin-walled, nodose-septate hyphae ramify throughout the tissues, branching repeatedly and forming numerous short branches bearing clusters of basidia at the hymenial surfaces of the tubes.

Decay and hosts

Polyporus occidentalis causes a white rot of hard-wood logs in dry, exposed positions in sub-tropical areas.

Specimens examined

Herb. DAOM: 31731, on *Cola cordifolia*, Jasikan, Togoland, May 1949; 38997, on wood, Rest Pew, Manchester, Jamaica, Feb. 1945; 52393, Municipio Benjamin Constant, Brazil, Aug. 1955.

Herb. PRE: 1372, on wattle stump, Cramond, Natal, Apr. 1911; 1697, on fence post, Letaba Drift, Zoutpansberg, Tvl., Aug. 1911; 5645, on fence post, Winkelspruit, Natal, Feb. 1912; 6685, on *Citrus simensis* stump, Nelspruit, Tvl., May 1913; 6926, on *Celtis rhamnifolia*, Lusikisiki, Transkei, Sept. 1913; 8818, on *Celtis rhamnifolia*, Pietermaritzburg, Natal, Feb. 1915; 9204, on *Celtis rhamnifolia*, Pietermaritzburg, Natal, Dec. 1915; 9482, on *Celtis rhamnifolia*, Inanda, Natal, Dec. 1915; 11249, on *Celtis rhamnifolia*, Durban, Natal, Nov. 1916; 11254, on *Pyrus malus*, Wolhuters Kop, Tvl., Feb. 1919; 13169, Flora of the Philippines No. 491, Nov. 1916, 13367, Flora of the Philippines No. 19101, Nov. 1916; 14072, Flora of Victoria Nyanza, Uganda, Nov. 1916; 14892, Flora of Kenya, Nov. 1916; 15016, on stump, Pretoria, Tvl., April 1921; 15051, on wood Selati River, E. Tvl., Nov. 1921; 15573, on wood, Durban, Natal, Nov. 1916; 15582, on *Rhus viminalis*, Branders High Forest, Aug. 1915; 23349, on wood, Alexandria, July 1927; 25491, on dead trunk, Kasane, Bechuanaland, July 1930; 25917, on tree stump, Zoutpansberg, Tvl., Dec. 1929; 26324, on tree stump, Elim Mills, Zoutpansberg, Tvl., March 1932; 26380, on tree stump, Eshowe, Natal, Jan. 1916; 26385, on tree stump, Margate, Natal, Feb. 1911, 27606, on tree stump, Pietermartizburg, Natal, Feb. 1934; 28250, Fungi Venezuelani No. 418, H. Sydow; 28707, on *Prunus domestica*, Pietermaritzburg, Natal, Nov. 1934; 30102, on *Acacia mollissima*, Willowvale Plant., C.P., July 1937; 30283, East Afr. Agric. Res. Stat., Amani, No. 1084; 30820, on dead wood, Port St. Johns, Aug. 1937; 31631, on dead wood, Eshowe, Natal, Jan. 1916; 31649, on dead wood, Durban, Natal, May 1916; 31675, on dead wood, Gingindhlovu, Natal, June 1915; 31686, on *Albizzia fastigiata*, Durban, Natal, Sept. 1916; 31693, on dead log, Durban Natal, Sept. 1916; 31701, on dead log, Botanical Garden, Durban, Natal, Oct. 1916; 31856, on dead log, New Germany, Natal, April 1917; 31857, on dead log, New Germany, Natal, Apr. 1917; 31945, on dead log, Stella Bush, Durban, Natal, Apr. 1917; 31980, on dead log, Pietermaritzburg, Natal, Nov. 1917; 35561, on *Nerium oleander*, dead branch, Pietermaritzburg, Sept. 1946; 33563, on *Brachystegia* log, Mufilira, Rhodesia, March 1942; 33754, on *Afzelia quanzensis*, Moçambique, Nov. 1942; 33991, on *Salix* sp. wood, Pietermaritzburg, Natal, 1943; 34373, on dead wood, Lake St. Lucia, Natal, 1935; 34376, on dead wood, Lake St. Lucia, Natal, 1935; 34461, on dead wood, Kazungulu, July 1930; 34558, on dead log, Kirstenbosch, Cape Prov., June 1934; 41357, on *Citrus aurantifolia*, Herb. C.M.I. no. 49391; *42144, on hardwood log, Honeydew, Johannesburg, Jan. 1961; *42445, decaying hardwood, F. C. Erasmus Nat. Reserve, E. Tvl., Feb. 1961; *42450, decaying hardwood, White River, Tvl., Feb. 1961; *42863, on *Pinus* sp. log, Bushbuckridge, E. Tvl., Feb. 1961.

Herb. STE: 104, on *Pinus*, near Durban, Natal; 151, on old stump, Durban, Natal; 275, on dead logs, Durban, Natal; 284, on dead logs, Zululand, Natal; 289, on dead logs, Zululand, Natal; 558, on dead *Persea gratissima;* 735, on dead *Persea gratissima*, Natal; 751, on dead *Persea gratissima*, Durban, Natal; 764, on dead *Persea gratissima*, Durban, Natal; 797, on old stump, Durban, Natal; 1043, old stumps, Ngare Mutoni, E. Africa, July 1922; 2415, on dead stump in bush, Umtali, Rhodesia; 2446, old stumps, Rhodesia, July 1927; 2553, old stumps, F. Eyles No. 4226, Feb. 1926; 2617, old stumps, Pietermaritzburg, Natal, May 1931.

Interfertility studies

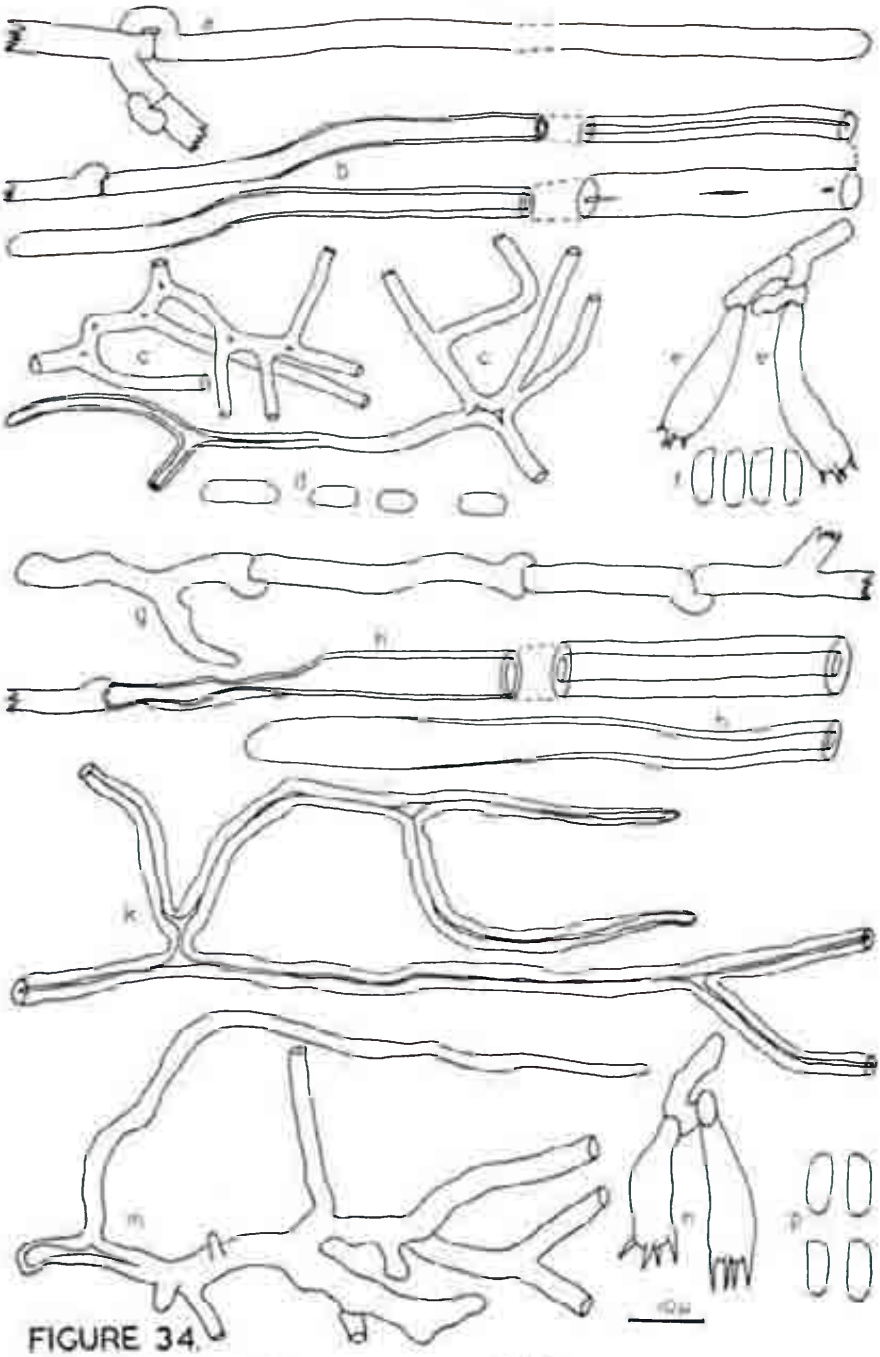

FIGURE 34.

Single basidiospores were collected from a carpophore of collection PRE 42863 kept in a moist chamber. In order to determine the type of interfertility of this species, 16 cultures, each grown from a single basidiospore, were paired in all possible combinations. It was found that *Polyporus occidentalis* has the tetrapolar type of interfertility with allelomorphs for heterothallism at two loci. The results, showing the distribution of mating types among the single spore cultures are presented in TABLE 8.

To test the conspecificity of collections of which cultures were available by means of the "Buller phenomenon", two mycelia from single spores of different mating types, PRE 42363 — 1 and PRE 42863 — 5 were used as haploid mycelia. Dikaryotic mycelia of collections PRE 42445 and PRE 42450 were tested by means of this technique. A set of six plates were prepared for each dikaryotic culture to be tested. Three plates in each set were then inoculated with each haploid monospore culture and incubated for five days. Each set of plates were then inoculated with a small piece of dikaryotic mycelium which was placed near the periphery of the growing haploid colony. After further incubation for four days, the haploid mycelium on each plate was examined for the presence of clamp connections at three positions along its periphery (Fig. 34 e).

Clamp connections were found in every case thus showing that dikaryotization of the single spore haploid mycelia by the added dikaryotic mycelia had taken place and confirming that the collections of *Polyporus occidentalis* numbered, PRE 42144, PRE 42445, PRE 42450 and PRE 42863 are interfertile and therefore conspecific.

Discussion

With the formation of thin-walled, nodose-septate hyphae, thick-walled fibre hyphae and extra-cellular oxidase enzymes in its cultures and its cylindrical basidiospores, *Polyporus occidentalis* fits well into Group 45 (Nobles, 1958 b). The cultures have the general and micromorphological characters of other species described above in this group. Cultures resemble those of *Trametes meyenii* most nearly but the buff coloured areas which develop on the mat and fruiting areas, together with the sub-hyaline to faintly yellowish walls of the fibre hyphae, serve to distinguish cultures of this species from others in the group. This fungus has not been described in culture before but it was included by Nobles (1958 b) in Group 45.

The tetrapolar type of interfertility present in *Polyporus occidentalis* also agrees with that of other species of Group 45 as well as Nobles' (1958 b) thesis that this type of interfertility is present in polypore species of which the thin-walled hyphae are nodose-septate and whose cultures produce extra-cellular oxidase.

The carpophores of this species consist of four types of hyphae, viz. thin-walled, nodose-septate hyphae, unbranched fibre hyphae, fibre hyphae with branches towards the distal ends and fibre hyphae with a number of long tapering branches often arising from a short length of main stem. The latter hyphae appear to be binding hyphae of the bovista type as described by Cunningham (1946) and the

FIG. 34.— **Polyporus occidentalis.** a - f. Structures from cultures: (a) thin-walled nodose-septate hypha from advancing zone; (b) unbranched fibre hypha; (c) narrow fibre hyphae with numerous long branches; (d) oidia; (e) basidia; (f) basidiospores.
g - p. Structures from carpophores; (g) thin-walled, nodose-septate hypha; (h) unbranched fibre hypha; (k) fibre hypha with one to three branches towards the distal end; (m) sub-solid or solid fibre hypha with numerous long, flexuous tapering branches; (n) basidia; (p) basidiospores.

branches of the fibre hyphae with branches towards the distal ends appear to assist in the binding function. The other hyphae correspond to Corner's (1932 a) definition of generative and skeletal hyphae so that carpophores of *Polyporus occidentalis* have a trimitic hyphal system in the terminology of Corner (1932 a) and Cunningham (1946).

The hyphal characters of *Polyporus occidentalis* were described recently by Fidalgo & Fidalgo (1966) who reported a trimitic hyphal system with thin-walled, nodose-septate generative hyphae, "skeletal hyphae thin- to thick-walled usually with a distinct lumen, walls hyaline to yellowish, unbranched, not septate . . . binding hyphae thick-walled to solid, hyaline, much branched, non-septate". This description agrees well with that given above but these authors did not mention the presence of thick-walled fibre, or skeletal hyphae, with branches toward the distal end which were fairly abundant in the carpophores examined by me. No other description of the hyphal characters of *Polyporus occidentalis* had been published but both Imazeki (1943) and Cunningham (1950 b) included this species in the genus *Coriolus* Quél. thereby implying similarities in hyphal and anatomical characters between this species and *Polyporus versicolor*. From the descriptions it is evident that many similarities in cultural and carpophore characters exist between *Polyporus occidentalis*, *Polyporus versicolor* and the other species of Group 45 described above. Certain differences, however, exist. *Polyporus occidentalis* is the only species studied in this group in which the fibre hyphae have faintly yellowish brown walls. All the other species have hyphae with hyaline walls. Carpophores of *Polyporus occidentalis* lack the solid, branched, nodose-septate hyphae which are present in the binding hyphal system of carpophores of *Polyporus versicolor*, *Lenzites betulina*, *Trametes suaveolens* and other species in this complex. The solid, branched processes formed on nodose-septate hyphae in cultures of *Polyporus versicolor* were not found in cultures of *Polyporus occidentalis*. The binding hyphae of *Polyporus occidentalis* do not have numerous short, curled branches like those of *Polyporus versicolor*, *Lenzites betulina* and *Trametes suaveolens* but instead have long, tapering branches resembling those of *Trametes cingulata* and the *Pycnoporus* spp. described by Nobles & Frew (1962). Indeed, in respect of hyphal characters, *Polyporus occidentalis* resembles *Trametes cingulata* and *Pycnoporus* spp. more closely than *Polyporus versicolor*. Some of the kinds of hyphae present in carpophores of the type species of *Trametes* Fr., *Lenzites* and *Coriolus* Quél. are thus lacking from carpophores of *Polyporus occidentalis*. Because Bondartseva (1961) and Teixeira (1962 b) regard the absence or presence of different kinds of hyphae as taxonomically important at the generic level, it appears that *Polyporus occidentalis* should not be regarded as congeneric with these three genera.

Murrill (1905) segregated the genus *Coriolopsis* with *Polyporus occidentalis* Klotzsch as type species, from the trametoid group of species on the basis of its dark-coloured context. For reasons advanced above, *Polyporus occidentalis* appears best placed in this genus which however is closely related to the trametoid-corioloid complex of species. It is however not impossible that future studies may show that other hitherto unknown species may reveal a combination of characters common to *Polyporus occidentalis* and other species of the trametoid-corioloid complex, thus offering evidence of congeneric relationship in a series of species.

From the descriptions it is evident that the structures formed in culture are also present in the carpophores from which they were made. The nodose-septate hyphae, fibre hyphae and hymenial structures formed in culture were identical to those of the carpophores but the oidia, which were abundant in cultures, were not found in the carpophores.

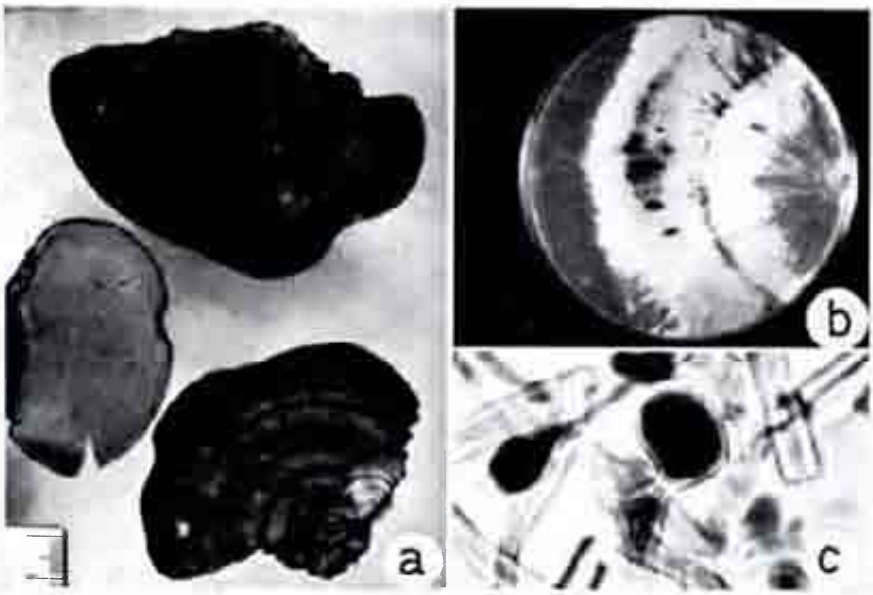

FIG. 35.— **Trametes cingulata.** (a) Carpophores of PRE 27506; (b) culture of PRE 42455 at six weeks; (c) thin-walled hypha with dark-brown resin-like contents from upper surface of carpophore. × 1000.

Trametes cingulata *Berkeley,* in Hook. Journ. Bot. 6, 164, 1854;
Coriolus cingulatus (Fr.) G. H. Cunningham, Proc. Linn. Soc. N. S. Wales 75, 221, 1950.

Cultural characters

Growth is moderately fast the mat reaching a radius of 40 mm in one week and covering the plate after two to three weeks. The advancing zone is even with the hyphae appressed, for one or two millimetres, then raised slightly at the edge of the mat. Mat behind margin at first thin, downy but becoming gradually more dense, somewhat raised, then collapsing somewhat toward the inoculum. Mat smooth at first but developing faint radiating grooves after two weeks with transverse ridges of dense, raised, thin, woolly to felty mycelium which abutt sharply on the thin, downy areas of younger mycelium. The mat is hyaline or white at first and remains so while thickening until, at 6 weeks, it is mostly characterized by areas of tough, dense, somewhat pellicular mycelium around the inoculum, radially sulcate and bordering sharply on thin, downy or sodden mycelium which gradually increases in density to form a transverse zone of dense, felty mycelium over the thin, subfelty mycelium of the newest growth. These zones of dense mycelium may develop irregular, granular-woolly patches which may form fruiting areas bearing minute, waxy, acicular spines, or, irregular lumps of dense, smooth, chamois-like mycelium may form on the sides of the dish or on the areas of thin mycelium and eventually form fruiting areas of minute, erect spines. The reverse of the culture bleaches gradually and a faint, sweetish, fragrant odour is given off. On gallic acid and tannic acid media no growth takes place but a strong diffusion zone is formed on gallic acid medium and a weaker one on

tannic acid medium. A strong blue colour is produced when an alcoholic gum guaiac solution is applied to the mat.

Advancing mycelium: hyphae narrow, hyaline, branching, thin-walled, nodose-septate, 3.0 — 4.0μ in diameter (Fig. 36 a).

Aerial mycelium: (a) hyphae as in the advancing zone; (b) fibre hyphae hyaline more or less straight, unbranched, the walls thick, refractive and lumina prominent, widening at their tips, aseptate, or, occluded and reduced to a thin, interrupted line, 2.5 — 4.5μ in diameter (Fig. 36 b); (c) fibre hyphae as above but with a number of branches over a short length, the branches long, flexuous and tapering, 1.5 — 3.0μ in diameter (Fig. 36 c); (d) oidia hyaline, smooth, cylindrical with rounded ends, 5.0 — 7.0 x 3.0 — 4.0μ (Fig. 36 d).

Fructifications: basidia broadly clavate 12.0 — 25.5 x 4.5 — 6.0μ with four short, straight sterigmata, 2.2 — 3.0μ (Fig. 36 e); basidiospores ovoid to short cylindrical, hyaline, smooth, thin-walled, obliquely apiculate 4.5 — 6.0 x 3.0 — 3.5μ (Fig. 36 f).

Submerged mycelium: (a) hyphae as in the advancing zone but more frequently nodose-septate; (b) chlamydospores intercalary or terminal sub-globose to ellipsoid, hyaline, thick-walled, 6.0 — 10.0 x 8.0 — 12.0μ (Fig. 36 g).

Carpophore characters

Carpophore annual, lignicolous, mostly solitary, sessile to dimidiate, rarely imbricate, occasionally laterally connate; pileus coriaceous to woody up to 9.0 x 5.0 x 0.3 — 0.7 cm; upper surface glabrescent, concentrically sulcate to tubercular and rough, with fine, irregular cracks or smooth, matt, dark grey to black, azonate or alternating dark and lighter-coloured zones; margin soft velutinate, entire, thick and rounded or thin, acute, pale cream to dark "cream color", sterile below; pore surface pale "cream color" drying darker, glistening, poroid; pores, rounded, 3 — 6 per mm; dissepiments thin, edges entire; tubes concolorous, 0.5 — 2.5 mm deep, not stratified; context white to pale "cream color", even textured, floccose punky to corky, 1.0 — 5.0 mm thick

Hyphal characters: (i) nodose-septate hyphae hyaline, branching, thin-walled and with deeply staining contents, 2.5 — 3.5μ in diameter, some inflated terminally with contents hard, resin-like, dark-brown (Fig. 36 m); (ii) fibre hyphae hyaline, long, unbranched, walls thick and refractive, widest over middle portion, aseptate, often with dark brown contents at the distal end, or, occluded, and reduced to an interrupted line, 3.5 — 6.0μ in diameter (Fig. 36 k, n); (iii) fibre hyphae thick-walled, hyaline, with one to three branches towards the distal end, lumina prominent, aseptate, 2.5 — 4.5μ (Fig. 36 p); (iv) branched fibre hyphae hyaline, thick-walled, with lumina aseptate, prominent or occluded, branches few or many, long, flexuous, tapering or short, flexuous and arising from a short distance of main stem, 1.5 — 3.5μ in diameter (Fig. 36 q).

FIG. 36.— **Trametes cingulata.** a - g. Structures from culture: (a) thin-walled, nodose-septate hyphae from advancing zone; (b) fibre hypha, unbranched; (c) fibre hyphae with numerous long, flexuous branches; (d) oidia; (e) basidia; (f) basidiospores; (g) chlamydospores.

h - t. Structures from carpophores: (h) thin-walled, nodose-septate hyphae; (k) unbranched fibre hyphae; (m) inflated thin-walled hypha with dark-coloured contents from upper surface; (n) inflated terminal portion of fibre hypha with dark-coloured contents from upper surface; (p) fibre hypha with one to three branches toward the distal end; (q) solid fibre hypha with numerous long, flexuous, tapering branches; (s) basidia; (t) basidiospores.

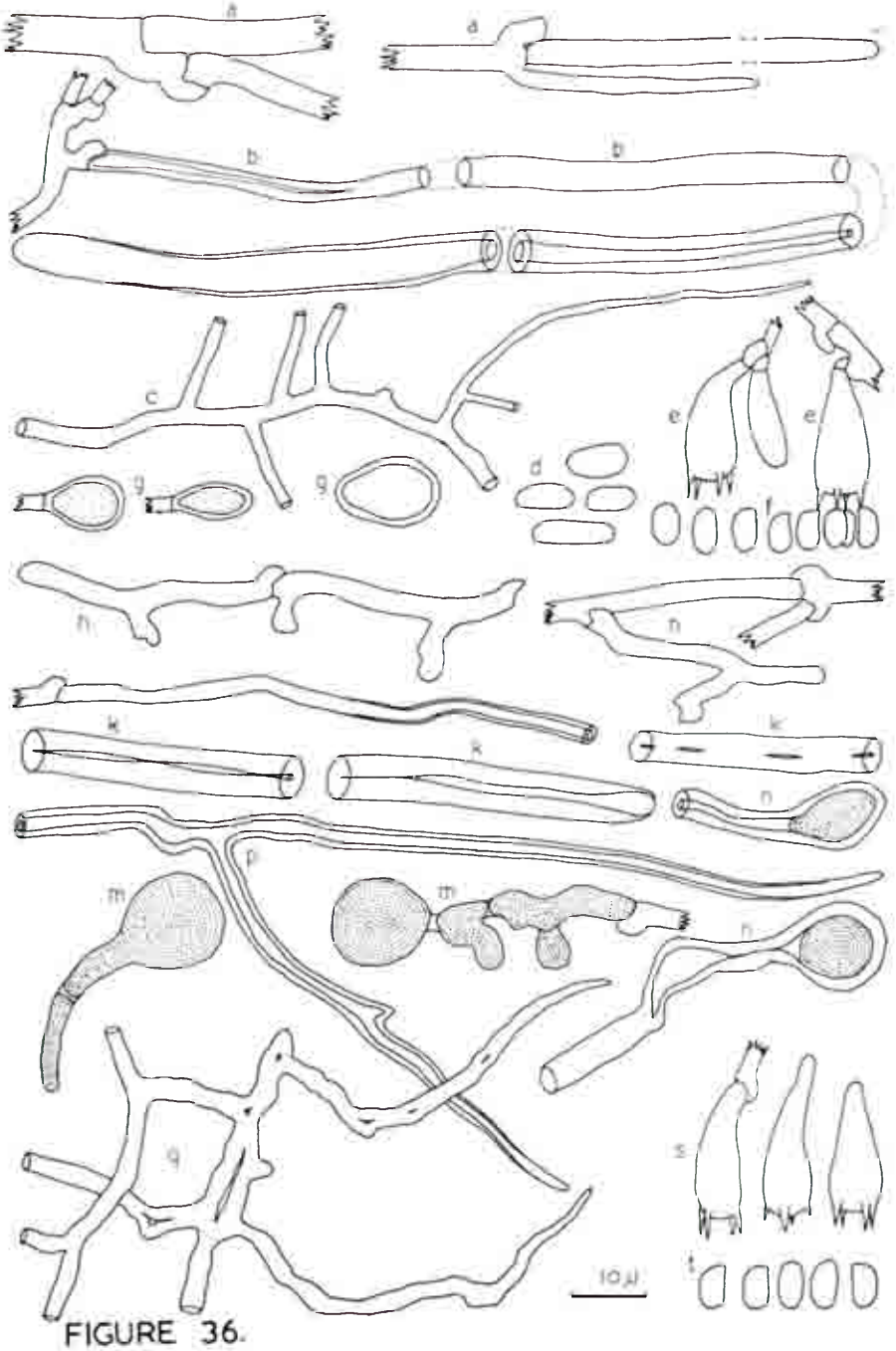

FIGURE 36.

Hymenium: basidia hyaline, long clavate to cylindrical, 12.0 — 22.0 x 4.5 — 6.0μ with four sterigmata 2.5 — 3.0μ long (Fig. 36 s); basidiospores ovoid to short cylindrical, hyaline, smooth, thin-walled, 4.0 — 6.0 x 2.5 — 3.5μ (Fig. 36 t).

Construction. The margin consists mainly of long unbranched fibre hyphae, mostly thick-walled and with aseptate lumina, orientated parallel to the direction of growth of the pileus. Loosely intertwined with them are branching, thin-walled, nodose-septate hyphae from which the fibre hyphae arise Immediately behind the margin in the context, fibre hyphae with one or two long branches or with a larger number of shorter branches, the branches tapering, flexuous and interwoven with the other hyphae, become abundant.

The older part of the context consists mainly of unbranched, sub-solid or solid fibre hyphae in more or less parallel arrangement and slightly intertwined, turning gradually upward towards the upper surface. Branched fibre hyphae, mainly solid, the branches long or short, tortuous, and tapering towards the ends are interwoven with the unbranched fibre hyphae across their direction of growth and bind them into a firm, homogeneous tissue. Occasional lengths of thin-walled, nodose-septate hyphae, mostly empty and collapsed, are present among the others. At the upper surface the ends of the unbranched fibre hyphae are closely packed at a common level. Their lumina are wide and mostly filled with dark-brown, resin-like contents. At the upper surface thin-walled, nodose-septate hyphae are very numerous, intertwined with the fibre hyphae and with ends projecting, often distended and at the same level as the fibre hyphae and filled with dark-brown, resin-like, hard contents (Fig. 36 m). The dark contents of the nodose-septate and fibre hyphae form a zone of about 90μ thick at the upper surface of the pileus. Below this zone the nodose-septate hyphae and many fibre hyphae have deeply staining luminal contents. In the lower context, the long, unbranched fibre hyphae turn downwards into the trama. Fibre hyphae with one or two branches towards the distal part become more numerous the branches becoming tortuous and fibre hyphae with many tapering branches over a short length of main stem increase in numbers towards the dissepiments where their branches are interwoven with the other hyphae, binding them into a tough tissue. The fibre hyphae are mostly tortuous and tightly intertwined and interwoven into the dense, homogeneous tissue of the lower trama and dissepiments. Most of these fibre hyphae have prominent lumina. Intertwined with the fibre hyphae in the lower trama and dissepiments are the narrow, thin-walled, nodose-septate hyphae, branching freely, the branches short, with numerous clamp connections and becoming very numerous at the hymenial surfaces where they bear basidia in small clusters. The edges of the dissepiments are sterile and consist of fibre hyphae with prominent lumina.

Decay and hosts

Trametes cingulata causes a white sap rot of various species of hardwoods (Banerjee & Naha, 1960 b).

Specimens examined

Herb. PRE: 2127, Pretoria, Jan. 1917; 8799, on *Eucalyptus globulis*, Pietermartizburg, Jan. 1915; 9145, Pietermaritzburg, Natal, Oct. 1915; 11246, on *Acacia mollissima*, Cramond, Natal, Jan. 1916; 12004, on dead log, Kyagwe, Uganda, Jan. 1916; 12465, Limpopo Valley, Transvaal, June, 1919; 14489, Pretoria, Transvaal, Apr. 1921; 14691, Glen, O.F.S., Apr. 1921; 14903, Samu, Kenya; 20289, Malay Peninsula, No. 10858; 20467, Knysna, C.P., Jan. 1925; 20610, dead wood, Pretoria, Transvaal, Aug. 1929; 25492, on dead tree, Kasane, Bechuanaland, July 1930; 26407, on dead wood, Pretoria, Transvaal, Aug. 1929; 26614, on dead tree, Mariental, S.W.A.; 27506, on dead log, Nelspruit, Transvaal, July 1934; 28970, on dead wood, Duiwelskloof, Transvaal, May 1937; 30521, on dead *Eucalyptus* sp., Swartruggens, Tvl., Feb. 1939; 30751, Rustenburg, Transvaal, Jan. 1939; 30876, on dead wood, Xumeni Forest,

Natal, Jan. 1938; 31458, Lobatsi, Bechuanaland, Apr. 1929; 31564, on *Acacia* sp., Balfour, Transvaal; 31628, Krantzkloof, Natal, Jan. 1916; 31629, Cramond, Natal, Jan. 1916; 31655, Ngoye, Natal, May 1916; 34984, on dead stump, Qudeni Forest, Natal, Feb. 1965; 36875, on fallen tree trunks, Amatongas Forest, Moçambique, June 1948; 41356, on *Albizzia zygia*, ex Herb. C.M.I. No. 37382; 41522, on *Olea laurifolia*, Knysna, C.P., Apr. 1965; 41737, on *Acacia mollissima* stump, Richmond, Natal, June 1951; 40297, on dead bark, Potgietersrust, Transvaal, March 1960; 42254, on fallen log, Sabie, Transvaal, Apr. 1962; *42433, on dead hardwood, Blouberg, Transvaal, Jan. 1959; *42448, on dead *Eucalyptus* sp., Bosbokrand, Transvaal, Feb. 1961; *42455, on *Eucalyptus* sp. log, Johannesburg, Tvl. Jan. 1961; *42456, on dead wood, Magaliesberg, Transvaal, Jan. 1961.
Herb. STE: 108, *Acacia mollissima* stump, Krantzkloof, Natal; 750, *Acacia mollissima* stump, Pinetown, Natal; 794, Pretoria; 805, on branch of apricot tree, Pretoria; 817, Lobatsi; 1074, Waterberg, Transvaal, Feb. 1923; 1464, on dry *Eucalyptus* pole, Tzaneen plantation, Transvaal, July 1924; 1671, Potgietersrust, Transvaal, July 1924; 1711, on old wood, Pietersburg, Transvaal, July 1924.

Interfertility studies

Single spores were collected from a fructification formed in a culture of PRE 42448. In order to determine the type of interfertility of this species, 16 cultures, each grown from a single basidiospore, were paired in all possible combinations. Clamp connections formed in the paired mycelia in a manner indicating the tetrapolar type of interfertility with allelomorphs for heterothallism at two loci, in this species. The results showing the distribution of mating types among the single spore cultures are presented below. These results confirm Naha's (1957) report that *Trametes cingulata* has the tetrapolar type of interfertility. This distribution of mating types among the basidiospores is set out in TABLE 9.

Single basidiospore cultures of other collections of *Trametes cingulata* from South Africa were later obtained from the respective dikaryotic cultures, viz: PRE 42433, PRE 42455 and PRE 42456. In order to determine the conspecificity of these collections with PRE 42448, four cultures, each obtained from a single basidiospore, from each collection, were paired in all possible combinations with four single spore cultures from PRE 42448. In all the paired mycelia, clamp connections developed thus proving that collections PRE 42433, PRE 42448, PRE 42455 and PRE 42456, are interfertile and therefore conspecific.

Discussion

The presence of nodose-septate, thin-walled hyphae and fibre hyphae in cultures which produce extra-cellular oxidase and the possession of cylindrical basidiospores, place *Trametes cingulata* in Group 45 (Nobles, 1958 b). In appearance and texture the mat resembles cultures of *Polyporus versicolor* and *Pycnoporus sanguineus*. From the former species it differs in the presence of the thinner, more fragile, radially striate mat in which nodose-septate hyphae with thickened walls and solid branched processes are lacking. These characters also distinguish *Trametes cingulata* from cultures of other species in this group. Its cultures differ from those of *Pycnoporus sanguineus* as described by Nobles & Frew (1962) by the absence of orange yellow colours. In respect of general appearance of the mat and the structures formed in culture, however, there are many similarities. This description agrees with previous descriptions by Naha (1957), Van der Westhuizen (1958) and Banerjee & Naha (1960 a).

In the carpophores four kinds of hyphae were found, viz: nodose-septate, thin-walled hyphae and aseptate fibre hyphae without branches, or with one to three branches towards the tip or with numerous long tapering branches. These latter appear to be "binding hyphae of the bovista type" as described by Cunningham (1946); but the fibre hyphae with one to three branches also contribute to the binding hyphal system. The carpophores of *Trametes cingulata* thus have a trimitic hyphal system as reported by Cunningham (1950 b) and Farinha (1964).

From the descriptions it is evident that the structures formed in the cultures are also present in the carpophores from which they were made. The nodose-septate hyphae, fibre hyphae and hymenial structures from the cultures are identical to those from the carpophores. Chlamydospores, which were fairly numerous in the cultures, were not present in the carpophores. This discrepancy had also been recorded for other species.

In descriptions of the hyphal characters of *Trametes cingulata*, Banerjee & Naha (1960 b) reported the presence of clamp connections on the thin-walled hyphae of its carpophores. Farinha (1964) reported that secondary hyphae of the carpophore were thin-walled, nodose-septate and, the tertiary hyphae, aseptate, thick-walled, branched and up to 7μ in diameter, while others were much-branched and narrow. Cunningham (1950 b) placed this species in the genus *Coriolus* Quél., which he had characterized as having a trimitic hyphal system with thin-walled, nodose-septate, generative hyphae, thick-walled aseptate, skeletal hyphae and thick-walled, aseptate, much-branched binding hyphae. These reports thus partially confirm the above observations but certain differences are apparent between carpophores of *Trametes cingulata* and those of *Polyporus versicolor* L. ex Fr. and *Trametes suaveolens* (L. ex Fr.) Fr. the accepted type species of the genera *Coriolus* Quél. and *Trametes* Fr. respectively. In carpophores of *Trametes cingulata*, solid or sub-solid, nodose-septate binding hyphae are not present as in the carpophores of these two species. Also, the binding hyphae of *Trametes cingulata* have long, tapering branches which arise over a short length of main stem. Binding hyphae of the other two species are short with fairly short, thick, branches. Hyphae with tapering branches are present in the carpophores of *Lenzites betulina* (L. ex Fr.) Fr., the type species of the genus *Lenzites* Fr. (Cooke, 1959) but they are lateral binding processes or branches of solid, nodose-septate hyphae. Carpophores of *Lenzites betulina* do not possess long fibre hyphae with branches near the end which contribute to the binding system. Carpophores of *Trametes cingulata* thus differ in respect of the types of hyphae present in them from the carpophores of the type species of the genera *Coriolus* Quél., *Trametes* Fr. and *Lenzites* Fr. On the other hand, the binding hyphae in carpophores of *Trametes cingulata* resemble those in carpophores of *Pycnoporus cinnabarinus* (Jacq. ex Fr.) Karst., the type species of the genus *Pycnoporus* Karst. as described by Nobles & Frew (1962) much more closely. Indeed, in cultural characters and hyphal characters *Trametes cingulata* appears to resemble species of the genus *Pycnoporus* Karst. more than they do those of the genera *Trametes*, *Coriolus* and *Lenzites* but lack the characteristic orange-red colours which distinguish species of the genus *Pycnoporus*. Species of the genus *Pycnoporus*, however, apart from their orange-red colours, have cultural characters which agree with those of Group 45 (Nobles, 1958 b) while their carpophore characters agree in many respects with those of the type species of the genera *Coriolus*, *Trametes* and *Lenzites*.

The cultural and carpophore characters of *Trametes cingulata* thus agree in many respects with those of the type species of the genera *Coriolus*, *Trametes* and *Lenzites*, but lack certain of the types of hyphae which are present in their carpophores. The differences in morphology of the binding hyphae of these species may be of specific significance only but the absence or presence of types of hyphae in carpophores are regarded as of generic importance by Bondartseva (1961), Teixeira (1962 b) and Donk (1964). It thus appears best to regard *Trametes cingulata* as generically distinct from *Trametes suaveolens* until detailed studies of the hyphal characters and hyphal morphology of more species in this group can clarify the significance of such differences in hyphal morphology. The genus in which *Trametes cingulata* Berk. will be more suitably placed, cannot be indicated at present, however.

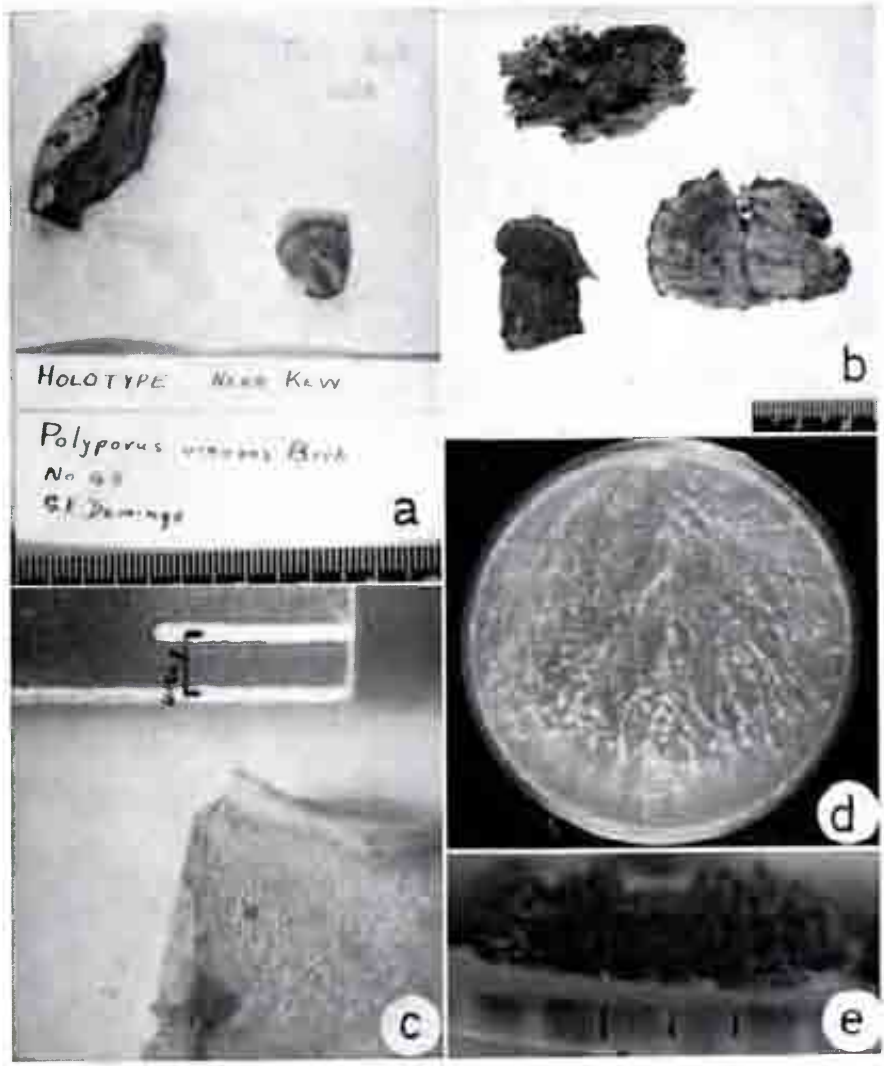

FIG. 37. — **Polyporus vinosus.** (a) Holotype; (b) carpophores from British Honduras; (c) pore surface of holotype; (d) culture of PRE 42154; (e) fructification in culture.

Polyporus vinosus *Berk.*, Ann. Mag. Nat. Hist. 11, 9, 195, 1852;

Coriolus vinosus (Berk.) Pat., Ess. Taxon. 94, 1900;

Nigroporus vinosus (Berk.) Murr., Bull. Torrey Bot. Club 32, 361, 1905;

Fomitopsis vinosa (Berk.) Imazeki, Bull. Gov. For Expt. Stat., Tokyo, Japan, No. 57, 111, 1952.

Cultural characters

Growth moderately slow to slow, the mycelium reaching a radius of about 10 mm in one week and covering the plate in four weeks. The advancing zone is very uneven with the mycelium mostly submerged and forming hyaline or white plumose outgrowths radiating out from prominent strands which originate from the inoculum. After three weeks small farinaceous pustules appear, scattered over the culture near the inoculum or along the main strands of submerged mycelium, white at first but gradually becoming "light greyish vinaceous" and slowly increasing in size. In an old culture a pad of pubescent "deep livid brown" mycelium developed on the side of the dish, from which thin, lamellar structures grew out laterally, uniting at various points to form daedaloid slits, which in turn rounded off to form minute tubes. A white spore deposit appeared below these tubes five months after inoculation of the plate. The reverse bleaches slowly and a faint mushroomy odour is given off. A strong blue colour is formed when a drop of alcoholic gum guaiac solution is applied to the culture. Strong diffusion zones are formed on gallic acid and tannic acid media but no growth occurs in seven days.

Advancing mycelium: hyphae hyaline, branching, nodose-septate, thin-walled, 2.2 — 3.5μ in diameter (Fig. 38 a).

Aerial mycelium: (a) hyphae as in the advancing zone; (b) fibre hyphae short, mostly unbranched, occasionally with one branch, thick-walled, the walls faintly reddish brown and thickest along the middle part, the lumina prominent, widening towards the extremities, aseptate, 2.2 — 5.0μ in diameter (Fig. 38 b).

Fructification: basidia hyaline, short clavate, 6.6 — 9.0 x 3.6 — 4.2μ with four straight, slender sterigmata 1.8 — 2.4μ long (Fig. 38 c); basidiospores hyaline, allantoid, smooth, thin-walled, 3.0 — 3.6 x 1.2 — 1.6μ (Fig. 38 d).

Submerged mycelium: hyphae hyaline, branching, nodose-septate, thin-walled, 1.5 — 5.5μ in diameter (Fig. 38 e).

Carpophore characters

Carpophore annual, lignicolous, solitary, sessile; thin, dimidiate to reniform, narrowly attached by a scutate disc or laterally connate and broadly decurrent, woody and brittle when dry, 1 — 4 x 3 — 7 x 0.3 — 0.7 cm; surface finely velutinate in young part, then glabrous, concentrically sulcate, mat, "dark vinaceous brown" to "hays brown" becoming "brownish drab" in age; margin acute, rounded, occasionally somewhat lobate, concolorous; pore surface "pale vinaceous drab" to "dark vinaceous brown" or "sorghum brown" poroid; pores angular, 6 — 8/mm; dissepiments thin, even; tubes up to 2 mm deep, occasionally stratified; context up to 5 mm thick, "sorghum brown", even, homogeneous.

Hyphal characters. Carpophores consist of: (i) nodose-septate hyphae hyaline, branching, thin-walled, with deeply staining contents, 2.2 — 3.5μ in diameter (Fig. 38 f); (ii) nodose-septate hyphae tortuous and branched with walls pale brownish and slightly thickened, with staining contents, or, empty and often with simple septa, 2.5 — 4.0μ in diameter (Fig. 38 g); (iii) fibre hyphae arising from nodose-septate hyphae, straight or flexuous, unbranched, pale smoky brown, thick-walled, lumina aseptate, wide at the extremities narrow or occluded in the middle parts, 2.5 — 6.0μ in diameter (Fig. 38 h).

Hymenium; basidia hyaline, clavate, 6.0 — 9.0 x 3.6 — 4.2μ, with four, straight sterigmata, 1.8 — 2.4μ (Fig. 38 k); basidiospores hyaline, allantoid, smooth, thin-walled, 3.0 — 4.0 x 1.2 — 1.6μ (Fig. 38 m).

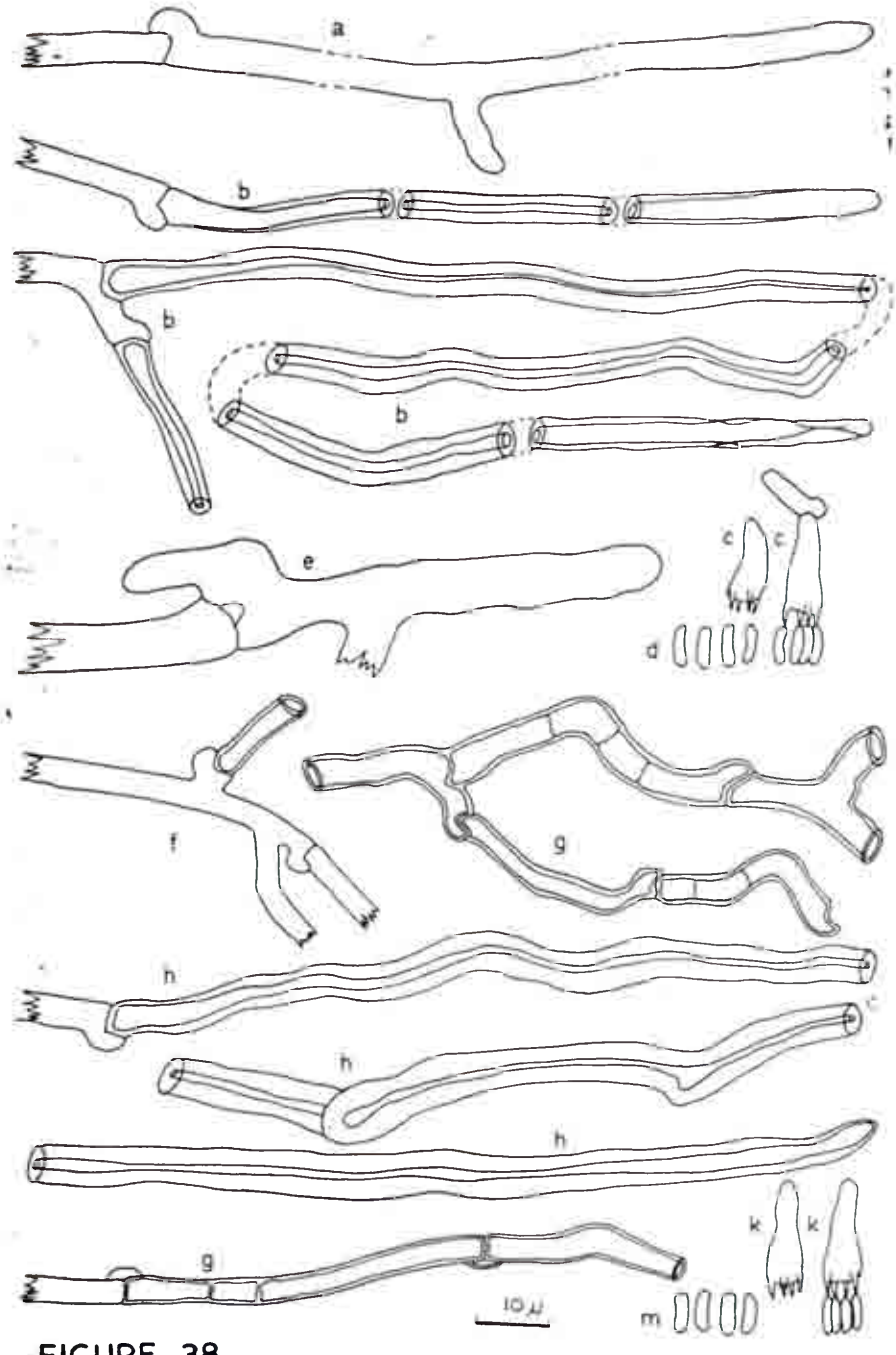

FIGURE 38.

FIG. 38.— **Polyporus vinosus.** a - e. Structures from cultures: (a) thin-walled, nodose-septate hypha from advancing zone; (b) unbranched fibre hyphae; (c) basidia; (d) basidiospores; (e) hypha from submerged mycelium.
f - m. Structures from carpophores: (f) thin-walled, nodose-septate hypha; (g) thick-walled, tortuous, branching nodose-septate hyphae with simple septa; (h) unbranched fibre hyphae; (k) basidia; (m) basidiospores.

Construction. At the margin the carpophores consist mainly of fibre hyphae with prominent lumina and staining contents, arranged parallel to and somewhat intertwined with one another and with branching, hyaline, thin-walled, nodose-septate hyphae. The context consists mainly of unbranched fibre hyphae with pale, smoky-brown, thickened walls, intertwined with one another and with nodose-septate hyphae with pale-brown, thickened walls. In the young parts behind the margin the ends of the fibre hyphae form the pubescent upper surface. Immediately behind this region the hyphal ends are bent over, flattened on to the surface in all directions and agglutinated by a thin layer of a clear, lacquer-like substance up to 30μ thick, into the smooth soft trichocutis (Lohwag, 1940) of the glabrous upper surface. Immediately below the trichocutis numerous hyaline, thin-walled, nodose-septate hyphae are present. The lower context consists mainly of pale, smoky-brown fibre hyphae intertwined with one another and turning downwards towards the trama of the dissepiments, becoming more tortuous and intricately intertwined. Just above the dissepiments the pale brown, nodose-septate hyphae with slightly thickened walls, become more numerous and tortuous, branching frequently and are tightly interwoven with the fibre hyphae, binding them into a tough tissue of which the elements are separated out with difficulty. In the dissepiments the fibre hyphae are tightly intertwined with numerous, hyaline, thin-walled, nodose-septate hyphae which branch freely to bear the basidia at the hymenial surfaces.

Decay and hosts

This species causes a white rot of hardwood logs and stumps in sub-tropical climates.

Specimens examined

Herb. PRE: 12022, on decayed log, Kyagwa, Uganda, July 1916; 14885, on decayed log, Victoria Nyanza, Uganda, July 1916; 27791, on gum tree, Pietermaritzburg, Natal, July 1916; 33125, on rotting log, Mt. Silinda Forest, S. Rhodesia, Jan. 1939; 34092, on old dead tree, Sichele For. Reserve, Zambia, Apr. 1944; 36585, on old dead tree, Sierra Leone, (Deighton No. 2571), March 1947; 40074, on logs in woods, Fungi Cubens., Wright No. 241, March 1947; *42154, on *Eucalyptus* sp. stump, Wilgeboom Plantation, E. Transvaal, Feb. 1961.

Herb. K: Berkeley Herbarium, 1879, *Polyporus vinosus* Berk. No. 43, St. Domingo. (Holotype).
Herb. STE: 139, on old log, Pietermaritzburg, Natal.

Herb. NY: 132, on prostrate log, Lamao River, Mt. Mariveles, Bataan, Luzon, 1903; 739, Alto Cedro, Cuba, 1903; 764, Cooper's Ranch, El Yunque, Mt. Baracoa, Cuba, 1903; 764, pine log, Gainesville, Fla., coll. Weber, May 1938; 873, on dead wood, Plants of Trinidad, Caroni, North Beach Road, May 1938; 873, on dead wood, Reinkliaar no. 305, St. Domingo, April 1906; 2148, on *Dipterocarpus vernicifluus,* Bosoboso, Rizal, Luson, 1907; 2148, on *Dipterocarpus,* Camp Keithley, Lake Lanao, Mindanao, 1907; 3695, on prostrate log, Mt. Mariveles, Bataan, Luzon, 1904; 7212, on half decayed logs and stumps, Palo, Leyte, Jan. 1906; 16469, Mt. Bulusan, Sorsogon, Luzon, June 1916; 17335, Mt. Bulusan, Sorsogon, Luzon, June 1916; 18444, Los Banus (Mt. Maquiling) Laguna, Luzon, 1917; 18444, British Honduras, 1906; 18444, Troye and Tyre, Cockpit County, Jamaica, Jan. 1909; 18444, Montgomery Co., Alabama, Jan. 1915; 19236, on prostrate log, Attapulgus Station, Decatur Co., Ga., 1903; 178527, Florida Agr. Expt. Station, Planera Hammock, Fla., Feb. 1938; 380, Porto Rico, 1923; 581, Porto Novo, St. Catharines, Brazil, 1928; 581, Herbarium, Expt., Station, Porto Rico Sugar Growers Association, No. 1504, El Dugue, 1914.

Interfertility studies

In order to determine the type of interfertility of *Polyporus vinosus,* sixteen cultures, each obtained from a single basidiospore from a small fructification formed in a culture of PRE 42154, were paired in all possible combinations on malt agar slopes. It was found that *Polyporus vinosus* has the tetrapolar type of interfertility with allelomorphs for heterothallism at two loci. Only three mating types were presented in the mycelia used. The distribution of mating types among the single basidiospore cultures are given in TABLE 10.

Discussion

Polyporus vinosus had not been described in culture before but with the positive reaction for extra-cellular oxidase, the presence of fibre hyphae and clamp connections on its thin-walled hyphae in culture, it agrees in most respects with Nobles' (1958 b) characters of Group 45. It differs from other species in this group by having fibre hyphae with coloured walls and basidiospores which are allantoid rather than cylindrical. Because no separate group for species with allantoid spores was available this species is placed in Group 45. The cultures of *Polyporus vinosus* differ from those of other species in this group because of the slow growth rate, scanty mycelium and reddish-purple colours of its fibre hyphae. These features, which serve to distinguish cultures of this species, also indicate that it is not well placed in this group and that its phylogenetic relationships may be with species outside this group.

The carpophores of *Polyporus vinosus* consist of three kinds of hyphae, viz: thin-walled, nodose-septate hyphae, thick-walled, nodose-septate hyphae and fibre hyphae. The small number of hyphal types present, suggest a simple construction of the carpophores of *Polyporus vinosus*, but, it was seen that thick-walled, nodose-septate hyphae were interwoven with the fibre hyphae of the lower context, binding them into a dense and very tough tissue. These hyphae cannot be regarded as binding hyphae in the sense of Corner's (1932 a, 1953) and Cunningham's (1946, 1954) definitions as they seem to be part of the generative hyphal system and are continuous with it. In this respect they do not resemble the thick-walled, nodose-septate, branching hyphae of the binding hyphal system seen in carpophores of *Lenzites betulina* and *Polyporus versicolor* in this group. These thick-walled, nodose-septate hyphae in the carpophores of *Lenzites betulina, Polyporus versicolor* and *Polyporus vinosus*, may be described as "sclerified generative hyphae" (Donk, 1964) with a binding function. Their presence in carpophores of *Polyporus vinosus* establishes a much more complex construction of these carpophores than in those of *Fomes pinicola*, which also has a dimitic hyphal system. This complexity of construction is not conveyed by the phrase, "carpophores with dimitic hyphal system" in the sense of Corner (1932 b, 1953), Cunningham (1946, 1954), Teixeira (1962 b) and Fidalgo & Fidalgo (1967).

From the descriptions it is clear that the structures found in the cultures of *Polyporus vinosus* are also present in the carpophores from which they were made. Fibre hyphae formed in culture were found to be much shorter than those of the carpophores. This appeared to be due to the very slow rate of growth of these hyphae in culture. In all other characters, the hyphae from these two sources were similar. No nodose-septate hyphae with pale-brown and slightly thickened walls were formed in the cultures although they were numerous in the carpophores. They may be expected to form in cultures under the right conditions since they were often seen to be continuous with the thin-walled nodose-septate hyphae in the carpophores.

When compared with other species of Group 45 described above, important differences in hyphal characters and carpophore construction are evident between their carpophores and those of *Polyporus vinosus*. The other species all have carpophores in which branched, aseptate, binding hyphae (Corner, 1932 a) bind the skeletal hyphae together. The presence or absence of different types of hyphae in carpophores is regarded by Teixeira (1962 b), Bondartseva (1961) and Fidalgo & Fidalgo (1966) as important at the generic level. Since branched, aseptate, binding hyphae (Corner 1932 a, b) are not present in the carpophores of *Polyporus vinosus*, this species cannot be regarded as congeneric with any genus in which such hyphae are present. For this reason Patouillard's (loc. cit.) transfer of this species to the genus *Coriolus* Quél., is untenable.

Imazeki (1952) transferred *Polyporus vinosus* to the genus *Fomitopsis* Karsten of which *Fomes pinicola* (Sw. ex Fr.) Cooke is the type species (Cooke, 1959). Carpophores of both these species have dimitic hyphal systems while their upper surfaces are covered by resinous or lacquer-like layers. In carpophores of *Polyporus vinosus* however, the fibre hyphae are dark-coloured and more closely interwoven than the hyaline fibre hyphae in carpophores of *Fomes pinicola*. Thin-walled, nodose-septate hyphae in carpophores of *Fomes pinicola* do not turn dark or develop thickened walls and bind the fibre hyphae in the tramal tissues as in carpophores of *Polyporus vinosus*. The carpophores of *Fomes pinicola* are thus simpler in construction than those of *Polyporus vinosus*. Furthermore, *Polyporus vinosus* has the tetrapolar type of interfertility and its cultures produced extra-cellular oxidase enzymes, whereas *Fomes pinicola* has the bipolar type of interfertility (Mounce, 1929) and its cultures lack extra-cellular oxidase. It appears therefore that *Polyporus vinosus* and *Fomes pinicola* cannot be regarded as being congeneric.

Murrill (1905) created the genus *Nigroporus* with *Polyporus vinosus* Berk. as the type and only species. In view of the above descriptions it appears that this genus may be retained for species with dark-coloured carpophores consisting of hyaline, thin-walled, nodose-septate hyphae, brown, thick-walled, nodose-septate hyphae and unbranched fibre hyphae with brown walls, hyaline, allantoid basidiospores and which cause a white rot of hardwoods. No other species possessing this combination of characters are known so that the relationships of this species are obscure at present.

Resumé.

The species included here in Group 45 have all those characters in common which are required for their inclusion in this group. On the basis of differences in the micromorphology of their carpophores however three smaller sub-groups may be distinguished, viz.: (i) a sub-group in which the binding hyphal system consists of thick-walled, aseptate fibre hyphae with short, tortuous branches and branching, thick-walled or solid, nodose-septate hyphae and which includes *Polyporus versicolor, Trametes suaveolens, Lenzites betulina, Polyporus pubescens, Trametes meyenii* and *Lenzites palisoti;* (ii) a sub-group in which the binding hyphal system is composed of aseptate, thick-walled fibre hyphae with long flexuous tapering branches and which includes *Polyporus occidentalis* and *Trametes cingulata* and (iii) a sub-group without a binding hyphal system which includes *Polyporus vinosus*.

The species in these three sub-groups thus share a number of correlated characters, viz.: production of extra-cellular oxidase, association with white rots, nodose-septate hyphae, fibre hyphae and the tetrapolar type of interfertility. It appears that these species share a common ancestry but show diversity in the elements of their carpophores and in their construction.

5.8 Group 51

Cultures of species in this group form white to cream coloured mycelial mats which soon develop extensive, appressed, brown, pseudoparenchymatous areas. Extra-cellular oxidase enzymes are produced. Their thin-walled hyphae have simple clamps at the septa and may remain so or may develop thick-walled, irregular projections and cuticular cells in the pseudoparenchymatous areas. Thick-walled, aseptate fibre hyphae are also formed. Their basidiospores are cylindrical. Interfertility is of the tetrapolar type in those species of which this character is known.

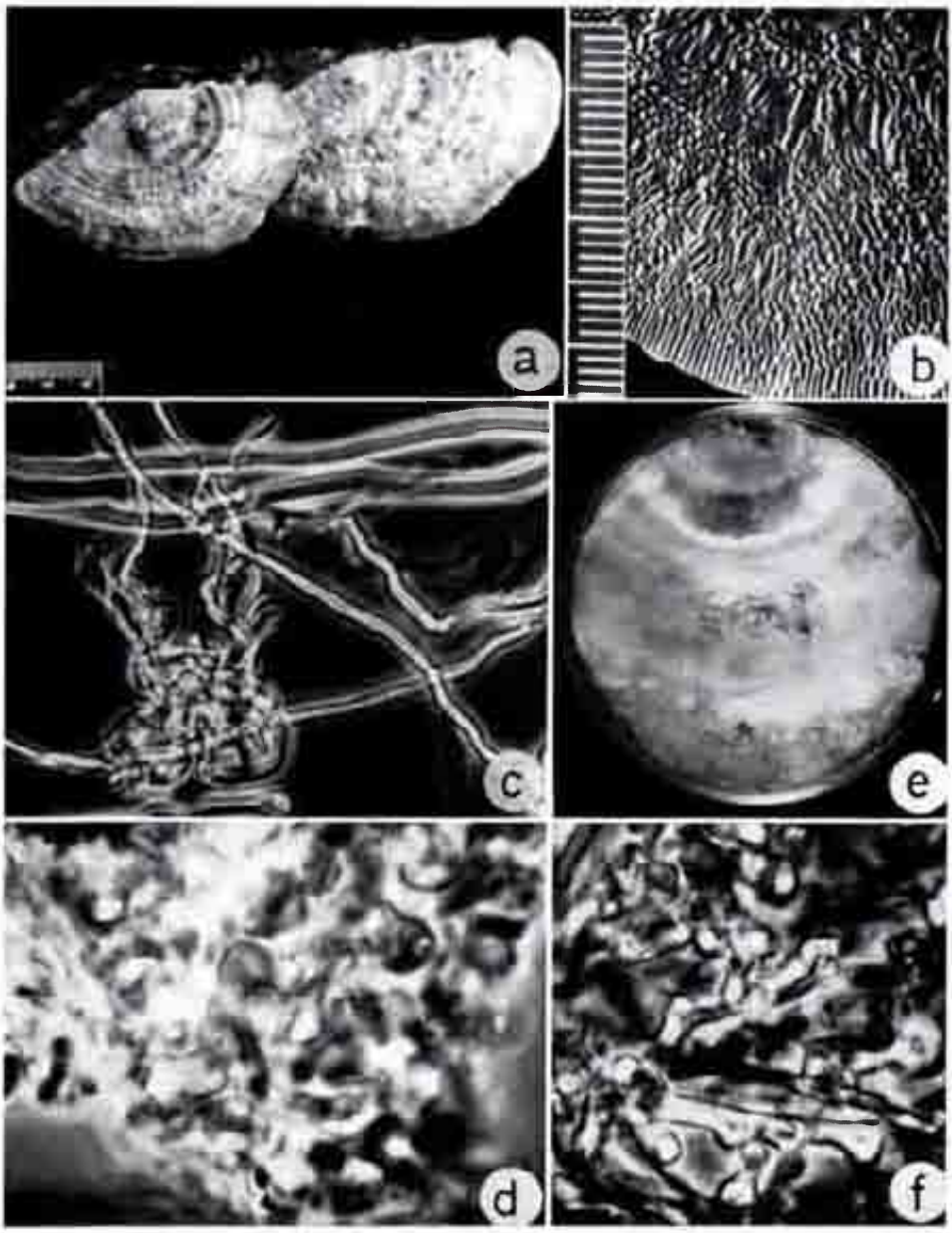

FIG. 39.— **Daedalea confragosa.** (a) Carpophores, upper surface, of PRE 42386 and (b) hymenial surface; (c) unbranched fibre hyphae and fibre hyphae with numerous branches from lower context, × 400 phase contrast; (d) cuticular cells from upper surface of DAOM 30121, × 1000, squash preparation; (e) culture of PRE 42345 at six weeks; (f) cuticular cells and hyphae with interlocking projections from culture, × 500 phase contrast.

Daedalea confragosa *Bolt. ex Fr.* in Syst. Myc. 1, 336, 1821;

Daedaleopsis confragosa (Bolt. ex Fr.) Schroet. in Cohn Kryptog.-Fl. Schles. Pilz. p. 493, 1888;

Trametes confragosa (Bolt. ex Fr.) Jörstad, Kgl. Norske Videnskab. Selskabs. 10, 28, 1936.

Cultural characters

Growth moderately fast to slow the mats attaining radii of 8 — 15 mm in one week and covering the plates in three to six weeks. Advancing zone even, closely appressed, hyaline or white becoming more raised and somewhat cottony to woolly towards the inoculum or remaining sub-felty and appressed with isolated felty patches. After about 2 weeks sunken areas of collapsed mycelium appear, bordering abruptly on the white aerial mycelium and on dark, crustose areas of "hazel", "russet", "avellaneous", "wood brown" to "army brown" colour which develop in some isolates. In others, the mat remains thin, sub-felty to sodden, with little or no aerial mycelium, developing patches of submerged mycelium, or, patches of raised, felty, aerial mycelium covered with irregular, crustose areas of "cinnamon buff", "Saccardo's umber" or "mummy brown" which gradually increase in size. White, aerial mycelium may darken gradually to "light buff", "light pinkish cinnamon" or "tawny". After six weeks the plates may be covered with thin, tough, felty mycelium, white in some parts or mostly in shades of brown varying from "light buff", "light pinkish cinnamon" to "avellaneous", "wood brown" or "cinnamon brown" and oozing droplets of dark brownish liquid, some covered by irregular, crustose areas of "natural brown" or "Mars brown", somewhat sunken and sharply demarcated from the felty mycelium. Or, the mat may be sub-felty and sodden with irregular, crustose areas with characteristic, sunken margins in "cinnamon brown" to "Saccardo's umber" along the margins, occasionally incompletely covered in their central parts. The reverse darkens gradually in reddish brown colours, mostly more deeply coloured under the crustose areas and presenting a marbled appearance. No odour is emitted by most isolates but a slight, pepper-like odour may be present in some.

On gallic acid and tannic acid agar strong diffusion zones are formed but no growth takes place on gallic acid and only a trace on tannic acid agar.
Advancing mycelium: hyphae hyaline, thin-walled, nodose-septate, branching at or near the septa often with numerous short branches from a short section of hyphae, 2.0 — 4.0μ in diameter (Fig. 40 a).

Aerial mycelium: (a) hyphae as in the advancing zone; (b) fibre hyphae hyaline at first, darkening later, branched, the branches long, tapering, solid or nearly so with the lumina narrow, aseptate or with one or two simple septa near the thin-walled tip, 1.5 — 3.0μ in diameter (Fig. 40 b); (c) cuticular cells ferruginous brown, thin-walled or thick-walled, of irregular shape, often distended into a number of irregular projections up to 20μ in diameter and arising from thin-walled,

FIG. 40.— **Daedalea confragosa.** a - d. Structures from cultures: (a) hyphae from advancing zone; (b) fibre hyphae; (c) cuticular cells; (d) nodose-septate hyphae with thick, brown walls and irregular projections.
e - q. Structures from carpophores: (e) thin-walled, branching, nodose-septate hyphae; (f) brown, thick-walled, nodose-septate hyphae; (g) unbranched, fibre hyphae; (h) fibre hyphae with branches towards the distal end; (k) fibre hyphae with numerous, short, tortuous branches; (m) thick-walled, nodose-septate hyphae with tortuous branches; (n) basidia; (p) basidiospores; (q) basidiole.

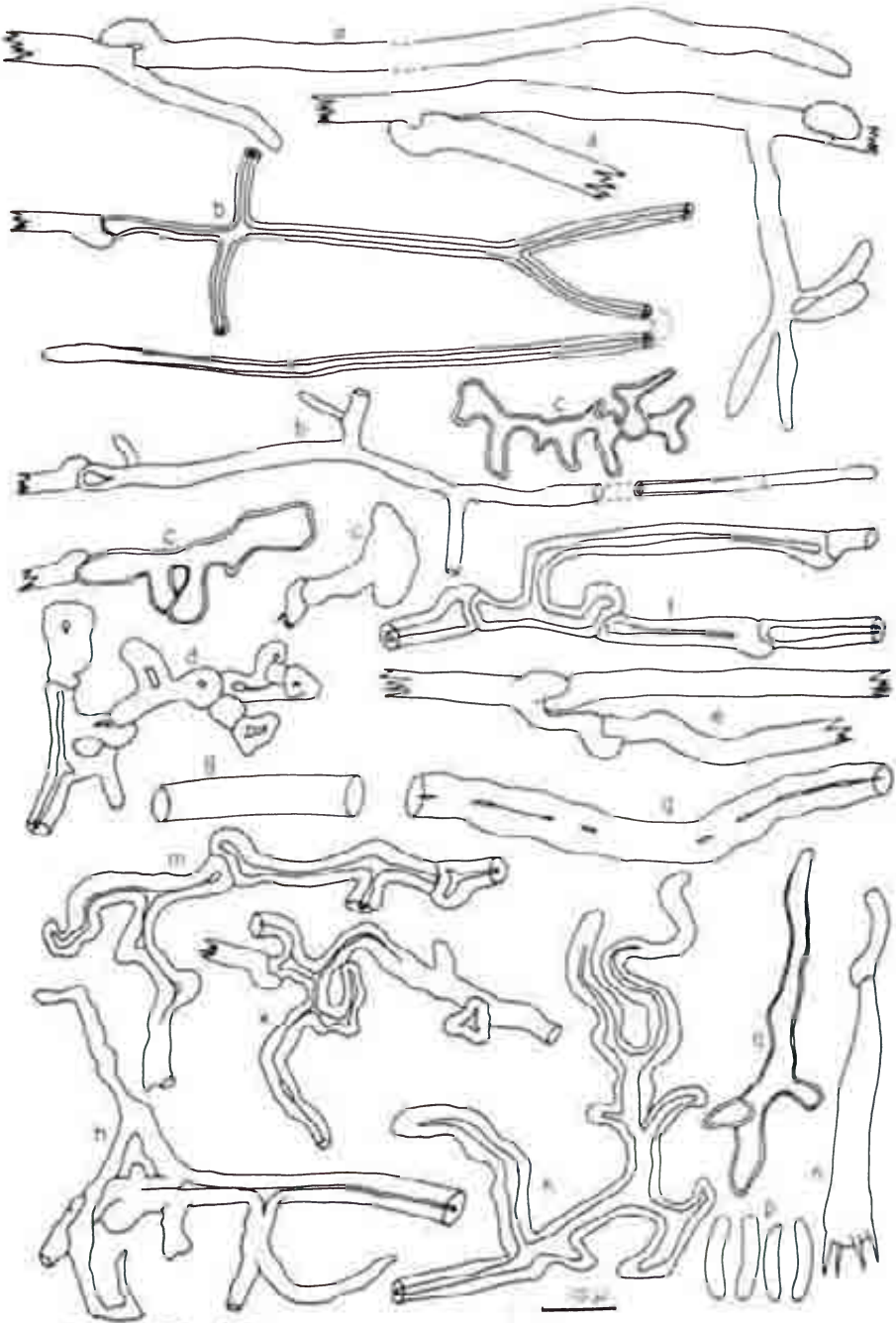

FIGURE 40.

nodose-septate hyphae, (Fig. 40 c) not present in all cultures; (d) nodose-septate hyphae with thickened brown walls, 2.0 — 4.5μ in diameter, branched, often with irregular projections and often agglutinated into strands, apparently intergrading into the cuticular cells and forming crustose areas (Fig. 40 d).
Submerged mycelium: hyphae as in the advancing zone.

Carpophore characters

Carpophore annual or reviving, lignicolous, solitary, sessile, dimidiate, applanate, plane to somewhat convex above, occasionally imbricate, or laterally connate; leathery and watery when fresh, drying to hard, rigid, woody, 2 — 10 x 3 — 15 x 0.2 — 3.0 cm; upper surface greyish, smoky, umber or sometimes with a reddish brown crust, finely pubescent to glabrous or nearly so, radiately rugose, often concentrically grooved; margin acute, thin; pore surface whitish to avellaneous drying to isabelline or pale brown, poroid to daedaloid or lamellate, pores 0.5 — 1.5 mm wide, dissepiments entire but often becoming lacerate or dentate; tubes concolorous 0.1 — 1.5 cm deep; context floccose to corky, whitish to pale brownish, zonate, 0.2 — 1.5 cm thick.

Hyphal characters. Carpophores consist of: (i) hyaline, thin-walled, nodose-septate hyphae branching close to the septa, 2.0 — 3.0μ in diameter (Fig. 40 e); (ii) nodose-septate hyphae with thickened walls and narrow or occluded lumina, the walls sub-hyaline or brownish and lumina empty or with deeply staining contents, 1.0 — 3.0μ in diameter (Fig. 40 f); (iii) fibre hyphae long, unbranched, straight or flexuous, smooth or somewhat uneven to almost moniliform towards the tapering ends, sub-hyaline to pale brown, the walls thick and lumina narrow or occluded to form a series of deeply staining dots along the moniliform parts, aseptate, widening only at the extremities, 3.0 — 9.0μ in diameter (Fig. 40 g); (iv) fibre hyphae, hyaline or sub-hyaline, flexuous or fairly straight, sub-solid to solid, aseptate, branching towards the distal end, the branches short tortuous and tapering towards their tips, 3.0 — 6.0μ in diameter (Fig. 40 h); (v) fibre hyphae with short, tortuous branches, sub-hyaline, thick-walled, lumina narrow or occluded, aseptate, 1.0 — 3.0μ in diameter (Fig. 40 k); (vi) nodose-septate hyphae thick-walled, sub-hyaline, with short, tortuous branches, 1.0 — 3.0μ in diameter (Fig. 40 m); (vii) cuticular cells brown, irregularly distended, often with irregular projections, thin-walled or thick-walled and occasionally with deeply staining contents, 8 — 12μ in diameter (Fig. 39 d).

Hymenium: basidia long, clavate, hyaline, 12.0 — 24.0 x 2.5 — 4.5μ, bearing 4 straight sterigmata 2.8 — 3.2μ in length (Fig. 40 m); basidiospores hyaline, long cylindrical to allantoid, smooth, thin-walled, 5.4 — 7.8 x 1.2 — 1.8μ (Fig. 40 p); basidioles sub-hyaline, thin-walled or walls slightly thickened, 28.0 — 36.0 x 1.5 — 3.0μ with one to four irregular, short, terminal branches up to 15.0 x 1.0 — 3.0μ (Fig. 40 q).

Construction. At the margin the fruit-body consists of long, unbranched fibre hyphae straight or somewhat flexuous and more or less parallel to each other, arising from thin-walled, branching, nodose-septate hyphae with deeply staining contents, intertwined with the fibre hyphae.

Behind the margin in the upper part of the context the tissues consist almost entirely of solid or sub-solid, faintly brownish, unbranched fibre hyphae arranged more or less parallel to one another, bending towards the upper surface where their tips, with slightly dilated lumina, end at a common level to form the finely pubescent upper surface. Interwoven with these fibre hyphae and running across their direction of growth are long flexuous or tortuous fibre hyphae binding the parallel hyphae into a firm tissue.

At the upper surface in the older parts the terminal portions of the fibre hyphae are closely intertwined and interwoven in all directions to form a cortex with a finely pubescent upper surface which soon becomes agglutinated into a thin, glabrous, cuticular layer by a hyaline lacquer-like substance. In this cortex narrow, hyaline, branching, thin-walled, nodose-septate hyphae 1.0 — 1.8μ in diameter and with deeply staining contents, are very numerous and interwoven with the fibre hyphae. On some fruit-bodies short, narrow, hyaline, solid hyphae grow upward from these nodose-septate hyphae and become lightly entangled and interwoven to form patches of pubescent tissues on the upper surface. Rarely, nodose-septate hyphae with pale brown walls may grow upwards from these thin-walled hyphae in the cortex and may develop irregular projections or become expanded into cuticular cells in some fruit-bodies. All these elements eventually become agglutinated together with fibre hyphae by a brown, amorphous, lacquer-like material into hard, crustose masses over the upper surfaces. The middle and lower context, consist of long fibre hyphae, fairly tightly packed, more or less parallel and bending downward towards the dissepiments. Just above the dissepiments the fibre hyphae become more tortuous especially towards their tips and many develop short, tortuous, lateral branches. In this region short, tortuous, fibre hyphae with many short, tortuous branches (binding hyphae, Corner, 1932 a) become very numerous and tightly interwoven with the other hyphae, binding them into a tough, homogeneous tissue. Also present in this region are narrow, branching, hyaline, thin-walled, nodose-septate hyphae with deeply staining contents interwoven with the fibre hyphae. The tissues of the dissepiments consist of tightly interwoven, branched, thick-walled, nodose-septate hyphae and fibre hyphae inextricably interwoven and narrow, thin-walled, nodose-septate hyphae branching repeatedly and ramifying among the fibre hyphae towards the hymenial surfaces where they bear the basidia in clusters on short branches.

Decay and hosts

Daedalea confragosa causes a white rot of dead sapwood of various hardwood trees but had been noticed on wounds as well (Overholts, 1953).

Specimens examined

Herb. DAOM: *F1577, on *Fagus grandifolia,* Meach Lake, Que.; F6307, on *Salix nigricotinifolia,* Ottawa, Ont., Nov. 1931; F6457, on *Betula alba* var *Papyrifera,* Cartier Lake, Petawawa, Ont., Aug. 1935; F7757, on *Betula* sp., Chalk Riv., Ont., Sept. 1937; F7763, on *Betula* sp., Chalk Riv., Ont., Sept. 1937; F8018, on *Betula* sp., Iberville, Que., Jan. 1938; F8063, on *Acer saccharum,* Petawawa, Ont., Aug. 1937; F8080, near Ludlow, Shropshire, Sept. 1937; F8340, on *Betula papyrifera,* Gatineau, Que., Aug. 1938; *F8997, on *Acer* sp., Ottawa, Ont.; F9111, on *Alnus incana,* Notakim Depot, Que., Sept. 1939; *F9210, on *Betula papyrifera,* Chelsea, Que., May 1939; F9411, on *Betula papyrifera,* Horseshoe Bay, Ont., Aug. 1939; F10783, on *Prunus avium,* Caledon East, Ont., Oct. 1941; *17555, on *Betula lutea,* Gatineau Park, Que., Sept. 1947; 22399, on *Betula occidentalis,* Kaslo, B.C., Aug. 1948; 22546, on *Salix bibbiana,* Steen River, Alberta, July 1950; 30121, on *Prunus* sp., Vancouver, B.C., 1948; 30269, on *Populus trichocarpa,* Kaslo, B.C., Oct. 1951; 30270, on dead *Salix* sp., Candle Lake, Sask., Aug. 1949; 31089, on *Salix bibbiana,* Riding Mountain, Man., May 1949; 52911, on *Betula* sp., Sicamous, B.C., Aug. 1912; 53773, on *Betula* sp., Esher, Surrey, Sept. 1959; 69975, on *Salix* sp., Agassiz, B.C., Sept. 1959; 72334, on *Betula papyrifera,* Petawawa, Ont., Sept. 1946; *94045, on dead yellow birch, Dorset, Ont., Sept. 1962; *94052, on dead hardwood branches, Dorset, Ont., Sept. 1962; *94054, on dead wood, Dorset, Ont., Sept. 1962.

Discussion

The cultural characters of *Daedalea confragosa* as described above, agree well with the requirements for its inclusion in Group 51. The description also agrees well with earlier descriptions by Davidson *et al.* (1938, 1942) and Nobles (1948, 1965).

Cultures of *Daedalea confragosa* develop dark-coloured, skin-like or crustose areas which are formed in cultures of species of stipitate polypores as described by Nobles (1958 b) in Group 53. Nobles (1948) stated that cultures of *Daedalea confragosa* may be confused with those of *Polyporus tuberaster* and *Polyporus brumalis* but that cultures of these stipitate species may be distinguished from those of *Daedalea confragosa* by having more extensive pseudoparenchymatous areas. The presence of cuticular cells, which are frequently found in cultures of *Daedalea confragosa* but not in those of *Polyporus tuberaster* and *Polyporus brumalis*, appears to be an aditional diagnostic character. Furthermore, cultures of *Daedalea confragosa* tend to have brownish compact, tough, felty or sub-felty mycelial mats while those of *Polyporus brumalis* and other stipitate species in Group 53 (Nobles, 1958 b) mostly possess white, woolly, aerial mycelium around the pseudo-parenchymatous areas. The distinctions together with consideration of host records may serve to distinguish cultures of *Daedalea confragosa* from those of the other two species.

The carpophores of *Daedalea confragosa* consist of five different types of hyphae, viz. nodose-septate hyphae, which may be thin-walled generative hyphae, or, thick-walled hyphae with tortuous branches which form part of the binding hyphal system, unbranched fibre hyphae or skeletal hyphae (sensu Corner, 1932 a), fibre hyphae with flexuous branches towards the distal ends, which also contribute to the binding hyphal system, and fibre hyphae with numerous short, tortuous branches (binding hyphae, sensu Corner, 1932 a, 1953). Since generative, skeletal and binding hyphae are present in the fruit-bodies, these fruit-bodies have a trimitic hyphal system (sensu Corner, 1932 a; Cunningham, 1946); but morphologically and ontogenically different hyphae comprise the binding hyphal system of the fruit-bodies.

Cuticular cells and brown, thick-walled nodose-septate hyphae with irregular projections were present on the upper surfaces of a very small proportion of the fruit-bodies examined. These structures arise as modified terminal parts of the thin-walled, nodose-septate hyphae present near the upper surfaces of the fruit-bodies. Numerous narrow, thin-walled, nodose-septate hyphae were present at the upper surfaces of all the fruit-bodies examined. It therefore appears that the growth and modification of these hyphae into cuticular cells, occur in nature under certain conditions only.

From the descriptions it is evident that structures formed in cultures of *Daedalea confragosa* may also be present in the carpophores from which they were made; but some differences in morphology are evident in certain structures. The fibre hyphae formed in culture are of one type only being narrow and branched with the branches long, narrow and tapering. These fibre hyphae differ in their manner of branching from the fibre hyphae present in the carpophores of *Daedalea confragosa* and appear to be intermediate between the unbranched and much-branched fibre hyphae of the fruit-bodies. Cuticular cells were not formed in all the cultures examined but thick-walled hyphae with irregular projections were mostly present. These structures developed even in cultures made from sporophores from which they were absent. It thus appears that the development of these structures depends on the conditions under which the mycelium is growing rather than its genetic complement. Conditions favourable for their development thus appear to exist more frequently in culture than in nature. Their presence in carpophores thus represents a character of doubtful taxonomic value.

The hyphal characters and construction of carpophores of *Daedalea confragosa* had been described before by different workers. Cunningham (1948 h) included the genus *Daedaleopsis* Schroet., of which *Daedalea confragosa* is the type species

(Donk, 1960), in the genus *Daedalea* Pers. ex Fr., which he characterized as having a trimitic hyphal system with skeletal hyphae unbranched, aseptate, some shade of brown; binding hyphae aseptate, commonly of the bovista type, some shade of brown and nodose-septate, hyaline, generative hyphae. Overholts (1953) reported that the hyphae of *Daedalea confragosa* were mostly simple, aseptate and thick-walled while some narrow hyphae were branched to form "a simple type of hyphal complex". Teston (1953 b) also reported nodose-septate generative and unbranched, thick-walled, skeletal hyphae in fruit-bodies of *Trametes erubescens* Alb. & Schw. ex Fr. (= *Daedalea confragosa* Bolt. ex Fr.), with much-branched, sinuous, thick-walled binding hyphae also present in the trama of the tubes. The hyphal characters and construction of the fruit-bodies of *Daedalea confragosa* as described above thus agree with reports by earlier workers but more detail is presented here.

Comparison of the above descriptions with those of the type species of other genera to which *Daedalea confragosa* had been assigned by earlier workers, reveals important differences. Fries (1821) placed this species in the genus *Daedalea* Pers. ex Fr. and was followed in this by many later workers (Pilát, 1936); but in cultures and carpophores of *Daedalea quercina* L. ex Fr., the type of the genus *Daedalea* Pers. ex Fr., nodose-septate hyphae with irregularly thickened walls are present. Its cultures do not produce extra-cellular oxidase and its carpophores lack binding hyphae. Nodose-septate hyphae with irregularly thickened walls are absent from the cultures and carpophores of *Daedalea confragosa*. Instead, cuticular cells and hyphae with irregular projections are present. Furthermore, cultures of *Daedalea confragosa* produce extra-cellular oxidase and binding hyphae are present in its carpophores. *Daedalea confragosa* thus cannot be regarded to be congeneric with *Daedalea quercina* despite many superficial similarities.

Ames (1913), in her study of the structure of polypore fruit-bodies, included *Daedalea confragosa* in the genus *Daedalea* Fr. of which she stated, "This genus differs from *Trametes* only in the form of the hymenial surface". She found no difference in the structure of different species in these two genera. Later, Jörstad (loc. cit.) transferred *Daedalea confragosa* to the genus *Trametes* Fr. and comparison with *Trametes suaveolens* (L. ex Fr.) Fr., the type species of that genus, reveals many similarities. The general plan of construction of the carpophores is similar in both species. Binding hyphae are numerous in the lower context and rare in the upper context of carpophores of both species. Unbranched fibre hyphae are more closely packed in the carpophores of *Daedalea confragosa* resulting in a corky texture of the fruit-bodies while those of *Trametes suaveolens* are loosely packed to form the soft, spongy tissue of carpophores of this species. The same types of hyphae occur in carpophores of both species but the cuticular cells and hyphae with irregular projections are never formed in carpophores of *Trametes suaveolens* of which the upper surfaces never become crustose. Also, the binding hyphae of *Trametes suaveolens* are more translucent than those of *Daedalea confragosa* which resemble the unbranched fibre hyphae. The basidiospores of *Daedalea confragosa* are allantoid in shape unlike the cylindrical spores of *Trametes suaveolens*. In cultural characters the differences between the two species are much more striking because of the presence of brown, skin-like or crustose areas and their associated modified hyphal elements are never found in carpophores or cultures of *Trametes suaveolens* so that their presence in those of *Daedalea confragosa* constitute a genetic difference between the two species. Because the absence or presence of different types of hyphae are considered to be of importance at the generic level (Bondartseva, 1961; Teixeira, 1962 b) and because of the differences in cultural and carpophore characters, these two species do not appear to be congeneric despite the presence of many similar characters.

Daedalea confragosa had also been referred to the genus *Lenzites* Fr. by various workers (Pilát, 1936). Many similarities in hyphal characters and construction exist between fruit-bodies of *Daedalea confragosa* and *Lenzites betulina* (L. ex Fr.) Fr. the type of the genus *Lenzites* Fr.; but *Daedalea confragosa* differs from *Lenzites betulina* in the same characters in which it differs from *Trametes suaveolens* so that these two species cannot be considered to be congeneric.

Because of these differences it seems best to maintain *Daedalea confragosa* in the genus *Daedaleopsis* Schroet. of which it is the type species (Donk, 1960). Future studies, however, may well reveal transitional species to the genus *Trametes* with which *Daedalea confragosa* has strong affinities.

Trametes corrugata *(Pers.) Bresadola* in Hedwigia 51, 316, 1912;

Polyporus corrugatus Pers. in Gaudichaud, Voy. Freyc. Uranie Bot. 172, 1827;

Earliella corrugata (Pers.) Murill in Bull. Torrey Bot. Club 34, 468, 1907;

Coriolus corrugatus (Pers.) G. H. Cunningham in Proc. Linn. Soc. N.S.W. 75, 222, 1950;

Formitopsis corrugata (Pers.) Imazeki in Bull. Tokyo Sci. Mus. 6, 92, 1943.

Cultural characters

Growth is moderately rapid the mat reaching a radius of 25 mm in one week and covering the plate in 3 — 4 weeks. The margin is even, mycelium appressed or submerged for a short distance, then raised, floccose-woolly, pure white at first but becoming somewhat collapsed, more woolly to felty with faint, brownish colours developing in spots on the felty mycelium, after two weeks. The mat gradually becomes more dense with balls of woolly, white mycelium forming on its surface and on the sides of the dish. One or two concentric, sulcate zones appear over the cultures and within two to three weeks crustose areas, at first smooth and "hazel" or "cinnamon", appear and increase in size, their margins contrasting sharply with the white, woolly mat. Crustose areas remain "hazel" or "cinnamon" or become "cinnamon rufous" or "cinnamon brown" and roughened, somewhat papillate and rugose in the older parts. Shiny, smooth, "cinnamon rufous" or "cinnamon brown" laccate areas form in the crustose areas against the glass sides of the dish After four to five weeks lumps of woolly mycelium may form against the sides of the dishes and gradually develop waxy or pasty, slightly sunken areas on which low, labyrinthiform lamellae, from which spores are discharged in inverted cultures, are formed. The reverse bleaches after two weeks and a faint mushroomy odour is given off. A strong positive reaction is obtained when the culture is tested for extra-cellular oxidase by means of gum guaiac solution. Strong diffusion zones are formed on gallic acid and tannic acid media with colonies reaching up to 15 mm in diameter on tannic acid agar after one week.

Advancing mycelium: hyphae hyaline, branching, nodose-septate, thin-walled, 2.2 — 4.5μ in diameter (Fig. 42 a).

Aerial mycelium: (a) hyphae as in the advancing zone; (b) fibre hyphae hyaline, straight, unbranched or occasionally branched, thick-walled, the lumina narrow, aseptate, 1.5 — 3.5μ in diameter (Fig. 42 b); (c) narrow hyphae repeatedly dichotomously branched, hyaline 0.7 — 1.5μ in diameter, forming a net-like structure just above the agar (Fig. 42 c); (d) hyphae with brown, thickened walls

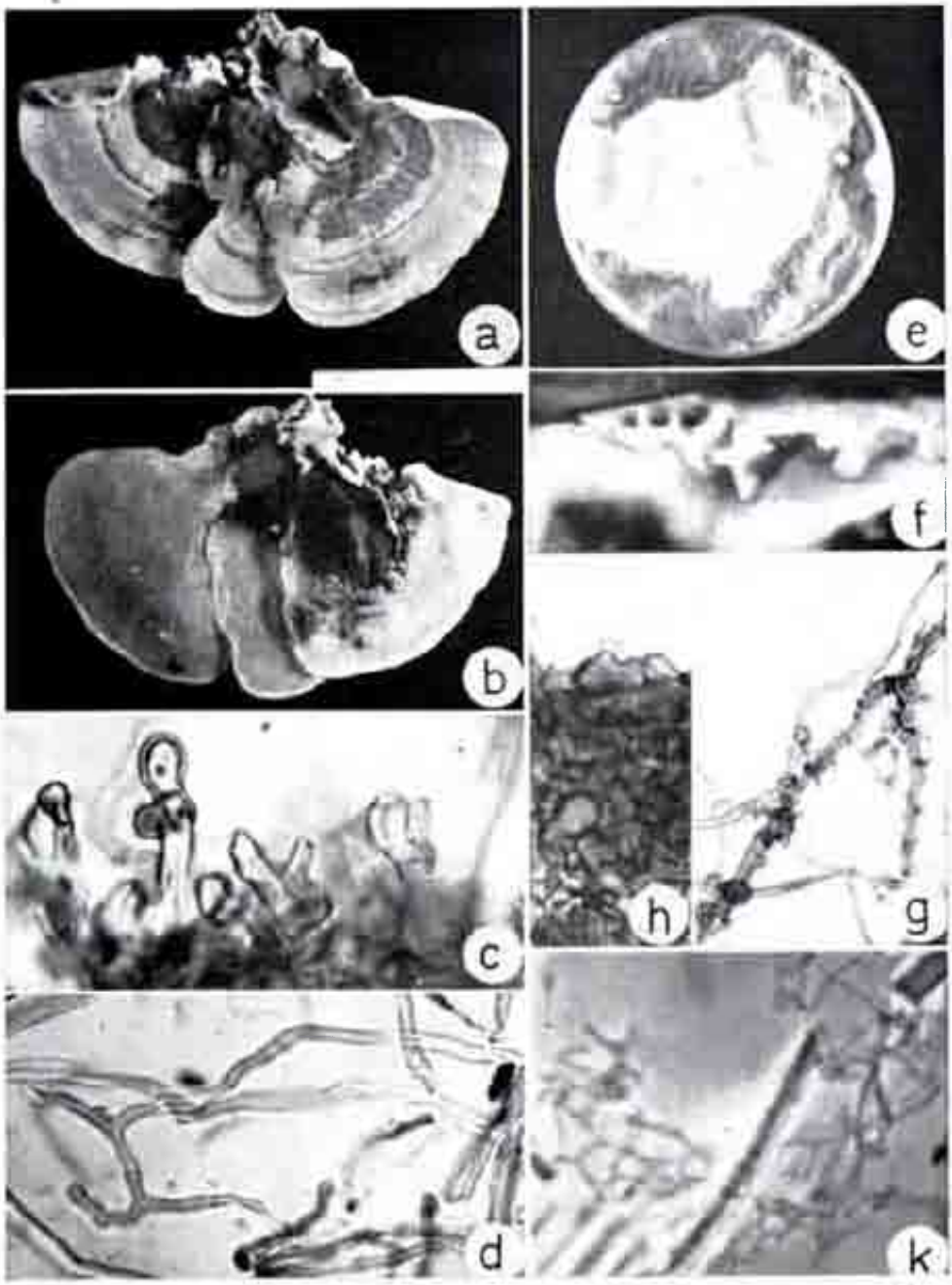

FIG. 41.— **Trametes corrugata.** (a) Upper surface and (b) hymenial surface of carpophore of PRE 34446; (c) cuticular cells from red stain on upper surface of carpophore of type specimen of *Earliella cubensis*, × 1000; (d) unbranched fibre hyphae and fibre hyphae with numerous branches from context of type specimen of *Earliella cubensis*, × 500; (e) culture of PRE 42454 at six weeks; (f) fructification in culture; (g) nodose-septate hyphae with irregular projections from culture, × 100; (h) cuticular cells from culture, × 100; (k) narrow, hyaline, branching hyphae from culture, × 1000.

bearing short lateral projections up to 7μ long, walls thickened to sub-solid or solid, 2.5 — 3.5μ in diameter and arising from nodose-septate hyphae (Fig. 42 d); (e) cuticular cells pale brown, sub-globose to ovoid or irregular in shape with fairly thin walls up to 25μ in diameter and arising from thin-walled pale or hyaline nodose-septate hyphae, and often embedded in a brown lacquer-like substance (Fig. 42 e).

Fructification: basidia cylindrical or narrowly clavate, 22.5 — 34.0 x 5.2 — 6.7μ, bearing four straight sterigmata 5.2 — 6.0μ (Fig. 42 f); basidiospores hyaline, smooth, thin-walled, long-elliptical to cylindrical, 6.7 — 10.5 x 3.7 — 5.2μ (Fig. 42 g).

Submerged mycelium: hyphae as in the advancing zone.

Carpophore characters

Carpophore annual, lignicolous, sessile, effused-reflexed, laterally extended, or conchate, connate, occasionally imbricate, woody, up to 15 x 3 — 6 x 0.2 — 2.5 cm; surface at first smooth, finely pubescent to glabrous, becoming rugose, zonate in older parts, creamy to "light buff" and thinly encrusted in "cinnamon brown" to dark "liver brown" or almost black areas in the oldest parts; margin obtuse at first, thick, later thin, creamy white, undulate, drying to "light buff"; pore surface pale pinkish when fresh drying to creamy white or "light buff", pores 2 — 4 per mm, poroid to daedaloid, rounded; dissepiments even, thick at first, later thin; tubes 1 — 8 mm deep; context white, corky to fibrous, zonate, drying to "light buff", 2 — 20 mm thick.

Hyphal characters. Carpophores consist of (i) hyaline, branching, thin-walled, nodose-septate, hyphae, 1.5 — 3.5μ in diameter (Fig. 42 h); (ii) fibre hyphae hyaline, straight or tortuous, unbranched or with an occasional long branch, the walls thickened, lumina prominent or narrow or occluded, aseptate or occasionally with one or two simple septa near the apex, 2.5 — 5.0μ in diameter (Fig. 42 k); (iii) fibre hyphae hyaline, sub-solid, repeatedly branched, the branches short or fairly long, flexuous, 2.5 — 3.5μ in diameter (Fig. 41 d, 42 m); (iv) narrow, hyaline, sub-solid hyphae, repeatedly branched, 0.5 — 0.7μ in diameter (Fig. 41 k); (v) cuticular cells with thickened, brownish walls distended into irregular shapes, 4.0 — 10.0μ in the widest parts and borne on thin-walled, nodose-septate hyphae (Fig. 41 c); (vi) nodose-septate hyphae with brownish thickened walls with irregular projections, 2.5 — 3.5μ in diameter (Fig. 41 c).

Hymenium: basidia hyaline, long, clavate 18.0 — 34.0 x 6.0 — 7.5μ and bearing four prominent sterigmata 4.5 — 6.0μ (Fig. 42 n); basidiospores hyaline, long cylindrical, smooth, thin-walled, obliquely apiculate, 8.0 — 12.0 x 4.5 — 5.5μ (Fig. 42 p).

Construction. At the margin the carpophore consists of long, more or less straight, fibre hyphae with thick, hyaline walls often thin-walled, and collapsed towards the extremities with lumina narrow, aseptate or with one or two simple septa, tightly intertwined with one another and with the branching, thin-walled, hyaline, nodose-septate hyphae from which they arise. Behind the margin the context consists of straight and tortuous, unbranched, fibre hyphae with hyaline walls partly thickened or sub-solid, and tightly intertwined. Nodose-septate hyphae, mostly empty, thin-walled and sometimes collapsed, are present in small numbers intertwined with the fibre hyphae. Interwoven with these hyphae are numerous hyaline, branching fibre hyphae, their branches long and tortuous, which bind all the hyphae into a tough, dense tissue. In the upper part of the context the fibre hyphae turn towards the upper surface where their ends are packed at a common level to

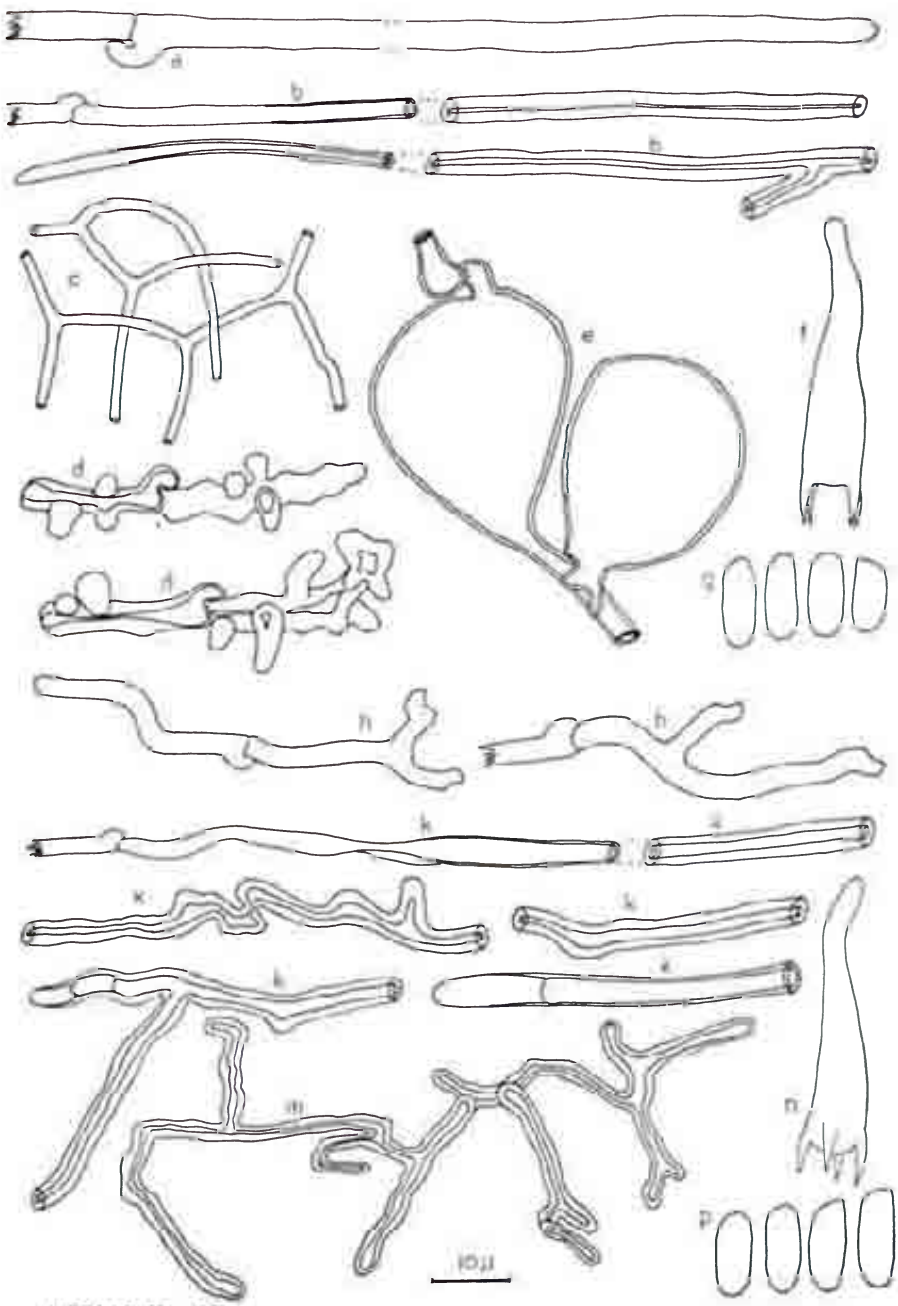

FIG. 42.— **Trametes corrugata.** a - g. Structures from cultures: (a) hypha from advancing zone; (b) fibre hyphae; (c) narrow, dichotomously branching hyphae; (d) hyphae with brown, thickened walls and irregular projections; (e) cuticular cells; (f) basidium; (g) basidiospores.
h - p. Structures from carpophores: (h) thin-walled, nodose-septate hyphae; (k) fibre hyphae, unbranched or with occasional long branch; (m) fibre hypha with many short, flexuous branches; (n) basidium; (p) basidiospores.

from the finely pubescent upper surface not covered by the deep, reddish-brown, crustose structure. At the upper surface below the dark-coloured, crustose areas, numerous thin-walled, nodose-septate hyphae, mostly narrow and frequently branched are present, intertwined with the ends of the fibre hyphae and forming a thin-walled, pseudoparenchymatous layer up to about 50μ thick over the ends of the fibre hyphae. Immediately above this layer are larger cuticular cells and nodose-septate hyphae with interlocking projections on their thickened brown walls. These structures are agglutinated by a pale brown lacquer-like substance into the hard crust in a layer up to 150μ thick over the older part of the upper surfaces of the fruit-bodies. In the older parts of the context of some of the sporophores examined a delicate network of very narrow, hyaline, repeatedly branched hyphae was visible, interwoven with the wider hyphae. Their origin could not be determined (Fig. 41 k)

In the lower context the fibre hyphae turn downwards towards the dissepiments. They are narrow and with more prominent lumina than in the upper context. The long fibre hyphae become more tortuous and are tightly interwoven with branching "binding hyphae", some with solid clamps, which bind them into a tough, dense tissue. Thin-walled, nodose-septate hyphae become more numerous in the trama and dissepiments where they branch repeatedly, the branches ramifying between the fibre hyphae in the direction of the pore surfaces. At the pore surfaces the nodose-septate hyphae form numerous, very short branches on which the basidia are borne.

Decay and hosts

Trametes corrugata causes a white rot of hardwood logs in sub-tropical areas.

Specimens examined

Herb. PRE: 15623, on living *Albizzia* sp., Durban, Natal, March 1917; 28968, on dead wood, Rooikoppies Plantation, Duiwelskloof, Transvaal, May 1937; 30230, indigenous wood, Krantzkop, Natal, December 1935; 31684, indigenous wood, Ifafa, Natal, August 1916; 34446, rotting logs of Kukin trees, Hawaii, July 1930; 31736, on dry branch, Chinizina, Beira, Moçambique, April 1957; *42454, on decaying lidchi stem, Tzaneen, Transvaal, January 1961.

Herb. NY: *Earliella cubensis* Murrill, on dead wood, Herradura, Pinar del Rio Province, Cuba, March 7 — 12, 1905, (TYPE).

Interfertility studies

In order to determine the type of heterothallism present in *Trametes corrugata*, 16 mycelia, each obtained from a single basidiospore produced from a small fruit-body formed in culture, were paired in all possible combinations. The formation of clamp connections on the paired mycelia took place in a manner which proved that *Trametes corrugata* has the tetrapolar type of interferitility. The distribution of mating types among the single spore mycelia is given in TABLE 11 in the abbreviated form used by Yen (1950).

Discussion

The presence of cuticular cells, fibre hyphae and nodose-septate hyphae, in cultures which produce extra-cellular oxidase enzymes, places *Trametes corrugata*, which had not been described in culture before, in Group 51. Its cultural characters agree in many respects with those of other species in this group but cultures of *Trametes corrugata* may be recognized by the reddish colours of the crustose areas which contrast sharply with the pure white, woolly mycelium, and the very large, thin-walled, cuticular cells present in these crustose areas.

The carpophores of *Trametes corrugata* agree in construction and hyphal characters with those of other species in this group and consist of six types of hyphae. Of these, the cuticular cells and thick-walled hyphae with irregular projections are modified portions of the thin-walled, nodose-septate hyphae but because of the presence of clamp connections in them, they must be regarded as generative hyphae sensu Corner (1953) and Cunningham (1946). The unbranched fibre hyphae and fibre hyphae with many long, tortuous branches agree with Corner's (1932 a) and Cunningham's (1946) definitions of skeletal and binding hyphae respectively. The very narrow, branched, aseptate hyphae present in some carpophores appear to serve a binding function and may be regarded as part of the binding system although their origin and true nature could not be determined. Carpophores of *Trametes corrugata* thus have a trimitic hyphal system sensu Corner (1932 a) but hyphae which differ in morphology and ontogeny are present in the generative and binding systems. The trimitic hyphal system in carpophores of this species was also reported by Fidalgo & Fidalgo (1966).

The very narrow, branched hyphae were not present in all the carpophores examined. They were present in the context of the carpophores of PRE 42454 and in the trama of the pores of the type specimen of *Earliella* Murr., but they are visible only after prolonged and extremely careful search of the carpophore tissues. It appears that they become very brittle on drying and disintegrate when tissues from old specimens are teased out for examination. Similar hyphae had been noted in cultures of this and other species but have not been found in their carpophore tissues.

Although very large, thin-walled cuticular cells were present in the crustose areas of the cultures, the dark reddish-brown, crustose areas of the fruit-bodies of *Trametes corrugata* were found to consist almost entirely of small, distorted cells with thickened, brownish walls which closely resemble the hyphae with interlocking projections, present in the cultures. It was, however, found in the cultures that some of these projections on the brown, thick-walled hyphae were distended into thin-walled vesicles resembling small cuticular cells. It thus appears that cuticular cells and hyphae with interlocking projections are different structures that develop from the same hyphae probably under different conditions. If this is correct, then the hyphae with interlocking projections found in the carpophores must be regarded as homologous structures to the cuticular cells formed in cultures. All the structures formed in cultures are thus present in the carpophores from which they were made.

Although *Trametes corrugata* fits well into Group 51 in cultural characters, its fruit-bodies differ in hyphal characters from those of other species in this group. In the fruit-bodies of *Daedalea confragosa, Hexagona tenuis* and *Fomes fomentarius,* the long, unbranched fibre hyphae (skeletal hyphae, Corner 1932 a) are readily distinguishable from the tortuous, much-branched fibre hyphae (binding hyphae, Corner 1932 a). In fruit-bodies of *Trametes corrugata,* the binding hyphae mostly have long branches which are usually narrower and more tortuous than the unbranched hyphae in the upper context and may be recognized by their smaller diameter, branching and more tortuous appearance; but in the lower context where the skeletal hyphae are narrower and more tortuous than in the upper context, the two types of hyphae are very similar and portions of the branched hyphae are often indistinguishable from flexuous portions of the unbranched hyphae. Furthermore the fibre hyphae of *Trametes corrugata* are consistently hyaline under the microscope while those of *Daedalea confragosa, Hexagona tenuis* and *Fomes fomentarius* (Teixeira, 1962 b) are sub-hyaline to pale brown. The hyphal characters of *Trametes corrugata* thus differ from those

of *Daedalea confragosa, Hexagona tenuis* and *Fomes fomentarius,* and *Trametes corrugata* cannot, because of these differences as well as other differences in carpophore morphology, be considered to be congeneric with these species.

Imazeki (1943) placed *Trametes corrugata* in the genus *Fomitopsis* Karst. but comparison with the cultural characters and micromorphological characters of the carpophores of the type species, *Fomes pinicola* (Sw. ex Fr.) Cooke, shows this transfer to be untenable. The hyphal characters and construction of the context and crusts of the carpophores of the two species are completely different. Furthermore, extra-cellular oxidase enzymes are produced by cultures of *Trametes corrugata* but not by those of *Fomes pinicola.* The latter species has the bipolar type of interfertility (Mounce & Macrae, 1938) whilst *Trametes corrugata* has the tetrapolar type of interfertility.

Cunningham (loc. cit.) transferred *Trametes corrugata* to the genus *Coriolus* Quél. thereby implying similarity in hyphal characters and carpophore construction between this species and *Polyporus versicolor;* but from the above descriptions it is clear that *Trametes corrugata* differs from *Polyporus versicolor* in respect of the morphology of the binding hyphae in their carpophores. Furthermore, the hyphae with irregular projections, present in the crustose areas of carpophores of *Trametes corrugata,* are absent from those of *Polyporus versicolor* although somewhat similar structures have been found in its cultures. Because the absence or presence of different types of hyphae in carpophores is regarded as significant at the generic level by various workers (Teixeira, 1962 b; Donk, 1964; Fidalgo & Fidalgo, 1966) it appears that *Trametes corrugata* cannot be regarded as being congeneric with *Polyporus versicolor* L. ex. Fr., the type species of the genus *Coriolus* Quél. *Trametes corrugata* also differs from *Trametes suaveolens* in the same characters in which it differs from *Polyporus versicolor* so that Bresadola's (loc. cit.) combination also appears to be untenable.

The long, branched binding hyphae of *Trametes corrugata* resemble those of carpophores of *Trametes cingulata.* Other hyphal characters and the construction of the carpophores of these two species are also similar but hyphae with irregular projections and cuticular cells are absent from carpophores and cultures of *Trametes cingulata.*

Carpophores and cultures of *Trametes corrugata* differ in respect of hyphal morphology from some other species in Group 51 and from the type species of the genera *Coriolus* Quél., *Fomitopsis* Karst. and *Trametes* Fr. to which it had been referred by various workers. The presence of cuticular cells and hyphae with irregular projections and trimitic hyphal system in its carpophores, indicate affinities with the type species of the genera *Daedaleopsis* on the one hand and *Coriolus* and *Trametes* on the other. If the construction of the carpophores of *Daedalea confragosa, Fomes fomentarius, Hexagona tenuis, Trametes acupunctata* and *Trametes corrugata* is considered, however, it becomes evident that the presence of cuticular cells and hyphae with irregular projections in their carpophores is the main character common to them all while differences in the hyphal characters and construction of their carpophores exist.

It thus appears that these species may have acquired this character by convergent evolution and that their phylogenetic relationships are less intimate than the presence of cuticular cells and hyphae with inter-locking projections in their cultures and carpophores imply.

The general morphology of the carpophores of *Trametes corrugata,* their hyphal characters, construction, texture and spore characters agree with those of some species included in Group 45 (e.g. *Trametes cingulata, Trametes meyenii).*

It thus appears that this species has strong affinities with others in that group; but the hyphal characters and construction of the carpophores of a larger number of species in both Group 45 and Group 51 will have to be examined before any definite conclusions can be reached, and the validity of the genus *Earliella* Murrill, of which *Trametes corrugata* (Pers.) Bres. (= *Earliella cubensis* Murr.) is the type species (Murrill, 1907 a), be established or rejected.

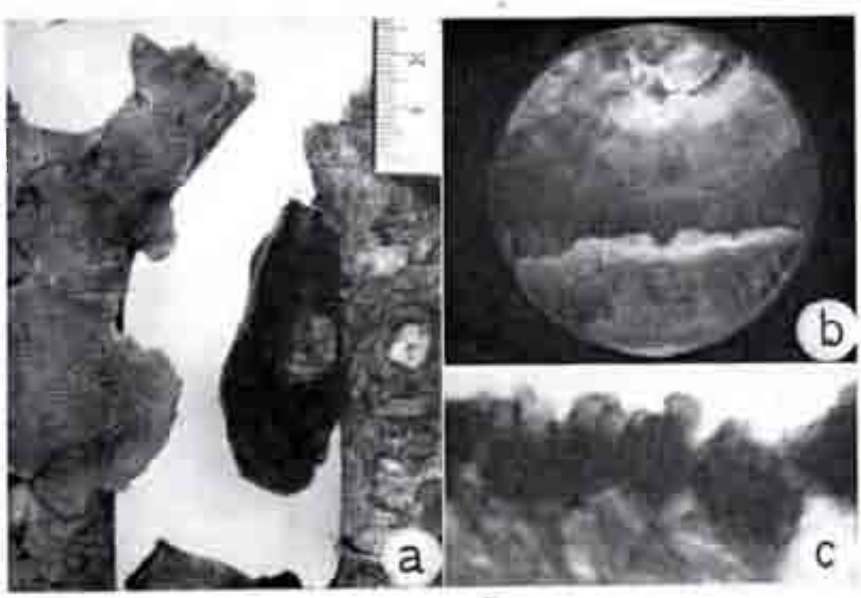

FIG. 43.—**Hexagona tenuis.** (a) Carpophores of PRE 43116; (b) culture of PRE 42159 at six weeks; (c) cuticular cells in red stain on upper surface of carpophore. × 500.

Hexagona tenuis *Hooker ex Fr.*, Epicr. Syst. Mycol., 498, 1838;
Daedaleopsis tenuis (Hooker ex Fr.) Imazeki in Bull. Tokyo Sci. Mus., 6, 78, 1943.

Cultural characters

Growth is moderately rapid, the mat covering the plate in 3 — 4 weeks. The advancing zone is bayed or even with hyphae raised to the limit of growth, the young mat thin, downy to floccose-cottony. Towards the inoculum the mat becomes more dense, woolly, white, radially sulcate, and, at about 10 — 20 mm around the inoculum, sunken and compacted into thin, appressed, pellicular, crustose areas of "cinnamon brown" to "wood brown" often with a thin, downy overgrowth of white mycelium after 2 — 3 weeks. With advancing age the white mycelium becomes increasingly woolly and dense, gradually becoming compacted into leathery, skin-like, wrinkled, crustose areas with colours ranging from "light ochraceous buff" to "tawny" to "russet," "natal brown" and patches of "mummy brown," irregular in outline and extending gradually until most of the surface is covered at six weeks. The reverse darkens with age, dark brown patches developing under the crustose areas often traversed by very dark, irregular lines and presenting a marbled appearance. A faint mushroomy odour is given off after two to three weeks but disappears later. A positive reaction is obtained when cultures are

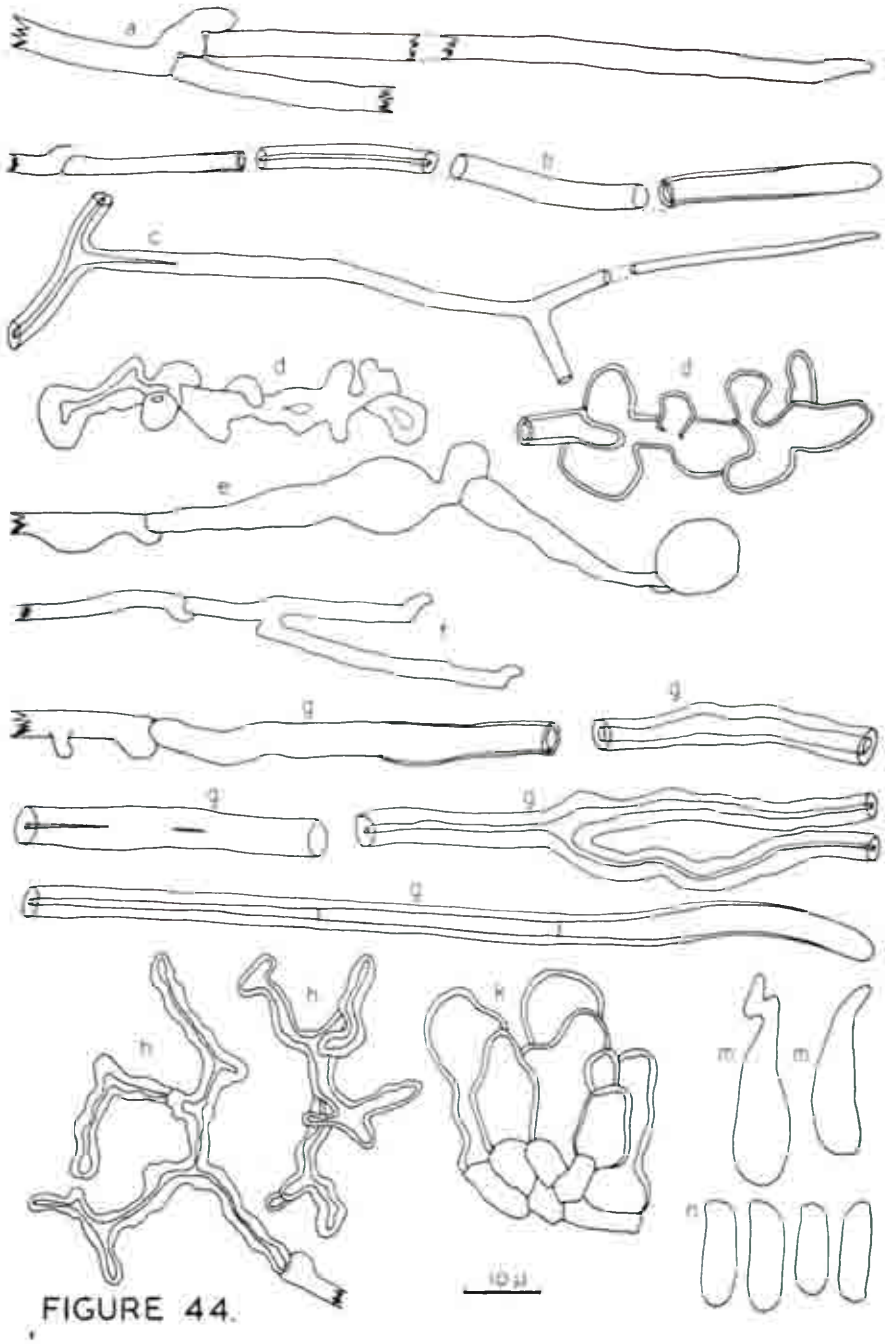

FIGURE 44.

FIG. 44.—**Hexagona tenuis.** a - e. Structures from cultures: (a) hypha from advancing zone; (b) unbranched, fibre hypha; (c) fibre hyphae with long tapering branches; (d) nodose-septate hyphae with irregular projections and cuticular cells; (e) swellings on hypha from submerged mycelium.
f - n. Structures from carpophores: (f) thin-walled, nodose-septate hyphae; (g) fibre hyphae, unbranched or occasionally branched; (h) fibre hyphae with numerous tortuous branches; (k) cuticular cells; (m) basidia; (n) basidiospores.

tested for extra-cellular oxidase by means of alcoholic gum guaiac solution. On gallic acid and tannic acid media, strong diffusion zones were formed but no growth occurred.

Advancing mycelium: hyphae hyaline, branching or simple, thin-walled, nodose-septate, with simple clamps and staining in phloxine, 2.2 — 3.7μ in diameter (Fig. 44 a).

hyaline to pale brown, walls thickened and lumina narrow or occluded, aseptate, 2.2 — 3.5μ in diameter (Fig 44 b); (c) fibre hyphae with long tapering branches, hyaline or pale brown, walls thickened, lumina aseptate, narrow or occluded or hyphae solid, .2 — 3.0μ in diameter (Fig. 44 c); (d) nodose-septate hyphae with walls slightly thickened, pale brownish to reddish brown and distorted into irregular projections and swellings or cuticular cells up to 15μ in diameter, tightly packed to form the dark-coloured, crustose areas (Fig. 44 d).

Submerged mycelium: hyphae as in the advancing zone and often developing swellings resembling the cuticular cells (Fig. 44 e).

Carpophore characters

Pileus annual, lignicolous, solitary, sessile, effused-reflexed, occasionally resupinate, applanate, conchate or flabelliform, free or laterally connate, coriaceous, 3.5 — 7.0 x 2.0 — 4.5 x 0.05 — 2 cm; surface glabrous, radially sulcate, rugose or smooth, "snuff brown" or "cinnamon brown" to "hazel" or "chestnut brown" often with dark "blackish brown" to "seal brown" areas towards the base; margin thin, acute, entire or rarely lobate, often undulate, "snuff brown," "cinnamon brown" to "hazel" or "chestnut brown"; pore surface "buckthorn brown" to "cinnamon brown," poroid; pores large, angular, 0.5 — 1 mm in diameter; dissepiments thin, even; tubes shallow, 0.5 — 1 mm deep; context rusty brown, darkening in KOH, fibrous, up to 1 mm thick.

Hyphal characters. Carpophores consist of: (i) hyaline, branching, thin-walled, nodose-septate hyphae with staining contents, 1.5 — 3.0μ in diameter (Fig. 44 f); (ii) fibre hyphae long, more or less straight or flexuous, unbranched or occasionally branched, the branches few, long, sub-hyaline to yellowish brown, the walls thickened or solid, lumina narrow or occluded widening at the extremities, aseptate or with one or two simple septa near the tip 3.0 —6.0μ in diameter (Fig. 44g); (iii) fibre hyphae hyaline to sub-hyaline, very tortuous, branching repeatedly over short distances, the branches short, tortuous, thick-walled, lumina narrow or occluded widening at the hyphal tips, aseptate, 1.0 — 3.0μ in diameter (Fig. 44 h); (iv) cuticular cells subglose to clavate with irregular, lobate projections, dark reddish-brown, thin-walled 5 — 15μ in diameter, arising from thin-walled, nodose-septate hyphae (Fig. 43 c, 44 k).

Hymenium: basidia hyaline, long clavate, almost cylindrical, 15.0 — 24.0 x 3.0 — 4.5μ with four slender, straight sterigmata 2.8 — 3.2u (Fig. 44 m); basidiospores hyaline cylindrical smooth, thin-walled 10.0 — 15.0 x 4.0 — 6.0μ (Fig. 44 n).

Construction. At the margin the carpophore consists of long, straight, unbranched, pale-brown fibre hyphae with prominent lumina, arranged parallel to the direction of growth and slightly intertwined with one another and with the hyaline, thin-walled, branching, nodose-septate hyphae from which they arise. Behind the margin the fibre hyphae have thicker walls and bend upwards towards the upper surface. Few nodose-septate hyphae are present in the upper context, which

consists mainly of parallel or intertwined, unbranched, fibre hyphae with yellow-brown, thickened walls and narrow or occluded lumina, and, numbers of hyaline or sub-hyaline, thick-walled or solid, fibre hyphae with short, tortuous, branches interwoven with long, unbranched, fibre hyphae. At the upper surface the ends of the fibre hyphae are packed at a common level and are bent over to lie flat on the surface. These elements are covered by a thin, transparent, lacquer-like substance to form the characteristic glabrous surface of the carpophores. In carpophores with dark, reddish-brown stains over their upper surfaces, thin-walled, nodose-septate hyphae with deeply staining contents are present in large numbers among the fibre hyphae below these areas. From these hyphae, dark-brown, swollen, cuticular cells and hyphae with irregular projections, extend into the dark, stained area. Here, these elements are agglutinated by means of a dark-brown, lacquer-like substance into a hard, brittle crust, up to 120μ thick, over the ends of the fibre hyphae (Fig. 43 c).

In the lower context, long, unbranched, yellow-brown, fibre hyphae are arranged more or less parallel to the direction of growth but some turn downwards into the trama of the dissepiments. Other unbranched, yellow-brown, fibre hyphae with prominent lumina, mostly unbranched, but very tortuous, are tightly interwoven with these straight fibre hyphae and with numerous, hyaline, short, much-branched, thick-walled or solid, fibre hyphae and branching, thin-walled, nodose-septate hyphae, to form the dense, tough tissues of the trama. In this tissue, thin-walled, nodose-septate hyphae ramify among the thick-walled hyphal elements, branching frequently towards the surfaces of the pores where they bear the basidia on numerous, short branches.

Decay and hosts

This species causes a diffused white rot of dead branches of hardwood trees.

Specimens examined

Herb. PRE: 11521, on decayed wood, Kentani, C.P., May 1918; 11545, on living branch, Buccleugh, Natal, July 1918; 15541, on *Albizzia gummifera*, Stellenbosch, C.P., Sept. 1916; 17099, Wilderness, C.P., May 1923; 23477, Mount-aux-Sources, Natal, July 1928; 23689, Margate, South Coast, Natal, Feb. 1931, 28259, on dead wood, Pretoria, Transvaal, March 1935; 28889, on dead branches, Drakensberg, Natal, July 1937; 31549, on dead branches, Ivy Range, Moodies, Natal, Aug. 1915; 31669, Ginginhluvu, Natal, May 1916; 31674, Ginginhluvu, Natal, July 1915; 31702, dead stump, Stellabush, Durban, Natal, Oct. 1916; 31850, New Germany, Natal, April 1917, 31865, on dead wood, Bluff, Durban, Natal, May 1917; 31894, on dead wood, Mazoe, Rhodesia, May 1917; 31900, Stellabush, Durban, Natal, July 1917; 31920, Bluff, Durban, Natal, Aug. 1917; 33066, on dead wood, Xumeni Forest, Donnybrook, Natal, Dec. 1940; 33207, on dead wood, Rustenburg, Transvaal, May 1939; 35329, on *Quercus* sp., Pietermaritzburg, Natal, 1943; 36422, on dead wood, Chiradzulu, Malawi, Sept. 1944; 36848; 36866, on dead wood, Vumba Mts., Umtali, Rhodesia, July 1948; 39112, on dry branch, Isipingo, Natal, Oct. 1950; 42067, Senanga, Barotseland, Aug. 1952; *42159, on dead hardwood branch, Bushbuckridge, Tvl., Feb. 1961; *42161, on dead hardwood branch, Bushbuckridge, Tvl., Feb. 1961; 43116, on *Acacia karroo* stump, Tongoland, Natal, March 1965.

Herb. STE: 222, old rotting wood, Durban; 223, Rhodesia; 224, old log, Durban; 1044, on wild *Ficus* sp., Kyrassa, E. Africa, July 1922; 1485, op droe hout, Houtbos, Transvaal, Julie 1924; 2414, in thick forset, Umtali, Rhodesia, No. 1926.

Discussion

Although the cultural characters of *Hexagona tenius* have not been described before, it is evident that, with its cultures which produce extra-cellular oxidase enzymes, and form fibre hyphae, cuticular cells and clamp connections on its thin-walled hyphae, this species fits well into Group 51. Indeed, it resembles a number of other species also present in this group (Nobles, 1958 b, 1965) so that confusion

may arise when it is attempted to identify isolates from unknown decays; but when the absence of secondary spores in cultures, the presence of fibre hyphae and the possession of white, woolly to felty mat which becomes largely covered by a reddish-brown crust, are considered together with the geographical origin of the specimen, cultures of *Hexagona tenuis* may be recognized with a fair degree of certainty.

The carpophores of *Hexagona tenuis* were seen to consist of thin-walled, nodose-septate hyphae, aseptate, branched and unbranched fibre hyphae or binding hyphae. The cuticular cells present in some carpophores are modified terminal portions of thin-walled, nodose-septate hyphae in which the septa and clamp connections are often involved. Since hyphae with clamp connections are regarded as generative hyphae by Corner (1953) and Cunningham (1946, 1954) only three types of hyphae are present in carpophores of *Hexagona tenius* which thus have trimitic hyphal systems, sensu Corner (1953).

The cuticular cells, which are the structural elements of the dark, reddish-brown, crustose areas of some carpophores, were not always present in all carpophores. They were often absent from some carpophores of a collection in which crustose areas were present on others, an inconsistency also reported by Van der Bijl (1922 a). No satisfactory reason for this sporadic appearance can be given although it is possible that this may be influenced by the conditions under which the carpophores develop. Because of this sporadic presence, however, the value of cuticular cells as a useful diagnostic character in carpophores is reduced considerably.

From the above description it is evident that the structures formed in cultures of *Hexagona tenuis* are usually also present in the carpophores from which they were made. It is noteworthy that the branched fibre hyphae of the cultures did not resemble those of the carpophores but similar differences were also observed in other species. Also, the cuticular cells formed in cultures were larger, had thinner walls and appeared more regularly and extensively than in the carpophores, but were undoubtedly homologous structures. Their more extensive development in cultures can be ascribed only to the existence of more favourable conditions for their development.

The anatomical characters of *Hexagona tenuis* have not been described before and little is known about them in apparently closely related species. Lloyd (1910) mentioned context colour but no hyphal characters in his Synopsis of the genus *Hexagona* Fr. Van der Bijl (1922 a) stated that hyphae of *Hexagona tenuis* were 4μ in diameter. Overholts (1953) described hyphae of *Hexagona variegata*, a species which he considered to be closely related to *Hexagona tenuis*, as "pale brown in KOH, long and flexuous, simple or nearly so, mostly with partly thickened walls, with no cross-walls or clamps, 4 — 6μ in diameter." Pinto-Lopes (1952) reported that secondary hyphae of *Hexagona nitida* Mont., are hyaline, nodose-septate and the tertiary hyphae are brownish, thick-walled or solid and septate. Fidalgo & Fidalgo (1962) reported that carpophores of *Hexagona apiaria* Pers. ex Fr. and *Hexagona hirta* (Beauv. ex Fr.) Fr., have trimitic hyphal systems. The above descriptions of the hyphal characters of *Hexagona tenuis* thus generally agree with observations by other workers on related species.

The description also agrees with Fidalgo & Fidalgo's (1962) report of the hyphal characters and hyphal systems of *Hexagona apiaria* Pers. ex Fr., the type species of the genus according to some authors (Cooke, 1959); but considerable uncertainty exists about the identity of the type species of the genus *Hexagona* Fr. This problem was discussed by Donk (1960) who concluded that *Favolus hirtus* P. Beauv. should be regarded as the type species. Until this problem is solved

however, the affinities of *Hexagona tenuis* with the genus *Hexagona* Pollini per Fr. cannot be determined with any degree of certainty.

Imazeki (1943), however, transferred *Hexagona tenuis* to the genus *Daedaleopsis* Schroet. with the remark that "it has no affinity to *Hexagona apiaria* the type of the genus *Hexagona* sensu stricto. This species is unique but it is safe for the writer that it would be placed under *Daedaleopsis* at least, if we do not erect a new genus for the species. The species connects with the genus *Daedaleopsis* through *D. conchifer* or *D. corrugata*." This is contradicted by the descriptions given here and the report by Fidalgo & Fidalgo (1962) who described the trimitic hyphal system in carpophores of *Hexagona apiaria*. In comparison with *Daedalea confragosa* L. ex Fr., the type species of *Daedaleopsis* Schroet., *Hexagona tenuis* differs from it mainly by the presence of binding hyphae throughout the context tissues of its thin carpophores, its large, cylindrical basidiospores and the large regular, shallow pores of its carpophores. These differences are of a similar nature to those between *Trametes suaveolens* and *Lenzites betulina* and because these are considered to be distinct genera, it appears best, at this stage, to regard *Daedalea confragosa* and *Hexagona* tenuis as species of separate genera although the two species are similar in many respects.

Comparison of *Hexagona tenuis*, with *Trametes corrugata*, presumably Imazeki's (1943) "*D. corrugata*," which is also included and described above in this group, shows the latter to have construction of the carpophores and binding hyphae which are unlike those of the fruit-bodies of *Daedalea confragosa* and *Hexagona tenuis*. It thus seems to be extremely unlikely that *Hexagona tenuis* can be related to *Daedalea confragosa* through *Trametes corrugata*.

More information, however, is required on the hyphal and anatomical characters of more species of the genera *Daedaleopsis* Schroet. as well as *Hexagona* Fr. before a satisfactory conclusion can be reached about the nature of their relationships. The solution of the problem of the type species of the genus *Hexagona* Fr. will be an important step in the determination of this relationship.

Note added in proof.

In later works K. Fidalgo advanced reasons for accepting the designation by Clements and Shear of *Hexagona crinigera* Fr. as lectotype of the genus *Hexagona* (Taxon 1968: 37-43) and excluded *Hexagona tenuis* Hooker ex Fries from this genus (Mem. N.Y. Bot. Gard. 1968: 100).

Trametes acupunctata *Berkeley*, Jour. Lin. Soc. 13, 164, 1873;

Coltricia acupunctata (Berk.) G. H. Cunningham, Proc. Linn. Soc. N.S.W. 75, 216, 1950.

Cultural characters

Growth is moderately rapid, the colonies reaching radii of about 115 mm in one week and covering the plates in 3 — 4 weeks. The advancing zone is even or slightly bayed, mat appressed for short distance, then raised, becoming thin, cottony and gradually passing into a thin, felty zone, or, bordering abruptly on a clear zone of submerged mycelium around the inoculum. After 2 — 3 weeks the mat becomes zonate with increasingly woolly texture towards the inoculum, with crustose areas of "verona brown," "natal brown" or "bister" developing over the clear areas and along the side of the plate. With increasing age the mycelial mat thickens and the dark-coloured, crustose areas increase in size until at six weeks the mat consists of thin, downy, white mycelium over the youngest parts,

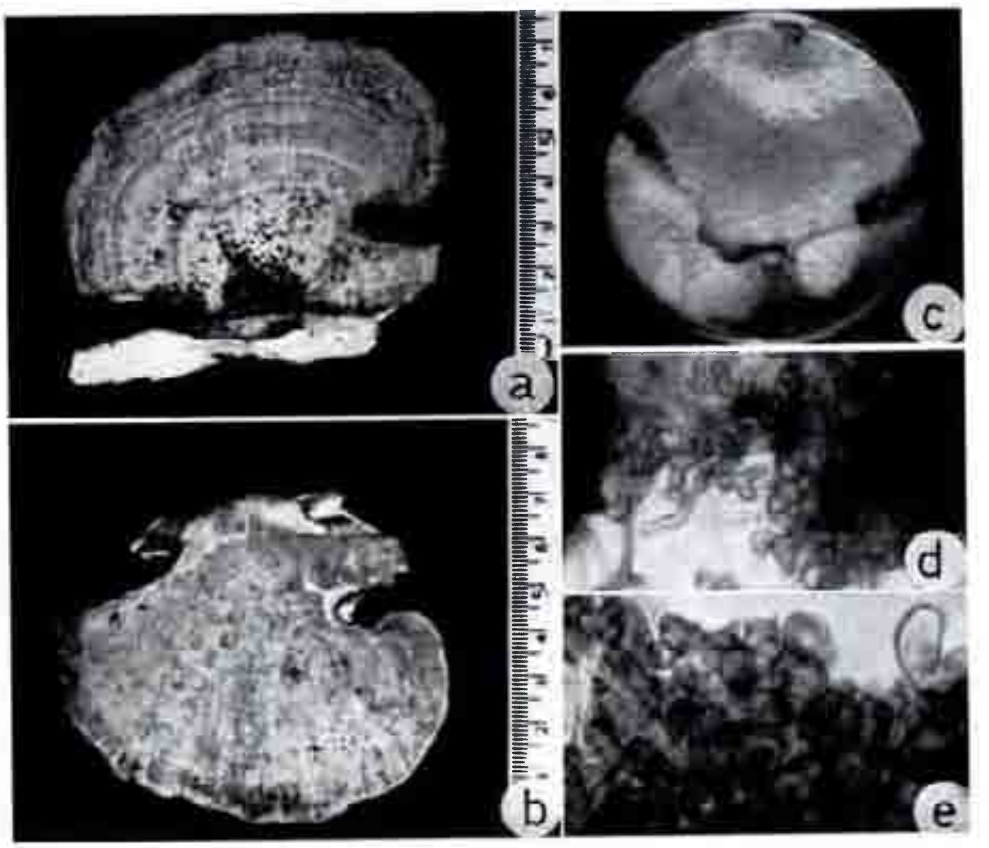

FIG. 45. — **Trametes acupunctata.** (a) Upper surface and (b) lower surface of carpophore of PRE 42440; (c) culture of PRE 42440 at six weeks; (d) cuticular cells from culture. × 100; (e) hyphae with partly thickened walls and irregular projections from dark-brown, crustose areas on upper surface of carpophore, squash mount in KOH, × 500.

often bordering abruptly on clear areas of submerged mycelium over which crustose areas of "Prout's brown," "cinnamon brown," "Verona brown" or "Natal brown" are forming, or, passing over successive zones of increasingly woolly to felty mycelium mostly fairly smooth or becoming pebbly towards the inoculum, white or "pale ochraceous buff" or "pinkish buff" in the older parts and bordering abruptly on the irregular, sunken "hazel," "ochraceous tawny," "cinnamon brown," "sayal brown," "Natal brown" or "Prout's brown," crustose areas which may cover up to half the area of the mat. The reverse bleaches at first, then darkens to deep, brown colours in which sharp, darker lines indicate the limits of the crustose areas. No odour or faint, mushroomy odour is given off. Cultures give a weak positive reaction when tested for extra-cellular oxidase enzymes with gum guaiacum solution (Nobles, 1958 a). On gallic acid and tannic acid media no diffusion zones are formed and no growth or a trace of growth occurs.

Advancing mycelium: hyphae hyaline, simple or branching, nodose-septate, thin-walled and staining deeply in phloxine 2.5 — 4.5u in diameter (Fig. 46 a).

Aerial mycelium: (a) hyphae as in the advancing zone; (b) fibre hyphae hyaline with thick, refractive walls and prominent, aseptate lumina, widening towards the thin-walled ends, unbranched, or branching occasionally, 3.0 — 5.0μ in diameter (Fig. 46 b); (c) narrow hyphae repeatedly branched, the branches tapering, walls hyaline partly thickened, the lumina prominent and aseptate, 0.5 — 1.2μ in diameter (Fig. 46 c); (d) nodose-septate hyphae with numerous short, stout branches or projections, thick, brown walls and narrow or partly occluded lumina, or, blown out into thin-walled processes or cuticular cells, 3.0 — 20μ in diameter (Fig. 45d, 46d).

Submerged mycelium: hyphae as in the advancing zone.

Carpophore characters

Carpophore annual, lignicolous, sessile, dimidiate, occasionally imbricate, often slightly concave, coriaceous, firm, rigid, almost woody, 3.5 — 20 x 2.0 — 9.0 x 0.2 — 2.0 cm; surface glabrous with fine radiating grooves and ridges traversed by concentric grooves, ridges, and tubercles, fawn to olive brown, often with patches of soft, dark cream-coloured or pale buff mycelium over the surface, or, dark reddish-brown crustose areas over the older parts; margin undulate and sinuose, concolourous with upper surface; pore surface dark olive-brown, poroid; pores rounded to somewhat daedaloid, 2 — 4 mm; dissepiments even, thin, tubes short, .02 — 0.5 mm deep becoming olivaceous brown inside; context olive-brown, fibrous, zonate, darkening in KOH, 0.1 — 12.0 mm thick.

Hyphal characters. Carpophores consist of: (i) hyaline, branching, nodose-septate, thin-walled hyphae with deeply staining contents, 2.0 — 3.0μ in diameter (Fig. 46 e); (ii) fibre hyphae long, unbranched, straight or somewhat tortuous, yellowish-brown, walls thickened, lumina narrow widening towards the thinner-walled ends, aseptate, often with staining contents, 2.0 — 5.0μ in diameter and arising from thin-walled, nodose-septate hyphae (Fig. 46 f); (iii) dark, yellow-brown, thick-walled hyphae, 3.0 — 4.0μ in diameter with short, thick, lateral projections or inflated portions up to 10μ in diameter (Fig 45 e).

Hymenium: basidia hyaline, long clavate, 16.0 — 22.0 x 6.0μ bearing four straight sterigmata, 3.0μ long (Fig. 46 g); basidiospores hyaline, long ellipsoidal to cylindrical, smooth, thin-walled, 5.0 — 8.0 x 2.5 — 3.5μ (Fig. 46 h).

Construction. At the margin, the carpophore consists of long, unbranched fibre hyphae, more or less straight, with the walls thickened and lumina prominent, aseptate, more or less parallel to one another and loosely intertwined. Intertwined with them are the narrow, branching, thin-walled, nodose-septate hyphae with deeply staining contents, from which they arise. In the upper context, behind the margin, fibre hyphae with much thickened walls and narrow, aseptate lumina, which constitute the bulk of the tissues, lie more or less parallel to one another and slightly intertwined, bending upward towards the upper surface where their ends are closely packed at a common level and become agglutinated by a thin layer of transparent lacquer-like material into a glabrous, cuticular surface. Narrow, branching, thin-walled, nodose-septate hyphae are intertwined with the fibre hyphae in the upper context and below the surface cuticle. On some specimens dark-brown, irregular, crustose areas may be present on the older parts of the upper surface. These consist of dark, yellow-brown hyphae with walls partly thickened or solid and with short, irregular, lateral projections and small, irregular swellings all agglutinated by brown, resin-like material into a hard, brittle mass forming a layer up to 50μ thick in which individual elements are distinguished with difficulty (Fig. 45 e). The lower context is similar to the upper but in the trama of the

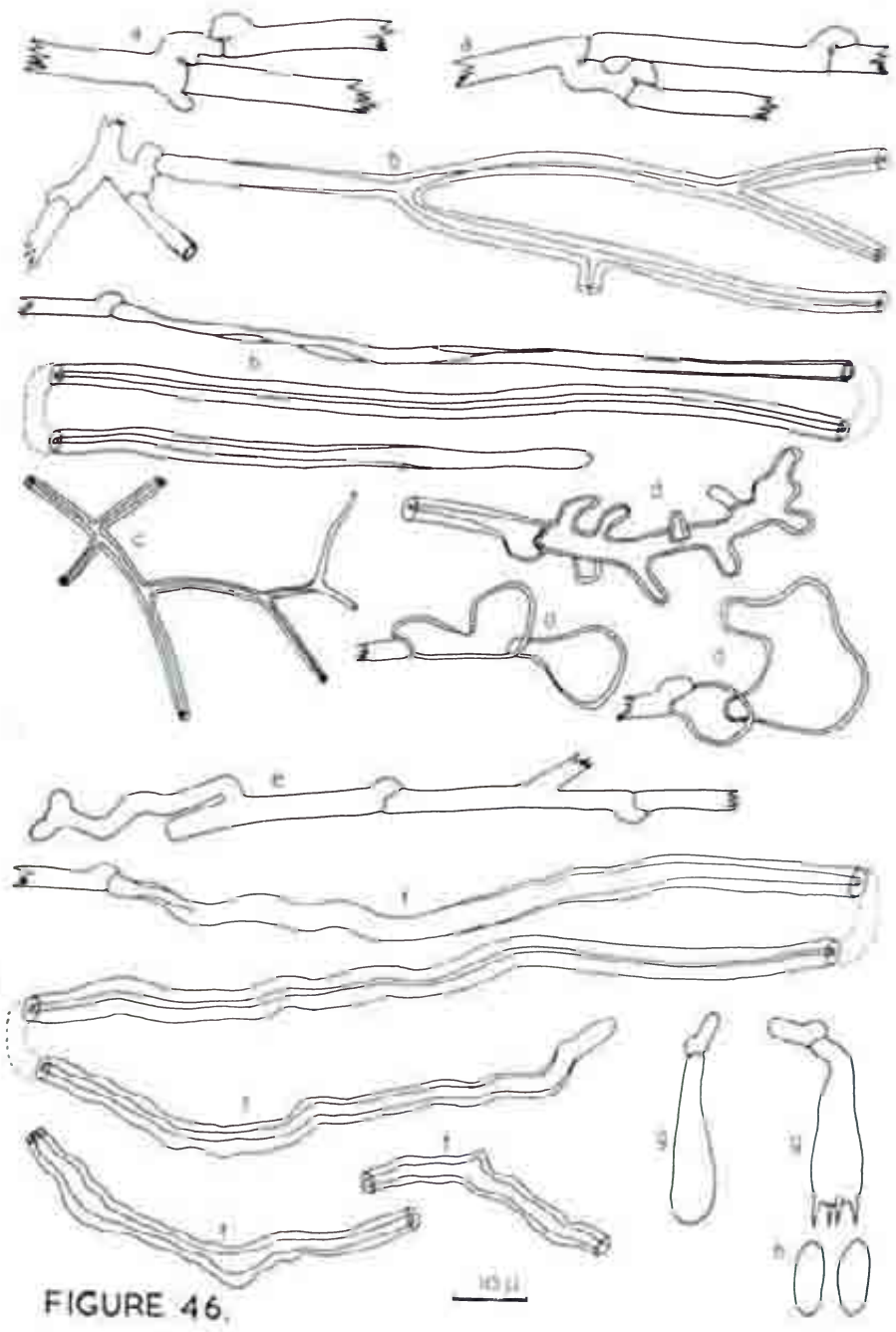

FIG. 46.— **Trametes acupunctata.** a - d. Structures from cultures: (a) thin-walled, nodose-septate hyphae from advancing zone; (b) fibre hyphae; (c) narrow, repeatedly branched hyphae; (d) nodose-septate hyphae with irregular projections and cuticular cells.
e - h. Structures from carpophores: (e) thin-walled, nodose-septate hyphae; (f) fibre hyphae; (g) basidia; (h) basidiospores.

tubes the fibre hyphae are narrower, more flexuous and with thinner walls and wider lumina than in the context. These hyphae become tightly interwoven to form a dense homogeneous tissue distinct from the context tissues. In the trama the thin-walled, nodose-septate hyphae become very numerous, narrow and branch frequently, the branches interwoven with and ramifying among the fibre hyphae, finally emerging at the hymenial surfaces where the clavate basidia are borne on short, terminal branches of these nodose-septate hyphae.

Decay and hosts

This fungus is fairly common on dead hardwood logs on which it causes a pale brown rot slightly lighter in colour than the wood.

Specimens examined

Herb. PRE: 11283, on *Acacia mollissima* stump, Cramond, Natal, April 1911; 13938, on *Acacia mollissima*, stump, Cramond, Natal, April 1911; 15546, on *Acacia mollissima* stump, New Germany, Natal, April 1917; 15591, on dead *Vepris lanceolatis*, Buxton, C.P., Aug. 1916; 27554, on dead wood, Table Mountain, Natal, Oct. 1929; 30821, on indigenous wood, Port St. Johns, C.P., Aug. 1937; 31555, on dead wood, Branders Main Forest, Natal, Aug. 1915; 31573, on dead wood, Branders Main Forest, Natal, Aug. 1915; 31587, on dead wood, Branders Main Forest, Natal, Aug. 1915; 31663, on dead wood, Ngoye, Natal, May 1916; 31733, on dead wood, Ngoye, Natal, May 1916; 31754, on dead wood, Durban, Natal, March 1917; 33208, on dead wood, Rustenburg, Tvl., May 1939; 34368, on dead wood, Hluhluwe, Natal, Oct. 1935; 42034, on dead wood, Knysna, C.P., 1959; *42171, decayed hardwood log, F. C. Erasmus Nature Res., Tvl., Feb. 1961; 42253, on dead log, Sabie, Tvl., Apr. 1962; *42440, decayed hardwood log, near Bushbuckridge, Tvl., Feb. 1961.
Herb. STE: 158, on dead logs, Bluff, Durban; 200, on dead logs, Krantzkloof, Natal, Jan. 1921; 350, on dead logs, Krantzkloof, Natal, Jan. 1921.

Discussion

The presence of nodose-septate, thin-walled hyphae, fibre hyphae and cuticular cells in its cultures, partly qualify *Trametes acupunctata* for inclusion in Group 51; but the weakly positive reaction of its cultures when tested for extra-cellular oxidase is in striking contrast to the strong positive reactions of other species in this group. The negative oxidase reaction of this species on gallic acid and tannic acid media together with the fact that this species causes a brown rot suggests that its inclusion in the large number of species of which the cultures do not produce extra-cellular oxidase may be justified. In that case it would then constitute a new group beyond Group 25, in which cuticular cells, fibre hyphae and nodose-septate hyphae are formed in cultures which lack extra-cellular oxidase. A group with this combination of characters is not provided in Nobles' keys, (Nobles, 1958 b, 1965); but because of the weak positive reaction for extra-cellular oxidase when its cultures are tested with gum guaiac solution, *Trametes acupunctata* must be included in Group 51 with which it also agrees in hyphal characters.

In carpophores of *Trametes acupunctata*, only two types of hyphae are present, viz.: thin-walled, hyaline nodose-septate hyphae and yellow-brown, thick-walled, unbranched fibre hyphae. No branched fibre hyphae or binding hyphae were found in any carpophore and the somewhat rigid, woody and fibrous texture of the fruit-bodies is due to the presence of these tightly packed and intertwined fibre hyphae. This species thus have carpophores with dimitic hyphal systems sensu Corner, (1932 b, 1953) and Cunningham (1946, 1954). In this respect fruit-bodies of *Trametes acupunctata* differ in hyphal characters and construction from those of all other species of which these characters are known, in this group.

Also present in some of the carpophores are dark-brown, thick-walled hyphae with the terminal parts inflated or distended into irregular projections which constitute the dark-brown crustose areas. These structures appear to be the counterparts in the fruit-bodies of the cuticular cells in the cultures. They occur in the same relative position as similar structures in other species in this group and apparently arise from thin-walled, nodose-septate hyphae in the upper surface of the carpophores. They are agglutinated into a very hard and very brittle structure which could not be prepared satisfactorily for proper examination. In view of their character and position in the fruit-bodies however, it seems extremely likely that they are the ends of thin-walled, nodose-septate hyphae modified into cuticular cells an dhyphae with irregular projections.

From the descriptions it is clear that most of the structures formed in cultures are also present in the fruit-bodies from which they are made. Only the narrow, hyaline, branched hyphae which are present in the cultures, over the agar, could not be located in the carpophores. Similar hyphae had been noticed in cultures of other species too e.g. *Polyporus versicolor,* but were absent from their carpophores. The absence of these hyphae from the carpophores could be due to their formation inside the wood on which the carpophores are formed, or to the existence of conditions in cultures which allow their formation and the absence of these conditions in growing carpophores. It was not possible to investigate either alternative.

Cuticular cells formed in cultures with greater regularity than in the relevant carpophores. The structures were more readily recognizable and could be traced to their origins with ease in the cultures. It appears that conditions which favour their formation occur more frequently in cultures than in carpophores. Their presence in cultures may thus be useful as a diagnostic feature when cultures from unknown decays have to be identified but their sporadic appearence on carpophores in nature diminishes their value as a character of taxonomic importance.

The hyphal characters and construction of the carpophores of *Trametes acupunctata* differ strikingly from those of other species in this group of which these characters are known. Much branched fibre hyphae or binding hyphae (Corner, 1932 a) are absent from carpophores of *Trametes acupunctata* but are present in those of *Daedalea confragosa, Hexagona tenuis, Trametes corrugata,* and *Fomes fomentarius* (Teixeira, 1962 b). As the absence or presence of types of hyphae in carpophores is considered to be of importance at the generic level by a number of workers (Teixeira, 1962 b; Bondartzeva, 1961), *Trametes acupunctata* cannot be considered to be congeneric with any of these species.

Although originally placed in the genus *Trametes* Fr. by Berkeley (loc. cit.) it is clear that *Trametes acupunctata* has little in common with *Trametes suaveolens,* (L. ex Fr.) Fr. the type of this genus. It differs from *Trametes suaveolens* by having a brown context of simple construction, by the presence of cuticular cells in its cultures and carpophores, by causing a brown rot, and in the weak production or absence of extra-cellular oxidase enzymes in its cultures.

Cunningham (1950 b) transferred *Trametes acupunctata* to the genus *Coltricia* S. F. Gray which he characterized as having pileate fruit-bodies with a "monomitic hyphal system, hyphae long, ribbon-like, branched and septate, without clamp connections." Since this description does not fit the hyphal characters and construction of the fruit-bodies of *Trametes acupunctata* as described above, this species cannot be assigned to the genus *Coltricia.*

Trametes acupunctata thus differs in respect of cultural characters, carpophore characters and type of decay from the type species of genera to which it had

been assigned. It is not well placed in Group 51 either, because of the inconsistent oxidase reactions of its cultures while its carpophores differ in construction from those of other species in this group of which these characters are known. The combination of characters found in its cultures and carpophores are not known to exist in any other species at present, largely because of the limited knowledge of hyphal characters and fruit-body construction of poroid Hymenomycetes. Its taxonomic position is thus uncertain but a more suitable position cannot be suggested. Description of a new genus based on this species may thus be justified but because future studies may reveal a genus to which *Trametes acupunctata* may be satisfactorily assigned it is proposed not to transfer it to a new genus which may well become an addition to an already long list of generic synonyms.

Resumé

From these descriptions it is evident that the four species of Group 51 included in this study possess the cultural characters which justify their inclusion in this group. With the exception of *Trametes acupunctata*, they share a number of correlated characters, viz.: the production of extra-cellular oxidase, association with white rots, the presence of nodose-septate hyphae, fibre hyphae and cuticular cells. It appears that these species share a common ancestry but show diversity in the elements of their carpophores. Its association with a brown rot, uncertain extra-cellular oxidase production in culture and absence of binding hyphae from its carpophores, suggest that the characters which *Trametes acupunctata* has in common with the other three species, may have developed as a result of convergent evolution.

5.9 Group 53

Cultures of species in this group have white mycelial mats covered by extensive, wrinkled, brown, pseudo-parenchymatous areas. Extra-cellular oxidase enzymes are produced. The thin-walled hyphae have simple clamps at the septa and may remain thin-walled or give rise to thick-walled, brown hyphae with interlocking projections. Thick-walled, aseptate fibre hyphae are also formed. Their basidiospores are large, cylindrical or ellipsoid-cylindrical and the interfertility for species of which this character is known, is the tetrapolar type. Carpophores of these species are alike in being stipitate.

Polyporus sacer *Afz. ex Fries*, Epicr., 436, 1836.

Cultural characters

Growth is moderately rapid the colony reaching a diameter of 15 mm after 1 week and covering the plate in 3 to 4 weeks. Advancing zone even, hyphae raised almost to the limit of growth Mat at newest growth white, cottony to woolly, thin, towards the inoculum at first appressed and becoming woolly-felty with faint, radiating grooves or woolly-felty streaks, then suddenly pale "cream color" with slightly uneven, lacunose surface and fine droplets of colourless liquid on it, around the inoculum. At three weeks the margin straightens as growth proceeds more rapidly adjacent to the sides of the dish. Mat becomes more appressed to sub-felty with pellicular areas developing at concentric grooves of previous week's growth and coalescing into pellicular areas which soon become

covered by raised, crustose areas. Mat remains white but crustose areas are at first "cinnamon buff" and bordering abruptly on the white mat, later darkening to "cinnamon." Or, zones of clear, submerged mycelium develop after 2-3 weeks over which crustose areas of "ochraceous tawny," raised mycelium, smooth at first but later wrinkled, and becoming "clay colour," soon form. At six weeks the mat is usually white or pale "cream color," downy or pellicular in the younger parts with smooth or somewhat wrinkled crustose areas in a wide zone around the inoculum and with scattered, raised, crustose patches over the older parts of the mat. Colours on these range from "ochraceous tawny" to "clay colour" or "light pinkish cinnamon" to "cinnamon." The reverse is bleached after 3 weeks but dark brownish colours gradually develop in the agar. A pleasant, fragrant odour is given off till about the fourth week but then gradually diminishes. A weak positive reaction is obtained when the culture is tested for extra-cellular oxidase enzymes. No growth takes place on gallic acid and tannic acid media but small diffusion zones are formed on both media within one week.

Advancing mycelium: hyphae hyaline, thin-walled branched or unbranched with simple clamp connections at the septa, 2.0 — 4.5μ in diameter (Fig. 48 a).

Aerial mycelium: (a) hyphae as in the advancing zone; (b) fibre hyphae unbranched or branching, long, more or less straight, hyaline, the walls thickened, lumina narrow or occluded for most of their length, widening at the extremities, aseptate, 1.0 — 3.0μ in diameter (Fig. 48 b); (c) narrow fibre hyphae, hyaline with numerous short tapering branches and mostly solid, 0.5 — 1.0μ in diameter (Fig. 48 c); (d) nodose-septate hyphae with interlocking projections and short, thick, lateral branches, sub-hyaline to pale yellowish brown, the walls thickened and lumina narrow or occluded, 3.0 — 8.0μ in diameter with projections up to 10u long (Fig. 48 d).

Submerged mycelium: hyphae as in the advancing zone but more tortuous and wider, 2.5 — 6.0μ in diameter.

Carpophore characters

Carpophore annual, terrestrial, solitary rarely grouped; pileus orbicular, tough coriaceous to woody, velutinate to glabrous, rugulose, slightly furrowed, concentrically sulcate or zoned, "tawny olive," "snuff brown" to "Verona brown," "Prout's brown" or "bister" and "dark olive" in concentric zones, centrally stipitate, 6.0 — 10.0 cm in diameter, 0.15 — 0.3 cm thick; margin acute, thin, entire, white or concolorous; pore surface white drying to "pale ochraceous buff", "warm buff" or "clay color," poroid; pores daedaloid, rounded or angular, 2/mm; dissepiments thin, even in younger parts but in older parts, radially raised; tubes concolorous up to 2.5 mm deep; context tough, fibrous, white to pale "cream color," 0.75 — 1.5 mm thick; stipe erect, tapering apically mostly slender, smooth, velutinate, "tilleul buff" to "wood brown" 0.3 — 1.4 x 4.5 — 15 cm, subtubular to tubular, context white, arising from basal sclerotium; sclerotium ovoid to irregular, rugose to rimose, horny, hard, concolorous with stipe, 1.5 — 5.0 x 2.5 — 7.5 cm; context white or "pale tilleul buff," firm, woody.

Hyphal characters. Carpophores consist of: (i) hyaline, thin-walled, nodose-septate hyphae, branching at the septa, 1.8 — 3.5μ in diameter (Fig. 48 e); (ii) fibre hyphae long unbranched or with an occasional long branch, more or less straight or tortuous, widest near middle, the walls hyaline, thick, refractive, lumina narrow or occluded, aseptate, 1.5 — 6.0μ in diameter (Fig. 48 f); (iii) fibre hyphae with many lateral branches, walls hyaline, thickened, lumina narrow or occluded, aseptate, 1.5 — 3.5μ in diameter (Fig. 48 g); (iv) nodose-septate hyphae with

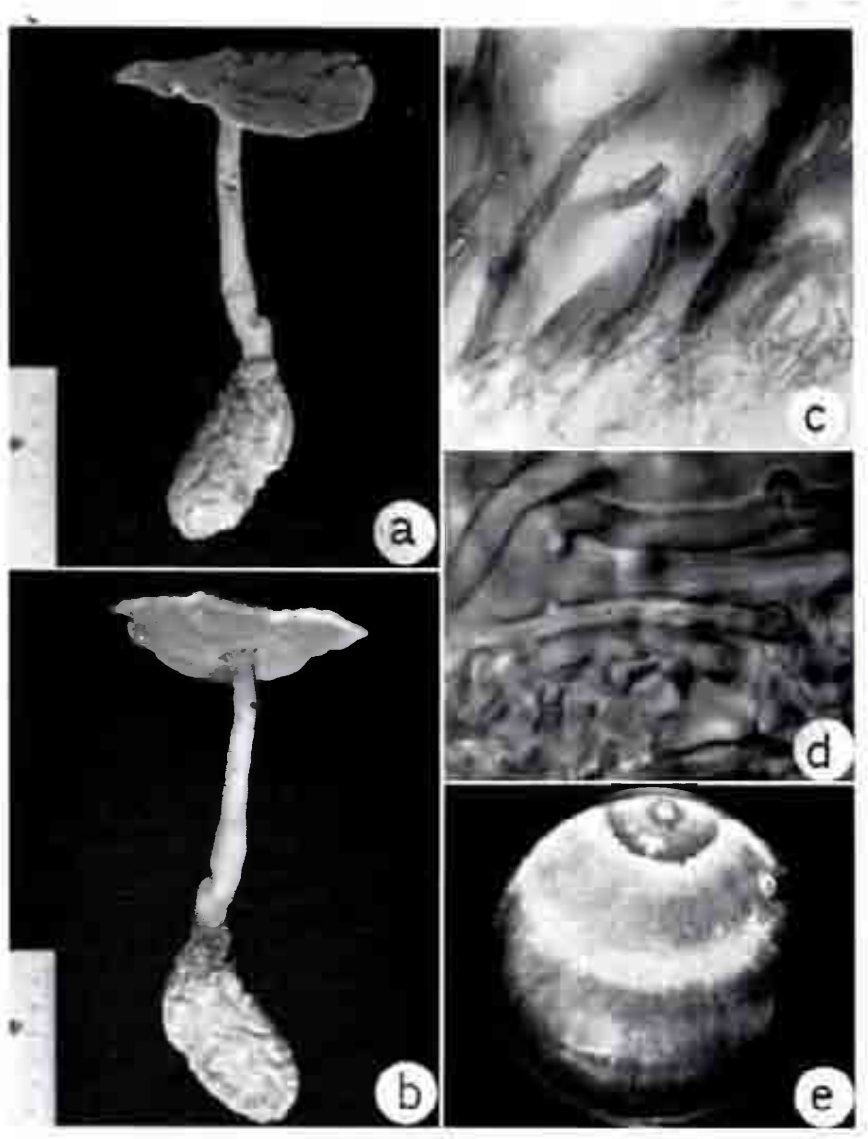

FIG. 47.— **Polyporus sacer.** (a) Carpophore of PRE 31545 showing upper suface and (b) hymenial surface; (c) dark-coloured, thick-walled, nodose-septate hyphae forming hairs on upper surface of carpophore. × 500; (d) cuticular cells and "hairs" from upper surface. × 1000; (e) culture of PRE 42163 at six weeks.

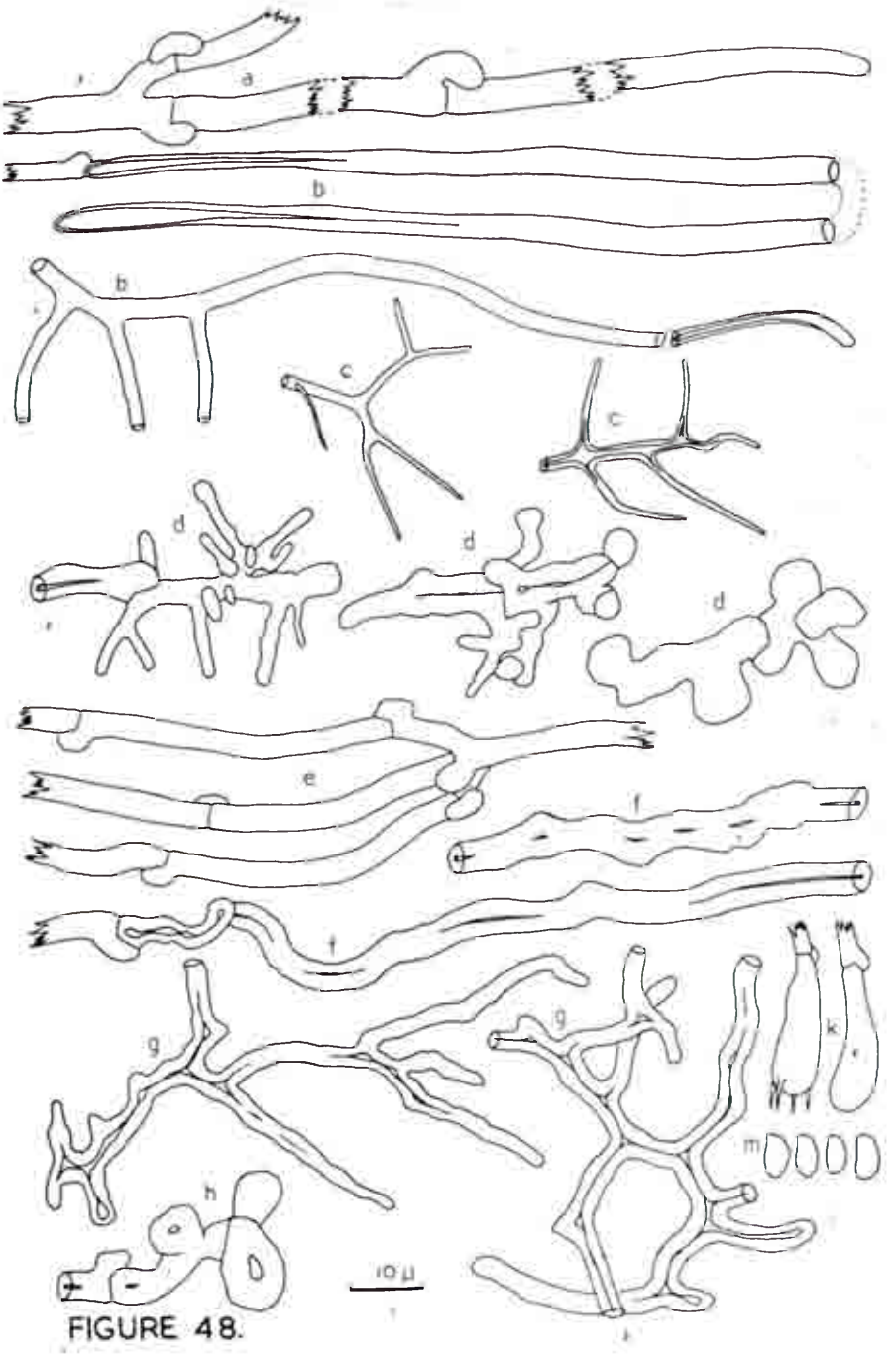

FIGURE 48.

FIG. 48.—**Polyporus sacer.** a - d. Structures from cultures: (a) thin-walled, nodose-septate hyphae from advancing zone; (b) fibre hyphae; (c) narrow hyphae with numerous short, tapering branches; (d) nodose-septate hyphae with interlocking projections.
e - m. Structures from carpophores: (e) thin-walled, nodose-septate hyphae; (f) unbranched fibre hyphae; (g) fibre hyphae with numerous short, lateral branches; (k) basidia; (m) basidiospores.

thick brown walls and narrow or partly occluded lumina and solid or sub-solid clamp connections, 4.5 — 10.0μ in diameter (Fig. 47 c); (v) nodose-septate hyphae with thick hyaline walls distended into interlocking projections, 4.0 — 8.5μ in diameter (Fig. 47 c, 48 h).

Hymenium: basidia hyaline long clavate 14.0 — 18.0 x 5.0 — 17.0μ bearing four sterigmata 2.0 — 3.0μ long (Fig. 48 k); basidiospores hyaline, ovoid to ellipsoid, flattened on one side, smooth, thin-walled, 5.0 — 7.0 x 3.0 — 4.5μ (Fig. 48 m); hyphal pegs numerous, white, long-conical up to 200μ long.

Construction: At the margin the pileus consists of fibre hyphae, hyaline and straight or flexuous, unbranched and with narrow or occluded lumina up to 6.0μ in diameter, intertwined with one another and interwoven with numerous hyaline, branching, thin-walled, nodose-septate hyphae 1.8 — 3.5μ in diameter, from which they arise. At the upper part of the margin, numerous nodose-septate hyphae are present, their walls distended into irregular, inter-locking projections which thicken and turn brownish simultaneously. A very short distance from the margin these hyphae are agglutinated into a hard, brittle, brown cuticle 30 — 50μ thick over the upper surface. The uppermost layers of this cuticle consists of nodose-septate hyphae with thick, brown walls lying parallel to the direction of growth of the pileus and agglutinated by a brownish, lacquer-like substance onto the surface to form glabrous zones (Fig. 47 c). Or, free, nodose-septate hyphae with thick, brown walls project upward from the cuticle to form the velutinate zones (Fig. 47 c). Below the cuticle and behind the margin the context consists mainly of intertwining hyaline, unbranched, straight or flexuous, fibre hyphae, solid or sub-solid with a thin layer of numerous, thin-walled, nodose-septate hyphae below the cuticle, freely intertwined with the ends of the fibre hyphae, some of which are agglutinated into the cuticle. Interwoven with the long fibre hyphae are fibre hyphae with short, sub-solid or solid, lateral branches which bind them together into the tough tissues of the pileus.

In the lower context and trama of the tubes the tissues are more dense and consist of long, fibre hyphae, more tortuous, generally narrower and more frequently branched than in the upper context, the branches long and tapering, and tightly interwoven with fibre hyphae with many short branches binding them together into a dense, even, tough tissue. Also interwoven with these hyphae are thin-walled, nodose-septate hyphae with deeply staining contents, branching repeatedly and becoming increasingly numerous towards the hymenial surfaces where they bear the basidia on numerous short branches. From the tissues of the dissepiments, hyphal pegs, each consisting of a bundle of parallel ends of fibre hyphae, project into the pore space for up to 200μ.

The tubular stipe consists mainly of long, unbranched, sub-solid to solid, hyaline fibre hyphae 3.0 — 6.0μ in diameter at the widest middle part, intertwined and parallel to the length of the stipe. Interwoven with them are narrower, hyaline fibre hyphae with numerous short tortuous branches with thick walls and prominent lumina, 1.0 — 1.5μ in diameter. Thin-walled, nodose-septate hyphae are interwoven with the fibre hyphae and become more numerous towards the outer and inner surfaces where they give rise to plectenchymatous layers of thick-walled cells 40 — 90μ in thickness on the inner and outer surfaces.

The sclerotium consists mainly of interwoven branched and unbranched hyaline fibre hyphae apparently without directional orientation and thin-walled nodose-septate hyphae in a homogeneous context and covered by a hard rind 90 — 180μ thick, apparently consisting of thick-walled, nodose-septate hyphae.

Decay and hosts

This fungus does not cause decay of timber but grows in humus rich soil in damp sub-tropical areas.

Specimens examined

Herb. PRE: 9112, Elandshoek, Tvl., Aug. 1915; 11519, Kentani Distr., C.P., May 1918; 31545; 36590, in soil in forest, Njala, Sierra Leone, Feb. 1947; *42163, on ground, F. C. Erasmus Nature Reserve, Tvl., Feb. 1961

Discussion

The cultural characters of *Polyporus sacer* have not been described before but there can be no doubt that the presence of thin-walled, nodose-septate hyphae, fibre hyphae and hyphae with interlocking projections in cultures which produce extra-cellular oxidase enzymes, places this species in Group 53. This group includes 11 other species of stipitate polypores, all of which display very similar characters in culture (Nobles, 1958 b). In cultures of these species "the dark-brown, wrinkled, pseudoparenchymatous areas contrast sharply with the white cottony or woolly parts of the mats" (Nobles, 1958 b). Cultures of *Polyporus sacer* are lighter in colour over the crustose areas tending towards brownish yellow and the aerial mycelium is sub-felty rather than woolly. These characters serve to distinguish cultures of *Polyporus sacer* from those of other species in this group.

The carpophores of *Polyporus sacer* were shown to consist of five types of hyphae. Of these, the two types of hyphae with thickened walls have clamps at their septa and must be regarded as generative hyphae, sensu Corner (1932 a) and Cunningham (1946) and of the same type as the thin-walled nodose-septate hyphae. The unbranched and branched hyphae correspond to the skeletal and binding hyphae respectively so that the fruit-body of *Polyporus sacer* has a trimitic hyphal system sensu Corner (1932 b, 1953).

In this species it is again evident that the structures formed in its cultures are also present in the fruit-bodies from which they were made. There are no differences between the thin-walled, nodose-septate hyphae and fibre hyphae from the cultures and fruit-bodies except that fibre hyphae from cultures are somewhat less flexuous than those from the fruit-bodies; but the nodose-septate hyphae with thickened walls which form the "hairs" of the upper surface of the fruit-bodies, were not found in the cultures. In the fruit-bodies, these hyphae are closely associated with the nodose-septate hyphae with inter-locking projections. Both types arise from thin-walled, nodose-septate hyphae; but nodose-septate hyphae with interlocking projections did develop in the cultures. It thus appears that these hyphae may be variations of the same modification of nodose-septate hyphae but which develop under different conditions of growth. Conditions favourable for their development probably did not exist in the cultures.

The hyphal characters of *Polyporus sacer* have not been described before but Furtado (1965 a) stated that "the hyphal system and general habit of the species suggest that *Polyporus sacer* may belong to the genus *Amauroderma*, but basidiospores were not seen." Furtado (1965 a) further stated that "the arboriform skeletal hyphae (Teixeira 1956, 1962 a, b) are commonly found in the ganodermoid polypores and it seems probable that they are characteristic of the sub-family *Ganodermoideae*." He included the two genera *Ganoderma* Karsten and *Amauroderma* Murrill in this sub-family and distinguished between them on the basis of the shape of the thick-walled echinulate spores; but the specimens of *Polyporus sacer* examined for this study have thin-walled, short-cylindrical spores and arboriform hyphae were not found in their fruit-bodies. This species thus does not have the characters of the genus *Amauroderma* Murr. as described by Furtado (1965 a) and can therefore not be included in that genus.

Of the eleven species of stipitate polypores included by Nobles (1958 b) in her Group 53, the hyphal characters of only one species, *Polyporus squamosus* Fr., is known in detail from the description by Corner (1953). In this description, Corner stated that the young fruit-body of *Polyporus squamosus* has a monomitic hyphal system consisting of clamped, generative hyphae only. After a certain stage of maturity is reached, the generative hyphae develop 2 — 4 lateral, branching processes, which Corner designated as "binding hyphae." By growing laterally between the generative hyphae and developing thickened walls, these hyphae bind the generative hyphae into the tough, dry tissues of the mature fruit-body which has a dimitic hyphal system consisting of generative and binding hyphae. The hyphal characters and construction of the fruit-body of *Polyporus squamosus* are thus completely different from those of *Polyporus sacer* as described here.

The pileus of another stipitate species, *Polyporus arcularius*, was found to consist of nodose-septate hyphae with short inflated cells from which fibre-like, thick-walled processes arise and generally resemble those of the mature fruit-bodies of *Polyporus squamosus* as described by Corner (Dr. D. D. McLain, personal communication and demonstration).

Overholts (1953), in his brief descriptions of the hyphae of the fruit-bodies of the stipitate polypores included by Nobles (1958 b) in Group 53, mentioned the attenuated, whip-like ends of the branches of the hyphae in the pilei of *Polyporus arcularius, Polyporus brumalis, Polyporus squamosus* and *Polyporus tuberaster*. In the fruit-bodies of *Polyporus elegans, Polyporus melanopus* and *Polyporus varius* the hyphae are thick-walled and much branched, while those of *Polyporus fagicola* and *Polyporus radicatus* are thin-walled and tend to collapse. The hyphal characters of these stipitate species thus also differ among species of this group and all of them differ from the hyphal characters of *Polyporus sacer*. This species can therefore not be regarded as congeneric with any of the species included by Nobles (1958 b) in Group 53 of which two had been designated as generic types. No other species of stipitate polypore of which the hyphal characters, construction and general morphology of the fruit-bodies resemble those of *Polyporus sacer*, is known at present.

Donk (1960) showed that Fries indicated some affinity between *Polyporus sacer* and *Polyporus versicolor* by placing each of these species as the first species in two of his nine stirpes of his genus *Polystictus*. Donk (1962) stated later that Fries had conceived the taxon already before he decided to treat it as the separate genus *Polystictus*, and that Fries' remarks tend to show that "the genus *Polystictus* started with the conception of a stirpes typified by *Polyporus perennis* L. per Fr., in the first place, and a stirpes typified by *P. sacer* Afz. ex Fr." This close affinity with *Polyporus perennis* is not evident when the hyphal characters of these two species are compared. Cunningham (1948 e) described the hyphal characters of *Polyporus perennis* as "hyphal system monomitic, hyphae long, ribbon-like, branched and septate without clamp connections." This observation was confirmed by Overholts (1953). Because *Polyporus sacer* has a trimitic hyphal system in Corner's (1932 a, b) and Cunningham's (1946, 1954) terminology, the two species cannot be regarded as closely related at all.

The affinity between *Polyporus versicolor* and *Polyporus sacer* first indicated by Fries (in Donk, 1960) received additional support when Nobles (1965) included *Polyporus versicolor* together with three species of stipitate polypores as well as *Daedalea confragosa* and *Fomes scutellatus* in her Key Code 2.3.8.11 on the basis of their cultural characters. This group includes species of which the cultures produce extra-cellular oxidase and the thin-walled, nodose-septate hyphae are differentiated to form fibre hyphae and hyphae with interlocking projections.

Because cultures of *Polyporus sacer* agree with these characters, this species may also be included in Key Code 2.3.8.11 thus revealing similarities with cultures of *Polyporus versicolor*. The similarities in hyphal characters and construction of the pilei of *Polyporus sacer* and *Polyporus versicolor* are even more striking and suggest a much closer relationship between them than between *Polyporus sacer* and the other species of stipitate polypores discussed above. An important difference between them, however, exists in the nature of the construction of the upper surface of their pilei. While the upper surface of both species may be described by the term "trichoderm" (Lohwag, 1940; Furtado, 1965 a) the "hairs" of the trichoderm of *Polyporus versicolor* consist of the ends of fibre hyphae (skeletal hyphae) which project from a dense layer of agglutinated hyphae (Fig. 47 c), whilst the "hairs" of the trichoderm of *Polyporus sacer* are thick-walled, nodose-septate hyphae which arise from the upper parts of a layer of agglutinated, thick-walled, nodose-septate hyphae and fibre hyphae. Furthermore, the binding hyphae in the pileus of *Polyporus sacer* have fairly long flexuous, tapering branches while those of *Polyporus versicolor* has short, tortuous branches. These differences in the nature of the trichoderm and the character of the binding hyphae together with the presence of an orbicular pileus borne on a well differentiated stipe arising from a hypogeous sclerotium, must separate *Polyporus sacer* from *Polyporus versicolor* at the generic level.

Differences between *Polyporus sacer* and *Daedalea confragosa* are of a similar nature to those between *Polyporus sacer* and *Polyporus versicolor*. The cultural characters and fruit-bodies of *Fomes scutellatus* could not be included in the present study.

The fruit-bodies of *Polyporus sacer* possess a combination of hyphal and morphological characters that have not been found in any other species till now. Its relationships and systematic position cannot be determined at present but future studies of more species of poroid Hymenomycetes may confirm Fries' idea of a taxon typified by *Polyporus sacer*.

6. DISCUSSION

The object of this study was to determine to what extent the structures formed in cultures of poroid Hymenomycetes are also present in their carpophores in order to determine whether their carpophores reveal the same relationships as their cultures. From the descriptions of cultural and carpophore characters of the species studied, it is evident that the structures formed in cultures are mostly present in the carpophores but that certain exceptions and discrepancies were observed. These concerned the different types of hyphae and hyphal modifications.

In all the species studied, nodose-septate hyphae were found to be present in both the cultures and carpophores of all specimens examined, but in some species the nodose-septate hyphae became thick-walled. In *Polyporus dichrous*, *Polyporus adustus* and *Polyporus subiculoides* these thick-walled, nodose-septate hyphae make up the bulk of the carpophore tissues although they are rarely found in the cultures. In other species, e.g. *Polyporus versicolor* and *Lenzites sepiaria*, thick-walled as well as thin-walled, nodose-septate hyphae were present in both the cultures and carpophores. In still other species, e.g. *Trametes cingulata* and *Polyporus occidentalis*, thick-walled, nodose-septate hyphae were never seen in the cultures or carpophores. It therefore appears that in some species the nodose-septate hyphae may be modified by thickening of their walls, under conditions

prevailing in the formation of fruit-bodies; but hyphae modified in this way were not present in all the species in which thin-walled, nodose-septate hyphae were present in both cultures and carpophores. It thus appears that the modification or differentiation of thin-walled, nodose-septate hyphae into thick-walled, nodose-septate hyphae or "sclerified generative hyphae" (Donk, 1964) can occur in certain species only. This character must therefore be recognized and these hyphae must be regarded as a distinct type of hypha. Their presence or absence in carpophores must therefore be taken into consideration in studies involving hyphal characters of fruit-bodies.

In the species studied in Group 25, another type of nodose-septate hypha of which the walls are irregularly thickened, were shown to be present in both the carpophores and cultures. These species were also shown to have other carpophore characters in common which would allow their inclusion in one genus. Nobles (1958 b) showed that a number of species, in which this type of hypha is present in their cultures, also have other hyphal and basidiospore characters in common which allow their inclusion in Group 25. These nodose-septate hyphae with irregularly thickened walls are present in certain species only so that it is clear that this character must be genetically constant. For these reasons, nodose-septate hyphae with irregularly thickened walls must be regarded as constituting a morphologically distinct type of hypha and should be recognized as such in studies involving hyphal characters of fruit-bodies. It is well-known that these hyphae are often found with difficulty in fruit-bodies of species in which they are present in cultures but they cannot be ignored for this reason. Careful search in parts where fibre hyphae are not numerous, will usually reveal their presence.

In those species in which fibre hyphae were present in cultures, fibre hyphae also occurred in their carpophores but differences in morphology of the fibre hyphae were noticed in some cases. In general, these differences were observed mainly in the extent of branching of the fibre hyphae and in their diameter. In *Daedalea confragosa* it was seen that the fibre hyphae in cultures were of one kind only, viz. narrow and branched with long branches while the fibre hyphae in the carpophores were either unbranched or had numerous short, twisted branches. In most species included in Group 45, with the exception of *Polyporus vinosus*, the fibre hyphae of the carpophores consist of unbranched skeletal hyphae and of binding hyphae with numerous, short, tortuous branches (sensu Corner, 1932 a, b); but the fibre hyphae of their cultures are mainly unbranched whilst some fibre hyphae have a number of fairly long branches, often fairly straight. In other species, mainly those of Group 25, where short-branched binding hyphae were not present in the carpophores, the fibre hyphae of the cultures were also mostly unbranched or had an occasional long branch. It can be concluded, however, that the fibre hyphae of the carpophores of all the species included in this study, agree with those of the fibre hyphae of the carpophores.

In cultures of *Polyporus versicolor, Polyporus pubescens, Trametes acupunctata* and *Trametes corrugata* a network of very narrow, dichotomously branched hyphae were observed in very tough parts of the mycelial mat. These hyphae, which were less than 1.0μ in diameter, could not be traced to their origin and were just barely discernible under the oil immersion lens. Such hyphae had been reported by Nobles (1965) in cultures of *Polyporus versicolor* and *Polyporus pubescens* but their presence in carpophores had not been reported by other workers. In this study they have been found only in the tissues of carpophores of two collections of *Trametes corrugata* including the carpophores of the type specimen of *Earliella*. Since these hyphae are so narrow and inconspicuous, their nature could not be determined and because the tissues are torn apart with needles,

to dissect out the different types of hyphae, they are subject to destruction because of their dichotomous branching habit. Small pieces may easily be overlooked as debris which is often present in the mounts; but their presence in the two carpophores indicate that such hyphae may also be present in carpophores of species in which they are formed in culture. The very tough nature of those parts of the mat in which these hyphae are present, suggests that these hyphae may serve as binding hyphae in the tissues.

In the five species studied in Group 51 and Group 53, nodose-septate hyphae of which the terminal portions were differentiated into cuticular cells or irregular projections, were present in the cultures. The cuticular cells were usually well-developed, mostly with thin walls and present in large numbers. In the carpophores, however, these structures were either not easily seen or were absent. Of the large number of carpophores of *Daedalea confragosa* that were examined, cuticular cells could be found in two only and they were smaller than those of the cultures. In the cultures of *Hexagona tenuis* and *Trametes acupunctata* the cuticular cells were well-developed but in their carpophores the corresponding structures did not resemble cuticular cells. Instead they resembled the "hyphae with irregular thick-walled branches, nodules or protuberances" described by Nobles (1965) under Code Symbol 11. Similar hyphae were also present in the cultures of *Daedalea confragosa, Hexagona tenuis, Trametes acupunctata* and *Trametes corrugata* as well as in their carpophores where they were present as the only specialized cuticular structures. Therefore, it seems that "cuticular cells" and "hyphae with irregular thick-walled branches, nodules or protuberences" are different manifestations of the same hyphal modification which develop under different conditions of growth. These structures, which form dark-coloured patches over the older part of the upper surface of the carpophores, occurred sporadically on the carpophores. They were often absent from some carpophores but present on others in the same collection. Because they are formed more frequently and regularly in cultures than in carpophores, it appears that their formation is influenced by the conditions of growth of the relevant mycelia. Their more regular presence in cultures of various species is thus of greater value in the recognition of cultures than in the identification and classification of the carpophores of these species.

Fructifications which produce fertile basidia and basidiospores were formed by a number of species in cultures. In every case the basidia and basidiospores were identical in respect of dimensions and morphology to those of the carpophores found in nature. This confirms the statements by Teixeira (1962 b) and Kotlaba (1964) that the characters of the basidia and basidiospores are fixed and constant for each species and emphasizes the great taxonomic importance accorded to these structures by all workers.

An interesting aspect of the formation of fructifications in culture is the fact that basidia and spores may be borne on structures which bear no resemblance to the corresponding fruit-bodies formed in nature. Further, the fructifications formed in cultures were seen to develop in distinctly different ways. In *Daedalea* spp. the fertile areas consisted of irregular, low, anastomosing ridges which grew out from the areas of compact mycelium. In *Fomes cajanderi* the fruiting areas developed as gradually deepening tubes in areas of felty mycelia. In *Lenzites trabea* flat, antler-like processes which united laterally to form large tubes, grew out of the mat. In *Polyporus versicolor, Polyporus occidentalis, Trametes meyenii* and some other trametoid species in Group 45, thin, acicular spines developed from felty patches and gradually widened into flat processes which united laterally to form tubes. These different ways of formation of fertile spore-bearing tubes,

occurred in cultures which differed in cultural characters. These observations thus indicate that these different ways of formation of spore-bearing tubes may represent phylogenetic differences between the species concerned. This conclusion is supported by the fact that differences in hyphal and anatomical characters were shown to exist between the carpophores of the various species in which fructifications formed in cultures. It is further supported by the fact that differences in the method of pore formation are known to occur in carpophores of different species under natural conditions (Ames, 1913; Corner, 1953). Savile (1955), suggested that ontogenic studies may throw light on the origins of tubes of various types of Hymenomycetes; but careful observations on fruit-body formation in culture and in nature of a large number of species will have to be made before practical use can be made of such observations in the taxonomy and phylogeny of these fungi.

From the above it is thus evident that the structures formed in cultures of Hymenomycetes are usually also present in the fruit-bodies from which they were made, although some exceptions to this general rule were encountered and certain structures were not quite identical in the cultures and in carpophores. This conclusion agrees with the statement by Pinto-Lopes (1952) and the results of work of Sarkar (1959), Davidson, Lentz & McKay (1960), McKay & Lentz (1960), Weresub & Gibson (1960), Nobles & Frew (1962) and Lombard & Gilbertson (1965, 1966). Consequently, the carpophores of the different species studied here can also be assigned to the same groups as the cultures made from them. The relationships between the carpophores of the different species as indicated by their cultures must be examined now.

In all those groups in which more than one species was studied, it was found that although the carpophores displayed the characters which allow their inclusion in the group, differences in the morphological characters of the hyphae and construction of the carpophores were present between the individual species or between smaller groups of species within the group. So it was shown that carpophores of *Lenzites trabea* with dimitic fruit-bodies (sensu Corner, 1932 a) differ from those of *Lenzites sepiaria* with trimitic fruit-bodies (sensu Corner) although both are included in Group 13. Of the four species studied in Group 25, the carpophores of *Daedalea quercina* and *Trametes moesta* are identical in hyphal characters but differ only in small morphological characters. The other two species, *Trametes roseola* and *Fomes cajanderi*, reveal similar micromorphological characters but differ from the two *Daedalea* spp. in respect of carpophore colour, texture and the presence of poroid hymenia. Despite these differences, which appear to be of interspecific importance only, it was suggested that these two species should be included in the genus *Daedalea* Fr. In Group 45, *Polyporus vinosus* differs from the *Coriolus — Lenzites — Trametes* spp. by the absence of binding hyphae from its carpophores. Among the other species in Group 45 a smaller group in which "sclerified generative hyphae" (Donk, 1964) are not present and another group in which "arboriform skeletal hyphae" (Teixeira, 1962 b) are present in the carpophores, could be distinguished. The four species in Group 51 have in common the presence of nodose-septate hyphae, fibre hyphae and cuticular cells in their cultures and their carpophores. They were found to differ widely in respect of carpophore construction, carpophore morphology and hyphal characters. Such differences are held to be sufficiently important to regard the relevant fungi as species of separate and distinct genera. Inclusion of some species in certain groups thus appears to depend on the presence of common characters which arose though convergent evolution (Savile, 1954, 1955) whilst other species may be grouped together because they are related through many common characters in respect of the morphology of their hyphae and other

microstructures and construction of their carpophores. These observations thus support Nobles' (1958 b) suggestion that her groups may constitute taxa of generic or higher rank but that some groups may be entirely artificial.

The characters that should be taken into account when considering affinities at generic level in the polypores have not been clearly enumerated as yet and the problem of delimitation of genera of the Hymenomycetes has developed as the most important aspect of their taxonomy. A number of workers including Corner (1948), Wakefield (1948), Pinto-Lopes (1952), Cunningham (1954) and Teixeira (1962 b) regard spore characters, and micromorphology and anatomy of carpophores as the most important indicators of generic affinities although Teston (1953 a) and Smith (1966) are rather sceptical. The views of the first-named workers are summarized by Kotlaba (1964) who stated that "the importance of these characters lie in their particular combinations." He admitted that a particular character may have different taxonomic values in different groups and that no generalizations can be made. He also considered a complex of characters to be the basis necessary for delimitation of genera. The problem thus evolves as the need to determine the relative values of various characters available for taxonomic purposes; but these relative values can be determined only after careful observations on a very large number of species had been made. Such observations had been made on a relatively small number of species only. The number of species included in the present study is insufficient to allow delimitation of genera but the observations made on them serve to emphasize some aspects of carpophore anatomy and micromorphology of hyphae and other structures, that should be taken into consideration in taxonomic studies of these fungi.

With the introduction of the concept of hyphal systems, Corner (1932 a, b) made available useful terminology to describe the construction of carpophores of macrofungi. This concept had been applied to the study of various groups of Hymenomycetes but without further extension or definition of hyphal types or attempts at finer distinctions in hyphal morphology except by Teixeira (1956, 1962 b), who described different kinds of skeletal hyphae. No attempts had been made to describe differences in carpophore construction in polypores, comparable to the different types of texture of carpophore of resupinate Hymenomycetes as defined by Talbot (1954 a), but the existence of similar differences is evident from the above descriptions of the carpophores. The carpophores of *Polyporus dichrous*, *Polyporus adustus* and *Polyporus subiculoides* consist entirely of nodose-septate hyphae. These carpophores thus have monomitic hyphal systems as defined by Corner (1932 a, b), Cunningham (1946, 1954) and Teixeira (1962 b). It is, however, evident from the descriptions that thin-walled, nodose-septate hyphae and thick-walled, nodose-septate hyphae are present in different amounts in carpophores of those species. It is further evident from the descriptions that the thick-walled, nodose-septate hyphae occur in definite regions of the carpophores and that they may be orientated in different directions in the tissues. These differences result in differences in complexity of construction and of texture of the carpophores. They are even more strikingly evident when the carpophores of these three species are compared with carpophores of some species of *Peniophora* and *Corticium*, with monomitic hyphal systems which consist of branched, thin-walled, nodose-septate hyphae terminating in clusters of basidia (Slysh, 1960); Cunningham, 1963; Talbot, 1951, 1954 a, 1958 b). It is thus clear that differences in carpophore construction and hyphal characters can exist in carpophores with monomitic hyphal systems and that these differences are neither recognized nor conveyed by the expression "monomitic hyphal system." Characters of carpophore construction, hyphal orientation and hyphal morphology observed in these species

are constant for each species and genetically fixed. They are therefore of phylogenetic importance. Furthermore, it had been shown that the thick-walled, nodose-septate hyphae, of which several types have been described, must be regarded as morphologically distinct from thin-walled, nodose-septate hyphae. Therefore, the presence or absence of thick-walled septate hyphae in carpophores, the relative position of the different types of septate hyphae, and their orientation in the carpophores must be considered in taxonomic studies and expressed in suitably descriptive terms which can convey characteristic types of construction of carpophores with "monomitic hyphal systems." In this way generic affinities may become more clearly apparent than is the case at present.

In species with carpophores with dimitic hyphal systems in Corner's (1932 a, b) terminology, similar differences in construction and hyphal characters exist. In carpopohres of *Lenzites trabea,* branched, thick-walled, nodose-septate hyphae which seem to form a primitive and poorly developed binding hyphal system are present besides the thin-walled, nodose-septate hyphae and fibre hyphae. In the carpophores of *Daedalea quercina, Daedalea moesta, Trametes roseola* and *Fomes cajanderi,* nodose-septate hyphae with irregularly thickened walls are present besides the thin-walled, nodose-septate hyphae and fibre hyphae. These different types of hyphal differentiation contrast strongly with that of the carpophores of *Fomes pinicola* where only thin-walled nodose-septate hyphae and fibre hyphae are present. They also differ from those of carpophores of *Trametes acupunctata* where some nodose-septate hyphae are differentiated into hyphae with irregular projections and cuticular cells. In carpophores of *Polyporus vinosus* some of the thin-walled, nodose-septate hyphae become thick-walled, turn brown and bind the fibre hyphae into a dense tissue. Yet, despite the morphological differences found in the nodose-septate hyphae they are regarded as generative hyphae by Corner (1932 a, b) and other workers and all these species are regarded as having dimitic hyphal systems. It is thus evident that differences in hyphal characters and carpophore construction of a similar nature to those found among species with carpophores consisting of nodose-septate hyphae only, are also present among species of which the carpophores consist of nodose-septate hyphae and aseptate fibre hyphae. These differences in carpophore construction and hyphal characters were also found to be fixed and constant for the different species. They are thus genetically constant and therefore of phylogenetic importance. Their presence in carpophores must therefore be recognized and taken into consideration when affinities at the generic level are being considered as had been done by Lentz (1960) with *Lopharia crassa* and *Lopharia cinerascens;* but these differences in carpophore construction and hyphal morphology of species whose carpophores have "dimitic hyphal systems" are not apparent from this expression.

Corner (1932 a, b; 1953), Kotlaba & Pouzar (1957) and Teixeira (1962 b) regard species of Polyporaceae having carpophores constructed of generative hyphae, skeletal hyphae and binding hyphae as the most highly evolved group of species in this family. All the species included in the present study in Group 45, Group 51 and Group 53 with the exception of *Polyporus vinosus* and *Trametes acupunctata* respectively, have carpophores of this type with trimitic hyphal systems (sensu Corner, 1932 a, b); but differences in hyphal morphology and carpophore construction similar in many respects to those found in carpophores of species with monomitic and dimitic hyphal systems, were also found to exist among carpophores of these species. In these species too, the modified nodose-septate hyphae are considered to be important because of their different forms in carpophores of different species. In carpophores of some species e.g. *Trametes cingulata* and *Polyporus occidentalis* the nodose-septate hyphae were consistently thin-walled. In others, e.g. *Lenzites betulina* and *Polyporus versicolor,* nodose-septate hyphae

with thick walls were present in the context as more or less straight, branching hyphae, parallel to the fibre hyphae, while in some other species, e.g. *Polyporus versicolor* and *Lenzites palisoti*, thick-walled, nodose-septate hyphae contributed to the binding hyphal system of the carpophores. These hyphae resemble the aseptate binding hyphae but are recognizable by the presence of clamp connections. In some carpophores of species in Group 51, terminal cells of nodose-septate hyphae are differentiated into cuticular cells or brown, thick-walled hyphae with irregular projections, whilst in Group 53, thick-walled, nodose-septate hyphae formed the hairy upper surface of the carpophores of *Polyporus sacer*. There are thus differences in the morphology and function of these hyphae in carpophores of different species and even in different parts of the same carpophore of some species.

Teixeira (1956, 1962 b) showed that different types of skeletal hyphae were present in carpophores of different species with trimitic hyphal systems. Although the skeletal hyphae found in the species mentioned above were mainly unbranched, corresponding to Teixeira's "vermiculiform skeletal hyphae" (Teixeira, 1962 b), fibre hyphae with one to three branches towards the distal end were found in carpophores of some species with trimitic hyphal systems in this study. These branches were found to contribute to the binding hyphal system of the carpophores. Morphologically they appear to correspond to Teixeira's (1956, 1962 b) "arboriform skeletal hyphae," but Furtado (1966) maintained that "arboriform skeletal hyphae" are found only in carpophores of Ganodermoid species. From observations made in this study, however, it appears that they may also occur in carpophores of species of *Trametes* and *Coriolus*. Differences in the morphology of fibre or skeletal hyphae thus occur and must be taken into consideration in taxonomic studies of these fungi. Differences in the binding hyphae of different species or groups of species were also evident. Cunningham (1946) recognized two types, viz.: the "bovista" type and the "long" type of binding hypha but failed to distinguish adequately between them. Morphological differences between binding hyphae of different species were observed in the species studied here. In some species of *Trametes* and *Coriolus* the binding hyphae were found to be rather intricately branched structures with the branches short, thick, often tortuous and of a different refractive index from that of the skeletal hyphae. In other species, e.g. *Trametes cingulata, Polyporus occidentalis* and *Polyporus sacer* the binding hyphae resemble skeletal hyphae but have fairly long, flexuous, tapering branches. The length and form of branches of binding hyphae may vary according to their position in the carpophore but differences in morphology of the branches and the difference in refractive index may be observed with little difficulty.

Corner (1953) described the binding hyphae from the carpophores of *Polyporus sulphureus* and *Polyporus squamosus*, species which he regarded as having dimitic hyphal systems with generative and binding hyphae. In both these species, the binding hyphae are formed by the evagination of the walls of intercalary cells of generative hyphae into a number of tortuous, lateral processes which later become thick-walled. Structures which bear some resemblance to these were seen in cultures and carpophores of *Lenzites sepiaria* and in the carpophores of *Polyporus adustus* (Fig. 2 p), but these structures, which have a binding function in the carpophores, do not arise in the same way as the binding hyphae which originate and develop as the terminal cells of lateral branches of generative hyphae. These structures are not separated from the parent cells by septa. For this reason these structures should be regarded as binding processes rather than binding hyphae. Differences in morphology and ontogeny of the elements of the binding hyphal system thus exist and should be of great value in taxonomic studies of Polyporaceae.

From the above it is thus evident that numerous differences in the morphology and ontogeny of the hyphae which comprise the different hyphal systems exist

in carpophores of different species. The different types of hyphae, their morphology, occurrence and function in fruit-bodies of polypores in the present study may be summarized as follows:—

1. *Septate hyphae*

1.1 Thin-walled, nodose-septate hyphae; branching, mostly with deeply staining contents; present in the growing regions of the upper surface, margin and hymenial surfaces; giving rise to all other structures in the carpophore, (generative hyphae, Corner, 1932 a, b); collapsed and empty in older parts of carpophores of some species.

1.2 Thick-walled, nodose-septate hyphae; walls regularly thickened, with or without staining contents, regularly septate, branching, (sclerified generative hyphae, Donk, 1964) occur as:

(i) hyphae supporting reflexed pilei and constituting major or only hyphal type, orientated mainly parallel to direction of growth of pileus;

(ii) hyphae as in (i) but present in small numbers in context, among fibre hyphae in species where these are present; function unknown;

(iii) hyphae with tortuous branches orientated across the direction of growth of the pileus and assisting in binding the tissues;

(iv) hyphae supporting pilei as in (i) but forming lateral, branched, binding processes;

(v) short, thick-walled or solid hyphae forming "hairs" of tomentose upper surface of pilei.

1.3 Nodose-septate hyphae with irregularly thickened walls, present in lower parts of context of certain species; function unknown.

1.4 Hyphae with irregular projections and cuticular cells; brownish, thick-walled elements arising from septate hyphae, present in dark-coloured incrusted areas over the older parts of some carpophores of certain species; function unknown, probably protective.

2. *Fibre hyphae*

2.1. Unbranched, straight or somewhat flexuous, hyaline to pale brown, thick-walled or sub-solid to solid, aseptate or with one or two simple septa towards the apex, arising from thin-walled or thick-walled regularly septate hyphae; when present, constituting bulk of tissues of carpophore, terminating in context or at upper surface and margin or below hymenial surfaces; arranged parallel to direction of growth of carpophore; supporting and protecting hymenophore and forming tomentum or pubescence or, by agglutination with lacquer-like material, incrusted or fibrillar or glabrous upper surface. (Aciculiform and vermiculiform skeletal hyphae, Teixeira 1956, 1962 b).

2.2 Branched fibre hyphae, as in 2.1 but with one to three branches towards the apex; the main stem parallel to the direction of growth of the carpophore and supporting the carpophore tissues, the branches arranged across the direction of growth of the carpophore and binding the tissues; occurs in lower context of certain species (arboriform skeletal hyphae, Teixeira 1956, 1962 b).

2.3 Branched fibre hyphae, the branches long and tapering, otherwise as in 2.1 branches interwoven with other hyphae across the direction of growth of the carpophore; bind hyphae into tough tissues; present in context of some species in which unbranched fibre hyphae are also present.

2.4 Branched fibre hyphae with numerous short tortuous branches, interwoven with other fibre hyphae across the direction of growth of the carpophores, otherwise as in 2.3.

2.5 Dichotomously branched, very narrow hyphae, forming a network in the lower context tissues of some species; apparently aseptate, origin and function unknown.

This list is by no means complete as many types of hyphae, such as simple-septate, thin-walled, generative hyphae (Corner, 1932 b), thick-walled, simple-septate hyphae (Pinto-Lopes, 1952), inflated hyphae (Corner, 1953) and others were not encountered in the carpophores of the species included in this study. It does however serve to illustrate the diversity in hyphal morphology and hyphal function which exists in carpophores of the poroid Hymenomycetes. It is evident from this, that this diversity and its possible phylogenetic connotations had not been fully utilized in taxonomic studies of these fungi. It is also evident that this diversity in hyphal morphology and function together with the resulting differences in carpophore construction and texture, are not adequately expressed and conveyed by the concept of hyphal systems. Consequently, the concept of hyphal systems had been criticized by Pinto-Lopes (1952), Teston (1953 a), Welden (1960), Smith (1966) and others.

Bondartzeva (1963) and Smith (1966) expressed the view that hyphal systems are indications of adaptive evolution and devices to restrict waterloss from the carpophores and prevent dessication and damage to the hymenium. Undoubtedly, there is strong evidence in favour of these views. Savile (1954, 1955) stated that if an ecological niche exists, it will be filled repeatedly by different organisms which find similar ways to achieve this. Problems involved in the extension of the hymenial surface, protection of the hymenial surface from rain and reduction of loss of moisture from fruit-bodies of Hymenomycetes can be overcome in a limited number of ways only so that similar structures must have developed repeatedly. It is thus conceivable that species of which fruit-bodies have similar hyphal systems (sensu Corner, 1932 a, b) may have developed repeatedly and independently. For these reasons species having similar hyphal systems cannot be regarded as being congeneric on that basis only. Indeed, it became evident in this study that important differences in morphological characters of the hyphae and in their arrangement and function in the carpophores can exist in different species with similar hyphal systems. It is, however, also evident from this study that the hyphae present in fruit-bodies of individual species are morphologically and genetically constant for each species unlike such characters as, habit, insertion, hymenial configuration and texture of the upper surface of the carpophores. It also became evident that the hyphal complement and construction of the fruit-bodies, i.e. the placing of different types of hypha in the carpophores of different species, are constant for each species although certain specialized structures, such as cuticular cells, may be absent from carpophores of species which are capable of forming them. For this reason these characters should be studied and recorded in detail in descriptions of carpophores of different species. All these characters must be considered together with other constant characters, such as spore shape and size and basidial shape and size, in the delimination and characterization of genera of the polypores. Applied in this way these characters become valuable components of the "complex of characters" which must be considered for generic delimination as stated by Ames (1913), Wakefield (1948), Pinto-Lopes (1952), Nobles (1958 b), Teixeira (1962 b) and Kotlaba (1964) among others; but careful observation and accurate descriptions of hyphal characters and construction of carpophores rather than generalizations by means of collective terms are essential prerequisites for their use in this connection.

7. SUMMARY

1. Twenty-four species of poroid Hymenomycetes from South Africa and Canada were studied. Of these, twelve species occur in South Africa, four in Canada whilst eight are found in both countries.

2. The micromorphological characters and oxidase reactions of the cultures and the micromorphological characters and construction of the carpophores together with the type of decay and host range of these twenty-four fungi were studied in order to determine: (i) which microstructures are formed in cultures of these species; (ii) their relationships as indicated by their cultural characters; (iii) whether the structures formed in culture are also present in their carpophores, and (iv) whether the relationships indicated by cultural characters are also revealed by their carpophores.

3. Mycelia obtained from single basidiospores were paired in culture in order to determine the type of interfertility of certain species or to determine conspecificity between different collections. In some species attempts were made to dikaryotize large haploid mycelia by pairing them with small dikaryotic mycelia in culture in order to establish conspecificity between the different collections from which the mycelia were obtained.

4. The literature on the classification of the poroid Hymenomycetes, the structure and anatomy of their carpophores in relation to their taxonomy and studies of Hymenomycetes in pure culture, was reviewed.

5. The cultural characters were studied by observations on cultures of the fungi incubated in the dark on 1.5 per cent malt agar plates for a period of six weeks according to the methods of Nobles (1948). Construction and micromorphology of the carpophores were studied by teasing apart thick sections of carpophores to obtain undamaged structures for examination according to the methods of Teixeira (1956). All microstructures were examined by means of the oil immersion lens and recorded by means of camera lucida drawings or photomicrographs.

6. It was found that the 24 species were distributed among nine of the 36 groups proposed by Nobles on the basis of their cultural characters. In five of these groups only one species was studied in each. Two of these species, *Polyporus dichrous* in Group 9 and *Polyporus subiculoides* in Group 32 displayed characters that made inclusion in their respective groups somewhat dubious.

7. The structures formed in cultures of the different species were also found in their carpophores with the exception of chlamydospores. Although chlamydospores were present in cultures of most species they were found in carpophores of one species only, *Fomes pinicola*.

8. As the structures formed in cultures are also present in the carpophores of the different species, the carpophores can be placed in the same groups as the cultures but do not show the same relationships.

9. Differences in the micromorphological characters of the hyphae and in the types of hyphae present in the carpophores of species from the same group were found in species of three of the four groups in which more than one species was studied.

10. Differences in construction of the carpophores and orientation and functions of their hyphae were observed in carpophores of species in which similar types of hyphae are present.

11. Important differences between the hyphal characters and construction of the carpophores of various species and the carpophores of type species of genera to which they have been assigned by different authors, were demonstrated.

12. Differences in the characters and origin of the "hairs" that constitute the trichocutis or upper surfaces of carpophores of a number of species, were noted.

13. Cuticular cells which characterize cultures of *Daedalea confragosa, Trametes corrugata, Trametes acupunctata* and *Hexagona tenuis,* are often lacking from individual fruit-bodies of these different species or are present as hyphae with irregular projections on the carpophores. Because of their sporadic appearance on carpophores, these structures are not regarded as being reliable characters for taxonomic purposes.

14. Three different ways of development of fruiting structures were observed in cultures of the various species, viz.: (i) formation of low anastomising ridges; (ii) tubules and (iii) erect acicular or flattened spines. These are considered to be of phylogenetic importance.

15. The type of interfertility of seven species was determined. All displayed the tetrapolar type of interfertility. Of these, *Polyporus dichrous* only, is associated with brown rot and its cultures do not produce extra-cellular oxidase enzymes. The other six species are associated with white rots and their cultures produce extra-cellular oxidase enzymes.

16. By pairing haploid mycelia derived from single basidiospores from different collections, it was found that haploid mycelia from a South African collection of *Lenzites trabea* were completely compatible with haploid mycelia from a Canadian collection. The conspecificity of the two collections were thus confirmed. The conspecificity of four collections of *Trametes cingulata* from South Africa were also confirmed by means of this technique. When this technique was used to determine the conspecificity of a South African collection of *Polyporus adustus* with Canadian collections of this species it was found that only a very low degree of compatibility existed between the haploid mycelia from the South African and Canadian collections although no differences in cultural and carpophore characters could be found.

17. The technique of dikaryotizing a large haploid mycelium grown in culture by pairing it with a small dikaryotic mycelium was used to confirm the identity of different collections of four different species. This was successful with four collections of *Trametes meyenii* and four collections of *Polyporus occidentalis.* This method failed however with five collections of *Polyporus dichrous* and seven collections of *Polyporus pubescens.*

18. It was concluded that the micromorphological characters of the hyphae and other microstructures as well as the construction of the carpophores are constant for each species. All these characters should be carefully described and recorded for each species and should be taken into consideration in taxonomic studies of these fungi. Differences and similarity of micromorphological characters and construction of carpophores of species are not adequately conveyed by the concept of hyphal systems.

8. TABLES

TABLE 1. — Oxidase reactions and colony diameter (in mm) of different isolates of *Polyporus adustus* on malt-gallic acid medium and malt-tannic acid medium and oxidase reaction as indicated by gum guaiac solution applied directly to cultures on malt agar, after 14 days' incubation.

Isolate No.	Oxidase reaction			Colony diameter (mm)	
	Gum guaiac	Gallic acid	Tannic acid	Gallic acid	Tannic acid
DOAM 9209	+ (1)	—	+	trace	trace
DAOM 17571	— (2)	—	—	trace	no growth
DAOM 17575	—	—	—	5	no growth
DAOM 22576	—	—	+	5	no growth
DAOM 53500	+	—	+	trace	trace
PRE 42039	+ + (3)	—	—	12	no growth
PRE 42328	—	—	—	12	no growth
PRE 42332	+	+	—	10	no growth
PRE 42350	+	—	—	15	trace
PRE 42365	—	—	—	trace	none

(1) Positive reaction;

(2) Negative reaction;

(3) Strong positive reaction.

TABLE 2.— Results of pairing four mycelia derived from single basidiospores of a South African collection, PRE 42039, with single basidiospore cultures of each of four Canadian collections PRE 42365, PRE 42328, PRE 42329 and DAOM 53500, of *Polyporus adustus*.

		PRE 42039				PRE 42365				PRE 42328				PRE 42329				DAOM 53500			
		1	2	1	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
PRE 42039	1					−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
	2					−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
	3					−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−
	4					−	−	−	−	−	−	−	−	−	+	−	+	−	−	−	−
PRE 42365	1	−	−	−	−					+	+	+	+	+	+	+	+	+	+	+	+
	2	−	−	−	−					+	+	+	+	+	+	+	+	+	+	+	+
	3	−	−	−	−					+	+	+	+	+	−	+	+	+	+	+	+
	4	−	−	−	−					+	+	+	+	+	+	+	+	+	+	+	+
PRE 42328	1	−	−	−	−	+	+	+	+					+	+	+	+	+	+	+	+
	2	−	−	−	−	+	+	+	+					+	+	+	+	+	+	+	+
	3	−	−	−	−	+	+	+	+					+	+	+	+	+	+	+	+
	4	−	−	−	−	+	+	+	+					+	+	+	+	+	+	+	+
PRE 42329	1	−	−	−	−	+	+	+	+	+	+	+	+					+	+	+	+
	2	−	−	−	−	+	+	+	−	+	+	+	+					+	+	+	+
	3	−	−	+	−	+	+	+	+	+	+	+	+					+	+	+	+
	4	−	+	−	+	+	+	+	+	+	+	+	+					+	+	+	+
DAOM 53500	1	−	−	−	−	+	+	+	+	+	+	+	+	+	+	+	+				
	2	−	−	−	−	+	+	+	+	+	+	+	+	+	+	+	+				
	3	−	−	−	−	+	+	+	+	+	+	+	+	+	+	+	+				
	4	−	−	−	−	+	+	+	+	+	+	+	+	+	+	+	+				

A (+) indicates formation of clamps on the mycelium.

TABLE 3.— Mating types of mycelia from single spores of *Polyporus dichrous* PRE 42384.

A_1 B_1: 1, 5, 10, 12;
A_2 B_2: 2, 7, 9, 11, 16, 17;
A_1 B_2: 3, 8, 13, 15, 18;
A_2 B_1: 4, 14.

TABLE 4.— Results, showing the formation of clamp connections (+), when four single basidiospore cultures from each of two isolates of *Lenzites trabea*, PRE 42457 and DAOM 72285, were paired in all possible combinations.

		PRE 42457			
		1	2	3	4
DAOM 72285	1	+	+	+	+
	2	+	+	+	+
	3	+	+	+	+
	4	+	+	+	+

TABLE 5. — Collections of *Polyporus pubescens* tested for conspecificity with monospore cultures Nos. 5 and 8 of *Polyporus pubescens* DAOM 94039.

DAOM 17577	DAOM 94017
DAOM 52833	DAOM 94026
DAOM 53503	DAOM 94039
DAOM 73309	

TABLE 6. – Mating types of single spores of *Trametes meyenii* PRE 42446.

A_1 B_1: 1, 9;	A_2 B_1: 3, 4, 5, 12, 13, 15;
A_1 B_2: 11, 16;	A_2 B_2: 2, 6, 7, 8, 10, 14.

TABLE 7. — Mating types of single spores of *Lenzites palisoti* PRE 42442.

A_1 B_1: 4, 5, 11, 15;	A_1 B_2: 8, 10;
A_2 B_2: 12, 13, 16;	A_2 B_1: 6, 9.
No mating: 1, 2, 3, 7, 14.	

TABLE 8. — Mating types of mycelia from 16 single spores of *Polyporus occidentalis* PRE 42863.

A_1 B_1: 1, 2, 3, 11, 12, 15;	A_1 B_2: 4, 6, 16;
A_2 B_1: 5, 7, 13;	A_2 B_2: 8, 9, 10, 14, 16.

TABLE 9. — Mating types of single basidiospores of *Trametes cingulata* Berk. PRE 42448.

A_1 B_1: 1, 9, 11, 14, 15, 16;	A_1 B_2: 3, 4, 5, 8, 10, 12, 13;
A_2 B_2: 6, 7;	A_2 B_1: 2.

TABLE 10. — Mating types of single spore of *Polyporus vinosus* PRE 42154.

A_1 B_1: 1, 7, 8, 9, 12, 13, 14;	A_2 B_1: not present;
A_1 B_2: 2, 4, 5, 10, 15, 16;	A_2 B_2: 3, 6, 11.

TABLE 11. — Distribution of mating types in 16 single spore cultures of *Trametes corrugata*, PRE 42454.

A_1 B_1: 2, 5, 7, 9, 16;	A_1 B_2: 4, 12, 13;
A_2 B_2: 6, 10, 11, 14;	A_2 B_1: 1, 3, 8, 15.

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