A STUDY OF CYSTIDIA IN EFFUSED APHYLLOPHORALES

by

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CONTENTS

SUMMARY

1. Selected species were studied, most of which were type species of genera of effused Aphyllophorales. The morphology and development of hyphae, cystidia, basidia and whole fructifications were traced by dissecting or sectioning primordia and growing edges of young fructifications, and also in more mature parts.

2. Six different categories of cystidia were recognised and described on the grounds of their morphology and development: skeletocystidia, metuloids, gloeocystidia, leptocystidia, radicate cystidia and hyphocystidia. The categories previously termed "tramal" and "hymenial" cystidia were shown to be misleading and of little practical use.

3. Measurements of cystidia and basidia in three species were statistically analysed. The analyses showed that not all cystidia may be interpreted as sterile homologues of basidia, thus confirming the conclusions drawn from developmental studies in these three species.

4. The crystals encrusting cystidia in three species were shown by X-ray diffraction to be composed of the dihydrate of calcium oxalate.

5. In the species studied, the fructifications showed three main patterns of development. On the whole

these correlated well with taxonomic groupings of species made on other grounds.

6. In most species the fructifications were found to thicken by the well-known process of hymenial thickening. In a few species the fructifications thickened by means of either a repetitive basal layer or a repetitive context.

7. Some observations are made on the factors giving rise to a stratified appearance in the context of some fructifications.

8. Some of the possible functions of cystidia are discussed.

9. The information gained in regard to cystidial types and developmental types in fructifications is put to taxonomic use. These are not important as taxonomic characters above the generic level but are used to clarify many controversial issues at the specific and generic levels.

STATEMENT

This thesis contains no material which has been accepted for the award of any other degree or diploma and contains no material previously published or written by another person, except when due reference is made in the text.

Isobel P. Price.

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I. INTRODUCTION

In the taxonomy of the Hymenomycetes there has been increasing emphasis on the use of microstructure in order to amend the highly artificial classifications produced by early workers, who mainly used macroscopic observation. The impetus came originally from the brilliant work of Karsten and Patouillard. Later, Bourdot & Galzin (1909 *et seq.*; 1928) created a number of subgeneric groupings in the Aphyllophorales which were the inspiration for more recent work by many authors. Rogers (1935), Jackson (1948 a, b; 1949 a, b; 1950 a, b, c), Donk (1954; 1956, a, b; 1957 1958) and Eriksson (1958 a, b), in particular, have amended old generic concepts and defined smaller and more natural genera comprising groups of species taken from the large artificial genera. These workers have stressed the need for re-evaluating basic characters used in the taxonomy of the Aphyllophorales.

The Aphyllophorales are especially notable for the wide occurrence of various types of distinctive sterile cystidiform structures which have been extensively used in taxonomy and which are usually referred to as "accessory organs". However, as emphasized by Lentz (1954), these are modified hyphae. These structures have been examined in the Hymenomycetes since Micheli in 1729 (cited in Lentz, 1954) called attention to structures which are now termed "cystidia". The majority of early investigations were no more than speculations on the functions of cystidia. The general concept of a cystidium was that it was a male organ of the sexual apparatus. This idea was discarded when the real nature of reproduction in the Basidiomycetes became known. Subsequent hypotheses have largely been concerned with possible mechanical, protective, or excretory functions of cystidia.

As knowledge about these structures was accumulated it became apparent that some fungi constantly had certain types of cystidia associated with them and that this could have a taxonomic use. Certain generic segregates have been based solely on the presence of cystidia. For example Coniophorella was erected (Karsten,1889a) for a species of Coniophora with large septate cystidia, and Peniophora (Cooke, 1879) was erected to accommodate all corticioid fungi with "metuloids". With the use of cystidiform structures in taxonomy came attempts to categorise and define them. Some categories were broad and ill-defined and often contained a heterogeneous collection of structures. For example, the illustration by Talbot (1954a fig.16) shows the wide range of structures which have been termed "cystidia". It is not surprising, then, that the erection of genera based solely on the presence of "cystidia" was not successful, as such genera on closer examination were usually found to comprise a very heterogeneous collection of species. Also, seemingly closely related species became separated because some possessed "cystidia" while others did not. All this has lead to confusion and to general dissatisfaction with the use of cystidiform structures as taxonomic characters. Relationships relying on the presence of cystidia are not necessarily natural, and the presence or absence of cystidia is not always significant in the classification of the Aphyllophorales (Eriksson, 1950; 1958a).

Because cystidiform structures have fallen somewhat into disrepute in taxonomy, efforts have been made, notably by Donk and Eriksson, to find more reliable characters on which to base genera; invariably it is found that genera have to be based on a composite of characters. However, as cystidia are obvious and describable they lend themselves to taxonomic use in the Aphyllophorales where taxonomic characters are often meagre; but the resulting classifications will be satisfactory only if cystidial types themselves can be classified in a way which reflects other taxonomic similarities and differences.

Previous classifications of cystidiform elements have been based on their shape, structure, contents, presence of a crystal encrustation and various other criteria, but many of these groupings are of questionable value. Their place of origin has sometimes been taken into account, but only in very broad terms (Burt, 1925; Lentz, 1954; Donk, 1964), and their development has largely been ignored. The chemical composition of the contents and mineral encrustation has usually not been defined. The lack of fundamental data about cystidiform structures, and also about the complete development of the fructification, has been stressed by Kendrick & Weresub (1966). If these structures are to be relied upon as taxonomic characters, a detailed study of their morphology and development should be undertaken, with particular emphasis on their relation to the development of the fructification as a whole. This was the purpose of the present study.

A survey of all the Aphyllophorales was beyond the scope and time of this study and research was confined mainly to the Thelephoraceae sensu Fries. In this traditional family, of broad limits, cystidiform structures are particularly common; they offer a wide range of morphology and a number of types of development are to be found. Observations were used to group these structures according to developmental as well as mature morphological features and an attempt was made to define the various types unambiguously. Other characters of taxonomic importance were also recorded in the specimens examined, and were used in conjunction with the cystidial types derived from this study to re-evaluate the classification of the species studied.

II. STRUCTURE AND TERMINOLOGY OF FRUCTIFICATIONS IN THE APHYLLOPHORALES

This review deals with the structure of fruit-bodies of effused Aphyllophorales and defines the terminology adopted in this study. As the taxonomy of the Aphyllophorales is in a state of upheaval it is appropriate to include some comments on the taxonomic use which has been made of some of these characters.

A. GENERAL

Hyphae

In the fruit-bodies of most Aphyllophorales, the hyphae do not become compacted into short-celled stromatic tissue but generally remain easily separable. They afford a number of taxonomic characters, used with varying degree of importance. Their width may be from about 2 u to as much as 30 u; wall thickness may be from about 0.1 u to so thick that the lumen is obliterated. Colour of the walls ranges from hyaline to dark-brown; in species of the Hymenochaetaceae ("Xanthochroic series", Corner, 1948) the brown color becomes intensified on addition of KOH (Burt, 1918; Donk, 1964). The hyphal walls are usually rigid but in some species are gelatinized.

The hyphae may become primarily or secondarily septate but only the primary septa are associated with clamp connexions when these are present. Primary septa are normally about the same thickness as the hyphal walls, and, in investigated species have the dolipore construction which is peculiar to most Basidiomycetes (Moore, 1965). Secondary septa are usually very thin, much thinner than the hyphal walls, and, as far as has been observed, do not have a dolipore construction. Secondary septa (Talbot, 1968) appear to be found mainly where there has been a regression of protoplasm, as in damaged hyphae, in old basidia, in sterigmata, and occasionally in cystidiform structures, e.g. in gloeocystidia of Gloeocystidiellum lactescens (Berk.) Boidin. The thin septa sometimes found in skeletal hyphae are here classed as secondary, but do not appear to be associated with regression of protoplasm.

In species with clamp connexions there is normally only a single clamp per septum, but in some species two, or a whorl of clamps are found (Boidin, 1958a; Maas Geesteranus, 1962). It is probably true to say that opposite or whorled clamps are found only in mycelial hyphae or in marginal hyphae of fructifications, but not in the denser tissues of fruit-bodies.

The value given to clamp connexions as a taxonomic character is not consistent. Some authors regard the presence or absence of clamps as significant only at the species level, while others believe that they are significant for higher taxa. This confusion is intensified by inaccurate observation on the occurrence of clamps; also clamps are sometimes present in cultures or somatic mycelium, but not in the natural fructification (Boidin, 1958a), and the pattern of distribution of clamps in some species shows considerable variation (Donk, 1964). Consequently much more information is required about clamp connexions and they must be used with caution in taxonomy (Furtado, 1966).

Hyphal branching is variable and has not usually been used taxonomically, although Rogers (1943) included cruciate and right-angled branching in the generic description of Pellicularia sensu Rogers. Side branches of hyphae usually appear just behind a septum, or may develop from a clamp connexion (Routien, 1948). The angle at which the branch arises may differ between species; those with wide-angled branching often have the lateral branches developing from the hymenial side, only, of the parent hypha. These details are usually not mentioned by authors, though if more information were available they might well prove useful in taxonomy.

Sometimes hyphae have specialized contents and are then termed 'vascular hyphae' (Lentz, 1954). Generally the different types of vascular hyphae are named according to the kind of contents, e.g. laticiferous (latex contents), oleiferous (fat-containing) and sanguinolentous (tannin-like materials which oxidise and become blood-coloured). Different types of vascular hyphae may characterize certain species or groups of species.

Hyphal Types and Hyphal Systems

Ames (1913) found that the texture of the pileus in polypores could be correlated with the arrangement of the hyphae, features of the hyphae themselves and the amount of water within the cells. She discussed the textures of fruit-bodies, describing the hyphal constructions which resulted in these textures.

A most important contribution to better understanding of the structure of fruit-bodies was made by Corner (1932a, 1932b) when he recognised and defined hyphal types and hyphal systems in certain polypores. His ideas were first used taxonomically by Cunningham (1946, 1947-1950; 1965) in studies of the New Zealand Polyporaceae. Subsequently Corner (1948, 1950, 1953) made certain small refinements in his nomenclature of hyphal types and systems. The present position is that three hyphal types are recognised in fruit-bodies of Aphyllophorales, and they may be combined variously into three hyphal systems. Generative hyphae are branched, thin-walled (rarely thick-walled) septate hyphae with or without clamp connexions; they give rise to the other hyphal types. Skeletal hyphae are unbranched, thick-walled, usually aseptate, hyphae which build a framework that is consolidated by the branched, thick-walled, aseptate, interweaving binding hyphae. A fruit-body with a monomitic hyphal system contains generative hyphae only. A dimitic hyphal system combines either generative and skeletal hyphae, or generative and binding hyphae. In a trimitic hyphal system all three hyphal types are present. Two previously recognised categories of hyphae are no longer differentiated; as Corner (1932b) himself pointed out, mediate hyphae are simply transitional between generative and skeletal types, and mycelial hyphae must always be present. Cunningham (1946) recognised a "bovista"-type of skeletal hypha and a "long"-type of binding hypha. However, Corner (1953) showed that the bovista skeletal hypha could well be classed as a binding hypha, while Cunningham himself (personal communication to P.H.B. Talbot) later doubted whether he could maintain the category for binding hyphae of the "long" type.

It is now generally recognised (Donk, 1964) that a knowledge of hyphal construction of fruit-bodies is essential for clarifying the taxonomy of polypores and other Aphyllophorales. Although must authors now include hyphal systems in their general descriptions of these groups of fungi, comparatively few thorough studies of hyphal systems in selected taxonomic groups have been produced. Besides the extensive works of Corner and Cunningham, the main contributions in this field are those of Teixeira (1956, 1958, 1960, 1962), Ragab (1953), and the recent comprehensive studies on Hydnaceae by Maas Geesteranus (1962, 1963a, b, c; 1967a, b).

A few authors have expressed doubts or dissatisfaction with Corner's system. Teston (1953) concluded that hyphal differentiation was a poor taxonomic base as it tended to fragment genera and moreover depended upon characters which are very variable in a single specimen and variable with age and size of the basidiocarp. She thought that it would only rarely characterize natural groups but could be used with advantage for series of species within such groups. Pinto-Lopes (1952) also expressed dissatisfaction with the system of Corner and reverted, with certain modifications, to a classification of primary, secondary and tertiary mycelium which had been proposed by De Bary (1884). Primary mycelium was defined as originating from germination of heterothallic spores and consisting of the haploid or non-diploidized hyphae. Secondary mycelium originated from the germination of homothallic spores, or from the fusion of two compatible primary mycelia, or from the spontaneous differentiation of the primary mycelium in homothallic species. Tertiary mycelium occurred as specialized tissue of fruit-bodies and was composed of secondary hyphae which had become wider, thicker-walled, or both, and was sometimes pigmented. Pinto-Lopes studied hyphal systems from a biological point of view rather than from the functional or morphological view of Corner, and his system of nomenclature for hyphae had the merit of being applicable to cultures as well as to natural fructifications. The opinion of Pinto-Lopes that each species has its own characteristic combination of secondary and tertiary mycelium emphasizes the argument that the simple 1-2-3 system of Corner may be inadequate. Corner (1954b) castigated the work of Pinto-Lopes; but when a character has such a profound effect on taxonomy as the introduction of hyphal systems did, then in my opinion it is desirable to study it from as many points of view as possible. If a system is sound it will be substantiated by further study and if not then well-founded criticism is beneficial.

The Basidium

The basidium is the site of the important functions of karyogamy and meiosis, and of the production and liberation of basidiospores. In the Aphyllophorales the basidium is an aseptate cell (holobasidium) but adventitious septa are sometimes encountered; they are secondary septa, not primary septa as in phragmobasidia (Donk, 1958; Talbot, 1968). The basidial terminology proposed by Donk (1931; 1956a) and amplified by Talbot (1954a) was used in the present study in preference to the terminologies used by Rogers (1934), Martin (1938; 1957) and Linder (1940), since it was consistent when applied to different types of basidia.

In the Aphyllophorales basidia may arise singly or in fascicles. Single basidia are formed from terminal cells of vertical context hyphae, or laterally (pleurobasidia) from horizontal basal hyphae. Only one terminal basidium may develop on a context hypha, or alternatively repetitive basidia may be produced. Repetitive basidia are not common in the Aphyllophorales. They are formed by a new basidium developing within a preceding one and growing through it, carrying the remains of the previous basidium around it as a mantle (e.g. basidia in the genus <u>Repetobasidium</u> Eriksson (1958a)). Most species of Aphyllophorales have fasciculate basidia. A fascicle is a botryose or cymose arrangement of basidia at different stages of development, arising from branching of a single context hypha. Although basidial fascicles are sometimes described as being botryose or cymose, generally very little notice is taken of how they develop. This is probably because few developmental studies on the fruit-bodies have been undertaken, and because development of fascicles is sometimes very variable. The detailed construction of basidial fascicles offers taxonomic possibilities. The features most likely to be useful are the type of branching of the basidial fascicle and the method of origin of the basidia, e.g. by proliferation from clamps (Rogers, 1936). Where possible in the fungi studied in the present work, details of the ways in which fascicles develop have been noted. As discussed below, it is difficult and often impossible to distinguish between basidiferous tissue of the context and hyphal portions of basidial fascicles, particularly if the fascicles are loose and if basidia are formed at successively higher levels.

Various features of basidia are used in the taxonomy of the Aphyllophorales. The position of the nuclear spindle was once considered a primary taxonomic character (Maire, 1902) but the resulting unnatural grouping of genera and the lack of knowledge on the subject led Rogers (1934) and Martin (1938) to regard the character as having no taxonomic value. However, some other authors believe that the position of the spindle may sometimes be a useful secondary taxonomic character if used with caution (Donk, 1931, 1964; Talbot, 1954a). An extensive review of nuclear spindles in the basidium is given by Donk (1964).

Significant differences in basidial shape are also used in taxonomy (Donk, 1964; Eriksson, 1958a, b; Lentz, 1957; Oberwinkler, 1964, 1965). In fructifications where the hymenium is a compact palisade, lateral expansion of basidia is usually limited and they tend to be clavate or cylindrical (Wakefield, 1935). However, in fructifications which are gelatinous, sparse or of a loose texture, basidia are usually not closely arranged and often are formed singly. In such fungi there is space for free development and a number of different basidial shapes are found. The typical clavate basidium of the Aphyllophorales is too widespread to be of diagnostic importance for most groups, but variations from this type are usually restricted in their incidence and can be of taxonomic importance for the groups in which they occur. The critical use of basidial shape in taxonomy is comparatively recent and further significant variations in shape are being reported as the microstructure of more species is studied in detail. There have, for example, been many recent extensions to the list of genera in which dimerous basidia are found. Observations of basidia are included in the present work, as it is necessary to extend knowledge on basidial shape to as many species as possible.

In the majority of Aphyllophorales there are normally four sterigmata and four basidiospores per basidium. However, two per basidium are usual for some species (e.g. species of the genus Clavulina (Corner, 1950)), and numbers of up to eight per basidium are normal in some genera (Donk, 1964; Oberwinkler, 1965). Sterigmata in the Aphyllophorales are typically tapered and curved, and variations from this standard have been used as an important taxonomic character (Donk, 1964). The basidiospores in Aphyllophorales are ballistospores and the majority are not repetitive. Morphological and microchemical features of the spores are useful in taxonomy; spore shape and size are particularly critical at the species level.

Form of the Fruit-body

The fruit-body of the Aphyllophorales is variously termed a fructification, basidiocarp or hymenophore. Donk (1964) suggests that the term hymenophore is more useful if restricted to that tissue of the fruit-body which subtends the hymenium and whose growth patterns are responsible for the various types of hymenial configuration.

The fruit-body may be stipitate, or subsessile usually with a well-defined point of attachment, or evenly attached to the substratum as in entirely effused types. As recommended by Donk (1964), the term effused, instead of resupinate, has been adopted for those fruit-bodies primarily attached to the substratum by their abhymenial side, and the term appressed for those which have become secondarily attached.

In stipitate forms, the pileus may be borne on a central, excentric or marginal stipe. The marginal stipe is sometimes reduced or lacking so that the side of the pileus itself is directly attached to the substratum. A sessile fruit-body is variously described, depending on the pileus shape and the area of attachment. For instance a dimidiate applanate fruit-body is sessile and semicircular, shelf-like, with a thin base of attachment, while an ungulate fruit-body is similar but with a very thick base of attachment. A flabellate pileus is wedge-shaped or fanlike and attached by a stipe or narrowed base. Effused fruit-bodies are evenly attached to the substratum over their whole proximal surface, but sometimes the margins may become free and the fruit-body then becomes effused-reflexed. Further variations of the form of fruit-bodies are discussed by Donk (1964).

The form of the fruit-body is important in classification of the Aphyllophorales but care should be taken in its use as sometimes a species exhibits different forms of fruit-body which, if found separately, could be placed in different genera or even different families (Donk, 1964). Eriksson (1958a) considers that the distinction between resupinate and pileate forms should be rejected completely as a taxonomic character because these forms of fruit-body may be present in closely-related species.

Structure of simple effused or effuso-reflexed fructifications

This thesis deals particularly with genera of Aphyllophorales with simple effused fructifications, and in part it is concerned with clarifying the various forms of development and structure of fructifications in particular species. At this point, therefore, it is desirable to give only a general picture of their structure. In most instances, generative hyphae emerge from the substratum at one or more focal points and branch and grow centrifugally while remaining appressed to the substratum. At the margin, or growing edge, of the fructification the hyphal ends are usually discrete; nearer the centre, a short distance behind the growing edge, branching of the appressed hyphae occurs. In most instances the branches remain horizontal at first, building up varying thicknesses of superposed hyphae to form a "basal layer". With some species, branches of the appressed hyphae or of a scanty basal layer, turn vertically downward almost immediately and give rise to basidia, thus forming a thin, arachnoid type of fructification, or by thickening of the hymenium, a membranous fructification. In other species the basal layer may be thin or thicker, but the vertical branches continue to branch and to build up an interwoven "context" tissue before the basidia are differentiated from terminal cells towards the outer surface of the context; the fructification in this case is usually membranous or pellicular, and of appreciable thickness. Depending upon the species concerned, the generative hyphae may at any stage give rise to skeletal hyphae; and both types of hyphae may at any stage give rise to various distinctive sterile hyphal endings, the "cystidia".

Context (Trama)

The context is the mass of hyphae between the hymenial layer and the abhymenial surface of the fruit-body.

The hymenial side of the context may be either smooth or convoluted into a series of spines, dissepiments of tubes, or crests. The tissue within these structures is often termed the 'trama' (De Bary, 1884; Lentz, 1954); however, the present author regards the terms 'trama' and 'context' as synonymous, as also did Donk (1964). Thus instead of 'trama', the tissue can be spoken of as context of the crest, dissepiment or spine, or as the hymenophoral context (Donk, 1964). Separate layers or zones may sometimes be differentiated within the context: two such layers are the basal layer and the cortex.

Basal layer

The basal layer is a region of repent hyphae growing parallel to the substratum and forming the abhymenial surface of the context in some types of effused fructifications. It consists of the first-formed hyphae in the fructification, which later branch and become overgrown. The thickness of this layer varies considerably in different species. It may be composed of only a few hyphae, as in *Hyphoderma tenue* (Pat.) Donk where a hymenium forms very early near the growing edge; or it may be very wide (40-50u and over) as in *Gloeocystidiellum porosum* (Berk. & Curt.) Donk. In the routine description of species, the term 'basal layer' is not often used. Cunningham (1963), however, consistently referred to this layer, and I have found the term necessary for describing the development of effused fructifications, as the growing edge consisted of repent hyphae in the majority of fruit-bodies studied.

Cortex and Trichoderm

In contrast to the basal layer of effused species, the cortex is a tissue forming the abhymenial side of the context of many reflexed or pileate species, e.g. in the genus *Stereum* sensu lato. It is a distinct layer, usually of darker color, composed of intertwined or parallel hyphae cemented together. The term 'cuticle' has been applied to this layer (Fayod, 1889) but was rejected by Lohwag (1937) because this term is generally accepted for use in higher plants for a tissue which is not homologous with that of fungi. The term "cortex" is, of course, objectionable on the same grounds.

The trichoderm is a hirsute layer arising from the cortex or abhymenial surface of the pileus. Lohwag & Peringer (1937) included the cortical tissue in the 'trichoderm'. Lentz (1954), however, defined the trichoderm as consisting only of the hirsute layer arising from the cortex, and this concept is used in this thesis.

Hymenial layer

The term 'hymenial layer' as applied by Cunningham (1963) includes the 'subhymenium' and the 'hymenium'. The term 'subhymenium' is difficult to define. It is used to describe a part of the fruit-body which is not a distinct tissue but rather a zone beneath the hymenium. The margins of this zone are indistinct, especially as it gives rise to, and blends with, the hymenium. In forms with a wide context, the subhymenium is a zone in which the hyphae branch more densely than in the context. Such a differentiation is often obscure, particularly in thin fructifications where the basidia arise from repent hyphae of the basal layer, but it is quite obvious in some of the thicker pellicular species (Talbot, 1954a, fig. 4(4)). As defined by Snell & Dick (1957) and by Cunningham (1963), the subhymenium is a zone of differentiated tissue, a densely intertwined layer of generative hyphae, which gives rise to the hymenium. This definition, however, raises another question of terminology, which becomes pertinent when developmental morphology is being described; as the literal meaning of subhymenium is 'under the hymenium', a layer which develops before the hymenium should not be termed a 'subhymenium'. A preferable term is 'basidiferous layer', that is, a layer of hyphae which gives rise to the basidia. In a mature, well-established thickening hymenium there is a different concept of 'subhymenium'; here the subhymenium consists of the original basidiferous layer plus the depth of old hymenium up to the current level of active basidia. As the hymenium is well established, this use of the term subhymenium is in keeping with its literal meaning.

The hymenium is the basidial and spore-bearing layer of the fructification, and in the Aphyllophorales the basidia are often mixed with sterile elements. The basidiocarp in the Aphyllophoralesbears the hymenium unilaterally, or amphigenously in clavarioid types. Extensive use is made of the form and components of the hymenium in the classification of Aphyllophorales.

Hymenial configuration

The hymenium is often smooth, or nearly so, especially among effused members of the Aphyllophorales, but it has a capacity for becoming convoluted into folds, spines, lamellae or tubes, particularly in pileate forms. Generally the configuration of the hymenial layer depends upon the shape of the underlying context, but Donk (1957a) pointed out that this is not always so. In certain circumstances the folds of the hymenial layer may be due to crowding of turgid basidia, as in some species of *Merulius*; when the basidia lose their turgidity the folds usually disappear.

Hymenial configuration was used by Fries (1874) as the main character in his classification which became standard for Hymenomycetes through its use by Saccardo in his Sylloge Fungorum (1887). Patouillard (1900), however, did not make extensive use of hymenial configuration in his classification of Hymenomycetes as he had studied microscopic features of the fruit-body and realized that similarity of hymenial appearance did not necessarily indicate close affinity as Fries had believed. Increasing emphasis on microscopic characters has led to the discovery of many instances of apparently natural series which cut across the groups of Fries's classification. Two series with fruit-bodies ranging from lamellate to poroid were described by Heim (1948). Several series, each containing different types of fruit-bodies and hymenial forms were discussed by Corner (1954a), his Xanthochroic series (Hymenochaetaceae Donk, 1948) being perhaps the best known of these. Therefore it is not surprising that in the literature it is frequently mentioned that hymenial configuration is not a satisfactory taxonomic character (e.g. Wakefield, 1948; Corner, 1954a; Eriksson, 1958a; Donk, 1964; Ingold, 1965). Despite this, it is still extensively used.

Convolution of the hymenium may be a biological advantage to the fungus as, for a given bulk of fruit-body, it produces a greater spore-bearing area than if the hymenium were smooth (Gäumann & Dodge, 1928. No matter which type of convolution is present, the spore-bearing surfaces are a "safe distance" apart. This "safe distance" is determined by the distance that spores are shot from the basidia; it is the minimum distance between spore-bearing surfaces which allows the spores to be discharged in the space and not onto the opposite hymenial surface (Ingold, 1965). This has limited the ways in which the spore-bearing area has been able to increase in the Hymenomycetes and has resulted in convergent evolution of hymenial configuration. If there are few possible methods of attaining important ends then convergent evolution is probable, if not inevitable (Savile, 1955). For example, the Polyporaceae and Boletaceae are regarded as quite separate groups, but the form of their hymenia is remarkably similar. This limit on the number of forms of hymenial configuration has ensured that natural groups of fungi have paralleled each other in the evolution of hymenial configuration from simple to complex. The several series mentioned by Corner (1954a) are examples. There is also evidence of parallel evolution of the same hymenial configurations in both Heterobasidiomycetes and Homobasidiomycetes (Teixeira & Rogers, 1955).

Thickening hymenia

Corner (1950), in describing the hymenia of clavarioid fungi, said that in some cases the hymenium remains as a single layer of basidia but that in most species it continually thickens. This is accomplished by branches which grow from below and between the current basidia and overlap them before producing new basidia, thus continually increasing the thickness of the hymenial layer. Corner regarded these two states of the hymenium as being of some systematic importance but did not have sufficient information to evaluate their significance. A valuable contribution to the understanding of hymenia was made by Donk (1957a). He noted that thickening of the hymenium is often encountered in members of the Aphyllophorales and especially in many species with effused fructifications. Originally the fructification may be barely visible to the naked eye, the hymenium very sparse and the context virtually absent, but by gradual intercalation of new hyphae and constant renewal of basidia the fructification may eventually become quite substantial. Donk (1957a) then divided hymenia into two main classes, euhymenia and hyphidial hymenia, with the reservation that not all hymenia in the Aphyllophorales would necessarily fit into these groups.

In euhymenia, basidia and their sterile homologues and derivatives are the first and principal elements to build up the hymenium and they are organized in a definite palisade. Euhymenia are divided into non-thickening ("static") and thickening types. The non-thickening euhymenium consists of basidia and sterile elements (if present) organized in a definite palisade with new hymenial elements being added at about the same level as the exhausted elements by a process of intercalation. A non-thickening euhymenium is probably not completely static but increases slightly in thickness, as can be seen from the detailed studies of Buller (1922; 1924). Thickening euhymenia, on the other hand, are characterized by the formation of new basidia at increasingly higher levels, from branches of the subhymenium which grow between the old basidia.

A hyphidial hymenium (Donk, 1957a) is one in which the basidia are not organized in a definite palisade layer but are scattered and embedded at various levels within a mass of hyphidia. Hyphidia are sterile hymenial elements which, in contrast to cystidia, gloeocystidia and others, are not swollen but remain hypha-like; previously hyphidia were termed paraphyses, pseudoparaphyses or paraphysoids. The hyphidia form a layer before the first basidia are formed. The basidia have to grow through these in order to produce their spores above the surface of the fruit-body. Lemke (1964) changed the name 'hyphidial hymenium' to catahymenium, because in _Aleurodiscus_ species there may be gloeocystidia present besides hyphidia. This latter term was accepted by Donk (1964) as a substitute for his original term.

In the group of species typified by _Xenasma_ _rimicolum_, there occurs a hymenial type which Donk (1957a) recognised as not being referable to any of his categories. Development of the fructification in this species and also in *Amphinema byssoides* and *Repetobasidium mirificum*, which show yet other types of development, is reported in detail in this thesis (p.78).

Texture

Texture is a property of the fruit-body which depends upon the physical arrangement and chemical composition of the structural components, and can vary with climatic conditions and age of the fungus. It is not unusual for a growing-edge of an effused fungus to differ in texture from a mature part of the same fruit-body. A variety of terms are used to describe texture, especially in relation to effused fruit-bodies where such a wide range of textures is exhibited that this character may sometimes have generic significance. For example, species of *Xenasma* are soft-waxy to gelatinous and dry to a varnish-like film (Donk, 1957a), whereas *Hyphodontia* species have fibrous fruit-bodies (Eriksson, 1958a). Bourdot & Galzin (1928) were conspicuously successful in their use of texture as a major taxonomic character for grouping species in subgenera, many of which have now been raised to generic rank.

Texture in the effused Aphyllophorales, though variable, can be grouped into six basic types as described by Talbot (1954a): gelatinous, arachnoid, byssoid, pellicular, membranous and crustose. Texture, however, is a compound character which is difficult to define precisely and is subject to personal interpretations (Ragab, 1953). Various terms are used by different authors to describe the same type of texture, or the same terms may sometimes be used in different senses.

B. CYSTIDIFORM STRUCTURES

The term cystidium was first used by Léveillé (1837) for the elongated, translucent vesicular bodies jutting out from the hymenium in a number of agarics. He regarded them as the same structures as those figured by Micheli in 1729. After the recognition of cystidia there developed two main ideas on their relationship to other structures in the fructification. Schultz (1882) recognized the presence of laticiferous vessels and many mycologists then believed that cystidia were the hymenial endings of a vascular system. On the other hand, De Seynes (1873) believed that the hymenium was composed essentially of one type of organ, the basidium, and that cystidium-like structures originating from about the same level as basidia should be regarded as sterile hypertrophied basidia; this idea has also been expressed by De Bary (1884), Maire (1902), Kühner (1925), Lohwag (1926) and especially Corner (1947).

Cooke (1879) based the genus Peniophora on the presence of structures he termed metuloids. These were larger than basidia, developed from the same level as basidia and extended well beyond the surface of the hymenium;

they were broadly fusiform in shape and obtuse at the apex, hyaline and externally rough with projecting "warts", which covered the whole of the exposed surface of the metuloid above the hymenium. No comment was made about the thickness of the walls of the metuloids. Massee (1889), in his monograph of the Thelephoreae stated his belief that the cells called metuloids by Cooke agreed exactly in origin, position and form with the bodies known as cystidia. He considered that cystidia were always colorless, thin-walled and variable in size in different, and to some extent the same, species. Cooke's drawings do not reveal any detail of the metuloids, but by studying the species which he had placed in Peniophora it is found that metuloids have thick, refractile walls and are not at all like the structures described and figured by Lèveillè. The external roughening with projecting "warts" (crystals) was emphasized by Cooke as a distinguishing feature of metuloids and, by extension, of the genus Peniophora. Subsequently, species which had bodies projecting beyond the hymenium that could not be described as setae and which had crystals on them, no matter how finely encrusted, were placed in the genus Peniophora and the bodies were termed cystidia. Thus cystidioid structures were confused from the beginning and their early terminology throughout the basidiomycetes was relatively simple: if sterile elements projected beyond the hymenium and could not be termed setae then they were termed cystidia; if they were corneous or gelatinous and usually embedded then they were still regarded as cystidia but were specifically termed gloeocystidia. This system had such latitude that the term "cystidium" could be applied to an extremely diverse array of structures, with disastrous effect on their taxonomic usefulness. A number of authors have tried to bring order into this confusion and the best discussions on this subject are those by Romagnesi (1944), Lentz (1954), Talbot (1954a), Singer (1962) and Donk (1964). There has now been considerable discussion in the literature on the subject of cystidia, but "the terminology connected with them is chaotic" (Donk, 1964). Donk himself made a major contribution by his perceptive groupings of sterile hymenial elements.

The terminology of cystidia will now be discussed under the various morphological features which have been used to classify them.

Composition of the cystidial wall

The composition of the cystidial wall has been used as a taxonomic character on which to base the genus *Tubulicrinis*. Walls of the cystidia in this genus dissolve or become distorted in KOH solution (this test is usually standardized by using a 10% solution) and the term lyocystidium has been applied to them (Donk, 1956). Cystidia in this category are typically bi-rooted or multi-rooted, with a capillary lumen that is inflated at the thin-walled apex. Recently, however, some species with lyocystidia have been removed from the genus Tubulicrinis (Oberwinkler, 1965; Parmasto, 1965) which indicates that more information is needed about the significance of this character, especially as it had previously been regarded as a major generic character.

Thickness of cystidial walls

Thickness of the cystidial walls is used to distinguish two types of cystidia (Romagnesi, 1944): leptocystidia and lamprocystidia.

Leptocystidia are cystidial structures with thin walls and are essentially what most authors usually termed cystidioles, i.e. abortive basidia which are more strongly developed than the fertile basidia. They have sometimes been termed basidioles but this term has usually been restricted to immature basidia or sterile cells closely resembling, but smaller than, basidia. Donk (1964) includes cystidioles and basidioles as leptocystidia, whereas Lentz (1954) defines a leptocystidium as a "thin-walled cystidium larger than a cystidiole". There appears to be little merit in differentiating the same types of structure merely on the basis of size. The term leptocystidium was not intended to include gloeocystidia, thin-walled structures with dense contents.

Lamprocystidia have thick, glassy (easily broken) walls and this term applies to the structures originally termed metuloids (Cooke, 1879) in Peniophora sensu stricto, and to similar structures in other genera; the term lamprocystidium is thus an unnecessary synonym of metuloid.

Shape

Terms based on the shape of cystidia are generally for descriptive purposes and do not indicate separate types of cystidia. For example, "vesicles" are simply pyriform gloeocystidia; nevertheless, it took a long time before this was appreciated.

Contents

Cystidia may be divided into two broad categories on the basis of their contents. Sterile structures with dense, deeply staining, oily, resinous or granular contents are termed gloeocystidia. Those without these contents are collectively left under the general term cystidium. Gloeocystidia may originate anywhere in the fructification and are characteristically embedded; often they extend as far as the basidial level but rarely project beyond the hymenium. Gloeocystidia have thin, hyaline walls and are generally narrow, flexuous and subcylindrical or wider and clavate; ovoid or vesicular shapes are not common. Gloeocystidia are also classified by the reaction of their contents to the sulfo-aldehyde test. Those which give a positive reaction have been termed macrocystidia (Romagnesi, 1944; Lemke, 1964) and the term gloeocystidium restricted to structures which are aldehyde-negative (Singer, 1962). I agree with Donk (1964) that the use of the term macrocystidium should be discouraged because gloeocystidia which react positively with sulfo-aldehyde are homologous with and no bigger than those which react negatively. Gloeocystidia reacting positvely with sulfo-aldehyde have been referred to as sulfo-cystidia (Boidin & Ahmad, 1963; Boidin, 1966). More information about the sulfo-aldehyde reaction is needed before it can be judged whether a separate term for the positively-reactive structures is warranted.

Within the category of gloeocystidia a number of more specialized types are recognised:

(a) Moniliform gloeocystidia have the typical contents and flexuous-cylindrical shape of gloeocystidia but their apices are moniliform. These are commonly found in *Aleurodiscus* where they have been termed pseudophyses (Höhnel & Litschauer, 1907), and paraphyses (Lentz, 1954). Lemke (1964) regarded the pseudophyses and gloeocystidia (elements which were not characteristically moniliform) present in *Aleurodiscus* as homologous structures and following Singer (1949) used the term pseudocystidium for both these structures. The pseudocystidia in *Aleurodiscus* may react positively or negatively with sulfo-aldehyde depending on the species. There appears to be no point in using these alternative terms as they now have ambiguous meanings and are also unnecessary when in the term "moniliform gloeocystidium" the type of cystidium and its morphology is indicated.

(b) The "vesicles" of *Stereum purpureum* are thin-walled ovate, pyriform to elongated (in the hymenium) structures with densely-staining contents. They are regarded by the present author as gloeocystidia of the uncommon ovoid shape and a more appropriate name for them would be vesicular gloeocystidia.

(c) Stephanocysts (Boidin, 1958a) have been found in only a few species and have a peculiar morphology. They are thin-walled, one-celled or two-celled, subspherical vesiculate organs with a girdle of digitate processes around the basal septum of one-celled stephanocysts or round the septum dividing the two cells of two-celled stephanocysts. Boidin restricts the term stephanocyst to the apical cell only, i.e. a stephanocyst would then be delimited by a basal girdle of digitate processes. However, in <u>Hyphoderma tenue</u> the two-celled stephanocyst is clearly differentiated from the hypha which it terminates, and it is therefore better to name the whole structure a stephanocyst. Stephanocysts are strange structures, but as their contents stain deeply it seems likely that they are gloeocystidial organs. Rogers & Jackson (1943) used the term "caliciform gloeocystidial bodies" for stephanocysts and found numerous intergrading structures connecting them with simple globoid gloeocystidia.

(d) Gloeocystidial hyphae are hyphae with the typical contents of gloeocystidia and they may have typical "gloeocystidial" terminations where they end in the hymenium. The hymenial terminations of gloeocystidial hyphae have been called gloeo~~v~~essels by Singer (1962).

Place of origin

Burt (1926) made considerable use of the position of cystidia in the fructification for differentiating species of Peniophora s. lat., but made no attempt to classify cystidia themselves by their position or by their origin and subsequent development. These should, however, be important factors in the classification of cystidia. The commonly used criterion is whether cystidia are "hymenial" or "tramal" (Lentz, 1954; Donk, 1964) but it is not always clear whether these terms refer to place of origin, or to position of the cystidia in the mature fructification. This difficulty arises largely because it is only relatively recently, through the review work of Donk (1957a, 1964), that there has been a clear appreciation of the fact that certain types of fructification increase in thickness by possession of a thickening hymenium; thus cystidia found in the trama of a mature fructification might well have been hymenial in origin but overgrown by the thickening tissues. With regard to origin of cystidia it must be remembered that although Corner (1932a,b) had defined hyphal types and hyphal systems in some polypores, his work was largely neglected until Cunningham (1946) applied it to a revision of New Zealand Polyporaceae. Even then it was some years before hyphal analysis became generally appreciated and used. Thus until quite recently there has been no accurate way of specifying the type of hypha giving rise to a cystidium. Knowledge of hyphal analysis and of the ways in which fructifications and hymenia develop now makes it possible to analyze the origin, development and final positioning of cystidia in effused Aphyllophorales; such work, indeed, forms the major part of this thesis.

Lentz (1954) defined hymenial cystidia as true cystidia which originate at about the same level as the basidia and sometimes in the basidial fascicle. Lentz did not conclude whether hymenial cystidia were equivalent to basidia or not, but found that their position, nuclear condition and sometimes form, suggested that they were sterile hypertrophied basidia. On the other hand, Donk (1964) restricts the term hymenial cystidium to those structures "in the hymenial layer produced by, or with, the subhymenium (basidiferous tissue) and homologous with the basidia". Leptocystidia and lamprocystidia are regarded as hymenial cystidia (Lentz, 1954; Donk 1964) and gloeocystidia which originate in the hymenium are termed hymenial gloeocystidia.

Tramal cystidia are those originating in layers deeper than the basidial level, generally in the context or trama (Lentz, 1954). When hymenial cystidia become embedded by a thickening hymenium they may appear to be tramal in origin; therefore it is important that the development of cystidia be studied so that they can be referred to their proper place of origin. Tramal cystidia penetrate from the context into the hymenium and often protrude beyond it. Gloeocystidia originating in the trama from either tramal gloeocystidial hyphae or generative hyphae are best termed tramal gloeocystidia. The term pseudocystidium has been applied to these gloeocystidia (Romagnesi, 1944; Lentz, 1954; Singer, 1962) but this is superfluous when gloeocystidium is a well established, satisfactory term (Donk, 1964). Skeletal hyphae which bend toward the hymenium and terminate in the hymenial region with unmodified or modified apices, sometimes with gloeocystidial contents, are termed skeletocystidia (Donk, 1964). The term pseudocystidium has also been applied to these structures but it is ambiguous as it has been applied to sterile structures originating from gloeocystidial, generative and skeletal hyphae; some authors restrict the term to gloeocystidial structures. To avoid such ambiguity the term skeletocystidium is preferred, especially because it implies that the cystidium develops as the hymenial ending of a skeletal hypha. When skeletocystidia terminate skeletal hyphae from deep in the fructification they are tramal in origin. But in fructifications with thickening hymenia new skeletal hyphae are continually being formed in the hymenial region and if these become modified almost immediately, the pedicels are very short and the cystidia could be classed as hymenial in origin although they are clearly homologous with those produced from tramal skeletal hyphae.

The term hyphocystidium has been introduced by Donk (1964) for tramal cystidia which originate from context generative hyphae and retain their hyphal character. This term includes the septocystidia of Cunningham (1953) but it is not clear from Donk's description if it also applies to any similar, aseptate hypha-like cystidia.

Cunningham (1955) used a different criterion of origin for classifying cystidia in the Thelephoraceae sensu lato: he differentiated between pedicellate and radicate cystidia. Pedicellate cystidia are composed of two parts, a basal pedicel and a modified apical part with crystal encrustation; they can arise from hyphae anywhere in the fructification. Radicate cystidia arise usually laterally and only from hyphae in the base of the fructification and are sessile; their bases are either inflated, extended laterally, or bear two or several radicate extensions. This type of cystidium is typical of the genus _Tubulicrinis_. The pedicellate group is not a useful concept as such a variety of cystidiform structures is included, but the notion of radicate cystidia is more useful because these are much more homogeneous in origin, development and morphology. The lyocystidia described above are a specialised form of radicate cystidium.

Hyphidia

Although hyphidia are not cystidioid structures they were present in a number of species in which the development of the fructification was followed during the course of this work and therefore their terminology is included in this section. Hyphidia are sterile elements produced by the hyphae of the context and retaining their hyphal nature by not becoming characteristically inflated in the manner of other hymenial elements and basidial homologues, to which the term cystidium is restricted (Donk, 1964). Most hyphidia belong to the generative hyphal system and typically are produced in advance of basidia, forming a catahymenium. Excluded from hyphidia are all bodies belonging to the gloeocystidial system which inflate in the hymenial region, and also hyphocystidia.

Donk (1956) introduced the term hyphidium for what had previously been called paraphyses, pseudoparphyses, paraphysoids, dikaryoparaphyses and like terms. The acceptance of this term brings order into the confusion of names applied to these structures and also removes the criticism that paraphysis was originally used for Ascomycetes and should not be applied to dicaryotic structures in Basidiomycetes (Lentz, 1954). Barely-modified hyphal endings are termed haplohyphidia; dichotomous ones are dichohyphidia; strongly branched ones are dendrohyphidia; and those with aculeate processes are acanthohyphidia. In a rapidly thickening hymenium it is difficult to distinguish between hypha-like hyphidia and the generative hyphae growing through the current level of basidia.

Lemke (1963) introduced some confusion into the terminology of hyphidia by accepting "hyphidium" for hyphoid structures but using acanthophysis and dendrophysis for non-hyphoid ones. Acanthophysis as used by Lemke corresponds to acanthohyphidium of Donk; dendrophysis is used for incrusted arborescent hyphidia which terminate in non-hyphal filaments in the ultimate parts of the branches; and dendrohyphidium is used for irregularly branched hyphidial elements.

A.H. Smith's Classification of Cystidia

Recently an attempt was made to reduce the number of terms applied to cystidia (A.H. Smith, 1966). Since this work appeared in an advanced treatise on the fungi (Ainsworth & Sussman, 1966), and is therefore likely to influence the thinking of many mycologists, it will now be reviewed in some detail.

Smith classifies cystidia by position and type (based largely on morphology) and believes that the combination of these two factors will enable quick identification of cystidia and concise descriptive work. He does not regard the point of origin of cystidia as significant enough to use in their classification. For classification on position he uses the terms pleurocystidium, cheilocystidium, pileocystidium and caulocystidium, after Buller (1922); dermatocystidium (Singer, 1962) for cystidia on either the pileus or stipe, or peridium of Gasteromycetes, and endocystidium for cystidia in the context of pileus, hymenophore or stipe. Buller's terms are applicable only to agarics, polypores, hydnums and other stipitate-pileate fungi.

For classifying cystidia by their type, Smith has four categories; leptocystidium, lamprocystidium, gloeocystidium and hyphoids.

Leptocystidia are smooth and thin-walled, with a shape different from that of basidia. They are presumed to be modified basidia and are the common type of cystidium found in the Agaricales. The term cystidiole, now generally considered synonymous with leptocystidium, is regarded by Smith as a needless introduction to the nomenclature of cystidia - nevertheless it preceded leptocystidium.

Lamprocystidia are thick-walled at least in some part, with or without encrustation, and with walls colored to hyaline. Smith lists three sub-types within this type.

(a) "Setiform lamprocystidia", which are awl-shaped with typically colored walls. Smith does not accept the term "seta" in its usual specialized sense (Lentz, 1954) and considers that setae in the Hymenomycetes are simply lamprocystidia, usually with colored walls which frequently darken in KOH. As a general rule, if the cystidium is ten times, or more, longer than it is wide in its widest place, and tapers to an acute apex, then it is regarded as meeting the criterion set for a setiform lamprocystidium. Smith believes that color should not be emphasized because there are examples of these structures in the Agaricales with all degrees of wall coloring. According to Smith the KOH reaction is well known on spore and hyphal walls of brown-spored agarics and he does not think that the reaction is of sufficient importance to justify restricting the term setae only to those thick-walled cystidia which show it. Thus a wider range of structures is included under this term than is generally admitted for the term seta. Donk (1964) has suggested that the setoid organs in the Agaricales might better be termed lamprocystidia although he still considers the structures in the Hymenochaetaceae to be setae.

(b) "Astrosetae", which are radially branched lamprocystidia. These have also been termed "stellate setae" and "asterophyses" by other authors.

(c) "Mycosclerids", which are versiform endolamprocystidia, and often hypha-like. Smith believes that descriptive terms should "mean what they say" and that there is no point in defining "skeletals" as thick-walled hyphae lacking clamps, since all the ground hyphae of a basidiocarp, no matter what their form, are skeletal hyphae in the sense that they are the framework of the basidiocarp. He therefore suggests that "mycosclerid" is a better term than "skeletal hypha". This seems to be rather a liberal extension of the original application of "mycosclereid" by Wright (1955), who introduced the term for certain conspicuous, thickened and colored terminal hyphae in the external portion of the walls of the endoperidium in Tulostoma berteroanum Lév.; these structures reminded him of the giant sclereids found in higher plants so he tentatively named them "mycosclereids". These mycosclereids are relatively short, wide thick-walled cells, obviously differentiated from the hyphae which bear them and not in any way like the skeletal hyphae found in polypores. In my opinion the use of mycosclerid as proposed by Smith is unsuitable. Smith has also suggested that mycosclerid be used for the cystidioid structures termed "false setae" (Talbot 1951: Lentz, 1954).

Gloeocystidia, according to Smith, are versiform cells distinguished by their contents, which either stain heavily, or are oily or amorphous and refractive. Two subtypes are possible within this category:

(a) "Chrysocystidia", which are like leptocystidia but with highly staining contents, refractive as revived in KOH. This type of gloeocystidium is not characteristically the termination of a laticiferous system whereas most gloeocystidia are.

(b) "Pseudocystidia", which are filamentous to fusoid elements with oily contents when fresh and represent the simplest gloeocystidia. As stated previously, I believe that the use of the term pseudocystidium should be discouraged. For laticiferous elements which do not project into or beyond the hymenium it is possible to use the term "endogloeocystidium".

Hyphoids are filamentous to cystidium-like cells characterized by peculiar systems of branching. Included in this category are:

(a) Dendrophyses with tree-like branching.

(b) Acanthophyses with aculeate projections.

(c) Dichophyses which repeatedly branch dichotomously.
As Smith accepted the term "hyphidium" proposed by Donk (1956), it is pointless for him to insist on using the suffix "-physis".

A.H. Smith's (1966) summary of cystidial classification, the most recent to have been published, appears to me to contribute little new information of value and to introduce further confusion into the terminology of cystidia. One especial weakness is that it does not take the point of origin of cystidia into account. Although Smith's system purports to reduce the number of categories of cystidia to four based on morphological type, it does not significantly reduce the number of terms, because each category has a number of subtypes corresponding roughly with existing named types; for example, setiform lamprocystidium instead of seta, and mycosclerid instead of skeletocystidium or skeletal hypha. His categories are based largely on cystidial forms found in agarics and undoubtedly do not cover the wide variety of forms found in the effused Aphyllophorales.

In this study I have mainly adopted the more conventional, and to my mind more rational, system of cystidial nomenclature outlined by Donk (1964).

III. MATERIALS AND METHODS OF EXAMINATION

A. MATERIALS AND METHODS

The species originally selected for developmental studies belonged to the genera Peniophora sensu lato and Stereum sensu lato. These genera were particularly suitable, as they are acknowledged as being heterogeneous and their species contain a diverse range of cystidiform structures distributed over a number of developmental types. Cystidiate species from other genera were included for study when fresh material became available or if a study of their particular cystidiform structures was desirable.

Specimens for study were collected from the Adelaide Hills and South Eastern districts of South Australia. In the living fungus, with turgid hyphae, microscopic examination of the thin growing edge and of the structural arrangement of the fructification is greatly facilitated. Fresh specimens are also necessary for conclusive results to be gained from sulfo-aldehyde tests (Boidin 1958a). However, as only a limited number of suitable species could be obtained in a fresh condition, herbarium specimens were used to supplement this material. A number of cultures of Aphyllophorales inhabiting litter of Pinus radiata were made available by Mr. J. Simpson and were used to supplement the collections from the field.

To deduce the manner of development of fructifications, microscopic sections from mature regions were first examined. These gave an idea of the structures present, their general appearance and their arrangement at maturity. Young structures were then examined, first in primordial fructifications or in the growing edge of more mature fructifications, and then serially in material taken from successively more mature parts of the fructification. This procedure enabled the development of hyphae and specialised structures to be followed with some certainty.

Preparations for study were made from hand-cut transverse sections and fragments of fructifications. The fragments were placed in a drop of mountant on a slide and teased apart with finely honed needles under a binocular dissecting microscope. To enable dried material to be effectively prepared in this manner, it was first soaked in 5% potassium hydroxide solution for some hours. The mounted material was finally examined and drawn, with the aid of a camera lucida, under an oil immersion objective.

Material was usually mounted in potassium hydroxide/phloxine solution (Martin, 1934). This was found to be very satisfactory, as the potassium hydroxide caused dried material to swell to normal proportions and the phloxine stained the cytoplasm. When potassium hydroxide/phloxine was not appropriate (e.g. for cystidia of Tubulicrinis or for seeing crystal encrustations which dissolve in KOH) aniline blue/lactic acid was used. Ammoniacal congo red mountant (Boidin, 1958a) mixed at the time of mounting with a trace of 2% aqueous phloxine (Warcup & Talbot, 1967), was sometimes useful as it stained cell walls as well as the cytoplasm. However, the staining can sometimes be too intense, especially when hyphae are closely packed or if the sections are moderately thick. Melzer's solution was used as a routine mountant because the amyloid color reaction sometimes exhibited by spore and hyphal walls when treated with this solution is a valuable taxonomic character. However, it is now apparent that caution should be exercised when interpreting reactions with Melzer's solution (Singer, 1962; A.H. Smith, 1965). Smith stated that there are reactions other than those involved with cell walls and that different degrees of amyloidity may be exhibited by some groups of spores. Also a range of shades is included in the amyloid or pseudoamyloid (dextrinoid) categories.

Fresh specimens with gloeocystidia were mounted in sulfo-aldehyde solution (Boidin, 1958a) and cresyl blue solution (Singer, 1949). In sulfo-aldehyde (sulphuric acid and formaldehyde) solution the contents of gloeocystidia of some species turn brown or violaceous-black which is termed a positive reaction; no color change is regarded as a negative reaction. Whether gloeocystidia react positively or negatively has been used as a taxonomic character (Weresub & Gibson, 1960; Slysh, 1960), but contradictory results obtained from this test by McLain and Weresub (1962) indicate that care is needed in interpreting and using the results. They found both positively and negatively reacting gloeocystidia in cultures of Peniophora pseudo-pini.

B. ORIENTATION OF STRUCTURES IN THE FRUIT-BODY

It is necessary for the purposes of description to have a convention regarding the orientation of the fungus. "The normal condition in the Hymenomycetes is that the one-sided hymenophore faces downward" (Donk, 1964, p.208); however, the hymenium does not consistently face downward. Talbot (1952) noted that resupinate Hymenomycetes "are frequently found growing on the upper or lateral surfaces of the substratum" --- and "are unable to undergo tropic movements to bring the hymenium into a downward-facing position if it does not face downwards naturally". Fructifications can be found on vertical surfaces (Christiansen 1959), especially under bark on the sides of fallen logs and "in effused or appressed-reflexed fruit bodies growing on a vertical substratum the hymenophore of the non-reflexed portions is directed sideways" (Donk, 1964 p.210). Sometimes hymenophores are found facing upwards; for example, Peniophora cinerea (Fr.) Cooke is commonly found on the upper surface of branches lying on the ground. In the laboratory, however, fructifications are invariably examined with the hymenium facing upwards. This can lead to losing an appreciation of the actual position of the hymenium in the field and to becoming more accustomed to regarding a hymenium as facing upwards. When illustrating these fungi it is a matter of personal preference whether the hymenium is drawn facing downwards, thus portraying it as it is normally found in nature (e.g. Eriksson; Rogers; Martin), or upwards, thus orientating it as examined in the laboratory (e.g. Boidin, and most other mycologists). But as this study is much concerned with growth directions of the fructification it is necessary to have the directional terminology in keeping with the normal relationship of the fungus to geotropic forces. Thus "upward" signifies a direction toward the substratum and "downward" signifies a direction away from the substratum.

The terms proximal and distal, hymenial and abhymenial, are used when referring to portions of fructifications. In this text "proximal" indicates that region nearest the substratum or the centre of the fructification and "distal" that region furthest away from the substratum or the periphery of the fructification.

The hymenial side of a structure is that part facing towards the hymenium and the abhymenial side is that part facing away from the hymenium.

IV. COMPARISONS AND CONCLUSIONS DRAWN FROM DEVELOPMENTAL STUDIES

The reader is referred to Appendix I for detailed descriptions and illustrations of development of cystidia and fructifications in the various species that were studied. These studies enabled me to group cystidia into a number of types which corresponded closely with some of those recognised previously and reviewed in the section on Terminology of Cystidia; I consider that the majority of other cystidial types to which names have previously been given, represent synonyms or are differentiated on trivial grounds only.

The following account first (Section A) compares cystidial types and their development in all the species studied, grouping the species under headings which indicate the cystidial types that I have recognised. This is followed by a short assessment of the taxonomic value which can be attributed to the recognised cystidial types. Next (Section B), the various types of effused fructifications are surveyed from the viewpoint of their development. Some observations on distinctive ways in which fructifications may thicken are recorded in Section C. And finally (Section D) the taxonomic use of the data is discussed, particularly at the generic level.

A. CYSTIDIAL TYPES AND THEIR DEVELOPMENT

Skeletocystidia

In species with a dimitic hyphal system, the growing margin is dominated by skeletal hyphae which curve downward a short distance behind the margin, grow vertically, and are mixed with generative hyphae to form a context. The hymenium is later produced at the level of the apices of the skeletal hyphae. Skeletocystidia ending in the hymenium usually have long curving pedicels; but because skeletal hyphae continue to form during subsequent thickening of the fructification the skeletocystidia tend to be shorter and more vertical when they are formed near or within the thickening hymenium. Thus skeletocystidia initiated in the hymenium may not appear to originate from skeletal hyphae and can be related to these only by tracing their development in the fructification as a whole.

The skeletocystidia in species of *Stereum* s.str. (*Stereum hirsutum*, *S.vellereum*, *S.fasciatum* and *S.sanguinolentum*) are the unmodified or slightly inflated apices of skeletal hyphae ending in the hymenium. In *S.sanguinolentum* the skeletal hyphae have contents which darken on contact with air and have been assumed to be tannin-like in composition (Boidin, 1958d); traces of similar substances occur in the skeletocystidia of other species of *Stereum* s.str.

In *Xylobolus illudens*, skeletocystidia were found to develop in the same way as those of species of *Stereum* s.str., but were more inflated at the apex. In *X.frustulatus*, thick-walled hyphae are present and simulate skeletal hyphae, but they can be linked through intermediates to the acanthohyphidia and are therefore not regarded as true skeletocystidia.

The skeletocystidia in both species of *Duportella* studied were somewhat setoid in appearance and arose by modification of skeletal hyphae ending in the hymenium. Both species were at one time placed in *Hymenochaete*, but their setoid hyphae are certainly not true setae. The apices of the skeletocystidia taper to narrow, rounded thick-walled ends and are usually minutely rugulose or lightly encrusted with crystals; their walls are light to dark brown. *Duportella tristicula* also possesses gloeocystidia, but their development was not elucidated.

The cystidia in *Amylostereum chailletii* and *Lopharia crassa* are rather similar in appearance to those of *Duportella*, but are not as cylindrical or as narrow. In *A.chailletii* the skeletal hyphae curve down to end in or beyond the hymenial level; their walls are darker than those of the generative hyphae and their apices in the hymenium are thick-walled, taper to a narrow rounded end, and are quite heavily encrusted with crystals. In mature fructifications where their origin is obscure, the apices of the skeletocystidia closely resemble metuloids. Although the cystidia in *A.chailletii* and *Duportella* species follow the same developmental pattern they differ in morphology.

In A. chailletti they are not so setoid, and are lighter-brown in color and more heavily encrusted with crystals. The cystidia of Lopharia crassa are sub-hyaline, crystal-encrusted and fairly thin-walled in young stages, but become almost devoid of crystals and with thick, dark walls in old stages. The more heavily-encrusted apices are sometimes metuloid in appearance (see p. 205). L.crassa is generally considered to be monomitic, but the long, thick-walled aseptate pedicels of the skeletocystidia resemble skeletal hyphae and originate in the growing edge in a similar way to other skeletocystidia. Possibly they may be regarded as forming a reduced type of skeletal hyphal system, but they are unlike skeletal hyphae in that they often branch to give rise to more cystidia. The skeletocystidia of A.chailletii sometimes branch near the apex.

Lopharia cinerascens is dimitic, with its cystidia formed from modified skeletal hyphae. They are large, heavily encrusted and metuloid in appearance, at least at the apex. Those formed in the growing edge have long, thick-walled aseptate pedicels and are clearly modified down-curved skeletal hyphae. The ones formed in the hymenium, however, have short pedicels and resemble typical metuloids. Only by tracing the development of the cystidia in different stages of thickening of the fructification, can the marginal and hymenial cystidia be related to one another; they are essentially the same type.

It may be concluded that the skeletocystidia of these species develop in a similar way, but show a certain amount of morphological variation, particularly towards their apices.

Metuloid cystidia

The metuloid cystidia as found in species of Peniophora s.str. are characterised by fusoid shape, short pedicels, peculiar thickening of the walls and dense crystal-encrustation. In the proximal two-thirds of the cystidium the lumen is comparatively wide, but below this it narrows abruptly into a capillary channel, except at the apex where it expands again into a small thin-walled bulb. Crystals encrust the walls of the cystidium from the apex to just beyond the point where the lumen narrows. In a recently-matured cystidium the crystal-encrusted area is the portion which projects beyond the hymenium.

Metuloids in Peniophora nuda, P.incarnata, P.cinerea, Phlebia gigantea and Phlebia hydnoides develop in the growing edge as modified downturned apices of basal hyphae, or from lateral swellings of the basal generative hyphae; consequently many of the first-formed cystidia have bi-rooted bases, and are usually nature by the time a hymenium forms from vertical hyphae. After vertical growth is established, cystidia develop as the modified apices of vertical hyphae. In P.cinerea there are also cystidia which develop in the same manner as metuloids but do not become encrusted with crystals; they lengthen as the hymenium thickens, their apices being at the current basidial level. They are best compared with skeletal hyphae (see p. 96).

The metuloid cystidia of *Hyphoderma pubera* develop in the growing edge from apical cells of the first-formed vertical hyphae. Basidia develop in a similar position to the cystidia and in the early stages of development the basidia and cystidia cannot be differentiated. The same relationship between basidia and cystidia continues as the hymenium thickens.

Peniophora cremea has crystal-encrusted cystidia resembling metuloids, but although the walls thicken the lumen remains comparatively wide and the apex is more rounded than in a typical metuloid. The crystal-encrustation on the mature cystidia is not as dense as that of a metuloid and is composed of discrete large granules rather than of a continuous mass of smaller crystals. In the fructification of *P.cremea* a floccose context develops from the basal layer a short distance behind the growing edge and the apices of some context hyphae become differentiated into cystidia. Basidiferous hyphae develop from side-branches of the cystidia and from the undifferentiated surface context hyphae. Young cystidia also form in the hymenium but bear the same relationship to basidia as did the ones in the growing edge.

The cystidia of *Lopharia cinerascens* are skeletocystidia by development but are metuloid in appearance and can therefore be placed in either category. Thus the metuloid cystidium is a morphological category and not correlated with a particular type of cystidial origin, but, instead it seems to be correlated with abundant excretion of calcium oxalate.

Gloeocystidia

Gloeocystidia were also not all initiated in the same way. In *Peniophora nuda*, *P. incarnata* and *Hyphoderma pubera* the gloeocystidia develop in the same manner as the metuloids present in those species and correspond with them in size and shape, except that some of the gloeocystidia in *H.pubera* lengthen greatly with the thickening of the hymenium. This also happens in *Hyphoderma tenue* where the gloeocystidia develop in the same way as the leptocystidia but remain embedded in the fructification.

Gloeocystidia in the fructifications of *Gloeocystidiellum lactescens* and *G.leucoxanthum* begin their development in the growing edge as modified apices of basal hyphae. The hymenium arises directly from the basal layer. After downward growth of hyphae is initiated, the apices of the gloeocystidia also grow down, elongating in pace with thickening of the hymenium. This eventually results in a palisade of gloeocystidia traversing a mature fructification from the base of the context to the level of the current hymenium.

A few gloeocystidia are formed in the hymenium and also elongate as the fructification thickens.

The gloeocystidia in the only species of *Aleurodiscus* which I studied, developed in the growing edge in much the same way as those of the *Gloeocystidiellum* species, but were abortive in this position; only the gloeocystidia developing with the hymenium from the first vertical elements persisted. They lengthened as the hymenium thickened but eventually lost their contents and became overgrown by the thickening hymenium. Additional gloeocystidia were continuously formed from hymenial cells and followed the pattern of development just described. The hymenial cells from which they could develop were also capable of giving rise to basidia, acanthohyphidia or dendrohyphidia.

In *Laxitextum bicolor* a broad interwoven context is formed before hymenial elements are differentiated. Gloeocystidia in this species are modified apices or modified side-branches of context hyphae. Most develop in the growing edge before a hymenium is formed but a few develop from hymenial hyphae and lengthen as the hymenium thickens. Thus the gloeocystidia may extend from near the base of the fructification to the current layer of basidia. Their contents become refractile and they eventually disintegrate.

Gloeocystidia in *Chondrostereum purpureum* are inflated, vesicular apices of context generative hyphae. They are formed in the growing edge before the formation of a hymenium and their hypha-like pedicels elongate horizontally until a hymenium is built over them; then they remain in a layer between the hymenium and the context. A few gloeocystidia are formed in the hymenium but these have a clavate shape which possibly results from lateral pressure in the developing hymenium, or may be an effect of positively-geotropic growth forces in the hymenium.

Leptocystidia

Hypochnicium punctulatum, *Corticium patricium*, *Hyphoderma tenue* and an unidentified species of *Hyphoderma* have cystidia which project well beyond the hymenium, are thin-walled to slightly thick-walled and are smooth or only sparsely encrusted with crystals. In all species the cystidia and basidia develop simultaneously from homologous apical cells of the first-formed vertical hyphae in the growing edge; they cannot be distinguished from one another in the early stages of development. The term leptocystidium can be suitably applied to these cystidia as they are homologous with basidia and are thin-walled. Admittedly the walls of older cystidia may thicken a little, but never to the same degree as the walls of metuloid cystidia. The term leptocystidium should be applied only to thin-walled cystidia which develop simultaneously with basidia and are homologous with basidia.

Radicate cystidia

In many of the species previously discussed, the cystidia which form in the growing edge develop laterally from basal hyphae and therefore may appear bi-radicate, with two lateral extensions at the base. One extension is often naturally short, forming a slight "heel" at the base of the cystidium, but in many instances the heel is formed by die-back of one of the long extensions, usually the distal one. In the group of species now to be discussed it is normal for the cystidia to have two or more persistent and well-developed roots; only cystidia of this sort are regarded as radicate cystidia. They are usually large compared with other elements in the fructification, and project for a considerable distance beyond the hymenium; the walls may become very thick and in some species are soluble in KOH solution (lyocystidia).

Radicate cystidia in all the species studied, were formed in the growing edge at a very early stage, well before the development of a hymenium. It was not possible to trace exactly how multi-radicate cystidia developed from lateral swellings of the basal hyphae, as the youngest stages found already had numerous roots from the base. A multi-radicate cystidium probably develops as a lateral branch from a basal hypha so that at first it would be bi-radicate; it is suggested that branches then quickly develop from the proximal side of the base or, in some instances, that each of the original lateral roots may branch very near to the base of the cystidium.

The multi-radicate cystidia of <u>Tubulicium</u> <u>vermiferum</u>

and *Litschauerella abietis* are very similar in appearance, but those of *T.vermiferum* are slightly amyloid and dissolve in KOH solution, whereas those of *L.abietis* are pseudoamyloid and do not dissolve. The cystidia of *Tubulicrinis umbracula* forming laterally from basal hyphae are bi-radicate; those that develop from vertical hyphae are terminal, but may appear bi-radicate through the formation of a lateral heel near the base of the cystidium. In *Tubulicrinis calothrix* there are bi-radicate cystidia in all parts of the fructification but those formed from the vertical hyphae usually have one vertical root and the other diverging at an angle. Two sizes of bi-radicate cystidia are found in *Xenasma rimicolum*; one is small and narrow with a capitate apex, the other is without an inflated apex, has relatively thick walls and an inflated base. *Xenasma pulverulentum* also has small thin-walled capitate cystidia which develop in the same way as those of *X.rimicolum*. The fructifications of these *Xenasma* species thicken by the addition of successive layers of horizontal hyphae; no vertical growth of context hyphae occurs (see p.78). Under these conditions the cystidia of these species always develop as lateral outgrowths from horizontal hyphae.

The cystidia of *Oliveonia pauxilla* are cylindrical and thin-walled, and project for a considerable distance beyond the hymenium. They develop from lateral outgrowths of the basal hyphae and are persistently bi-radicate.

Hyphocystidia

The development of septate hyphocystidia was followed in a number of species.

In Phlebia hydnoides septate hyphocystidia originate in the same manner as the metuloids of this species, and cystidia intermediate between the two forms can be found. The septate cystidia have indeterminate growth, elongating apically and laying down septa at fairly regular intervals. The walls and septa become thickened and crystals form externally.

Both Amphinema byssoides and A.tomentellum develop a byssoid context of generative hyphae at the growing edge before a hymenium is formed. Some distance from the growing edge many of the surface context hyphae develop into hyphocystidia which, when young, are very difficult to distinguish from vegetative hyphae. Not until the cystidia have lengthened and developed many septa and slightly thickened walls, is it possible to discern them easily. A hymenium develops soon after the initiation of cystidia. Lateral branches from above the base of the hyphocystidia may develop into either basidial fascicles or cystidia. The cystidia in both species of Amphinema have indeterminate growth.

The development of septate hyphocystidia in Hyphoderma setigerum followed the same pattern as in the Amphinema species, except in some collections where the hymenium developed directly on the basal layer. Also in H.setigerum the young cystidia are often part of a basidial fascicle but at no stage do they follow the developmental pattern of basidia.

Two forms of generative hyphae, one darker than the other, are differentiated in the early vertical growth of fructifications of Coniophorella olivacea. After the formation of a byssoid context the light-colored hyphae branch profusely forming a hymenium. At about the same time large septate cystidia develop from the darker hyphae. The cystidia may be formed singly, or several together from the branching of one parent hypha. Although cystidial and basidial systems appear to be separated at an early stage they are not strictly so, since the basidia may develop from cystidial hyphae and vice versa. The cystidia continue apical growth, eventually becoming long, multi-septate and overgrown by the thickening of the hymenium.

Hyphodontia alutaria has two types of cystidia: clamped, septate hyphocystidia, and subulate cystidia which are possibly a form of leptocystidium although they are not all hymenial in origin. The apex of a hypha anywhere in the fructification, but particularly in the hymenium, may become abruptly narrowed into a long thin point which is thick-walled and covered with crystals, thus forming the subulate type of cystidium. The septate hyphocystidia develop from context hyphae just prior to the formation of a hymenium; at first they are relatively short and capitate, but they have indeterminate growth and each new growth-phase leaves a swelling in the cystidium marking the position of what was previously its apex. The intercalary swellings and the capitate apex may be encrusted with crystals. A hyphocystidium of this sort may develop side branches which continue growth as cystidia.

Donk (1964) considered that hyphocystidia are tramal cystidia, originating deep in the context then extending into the hymenial region and often beyond it. However, this study of septate hyphocystidia shows that they develop at the surface of the context and that the hymenium is formed soon afterwards. In some species the cystidia are closely connected with basidial fascicles and are therefore hymenial in origin; they appear to be tramal in origin when they become embedded by the thickening of the hymenium. It is proposed to define hyphocystidia as those cystidia which are hypha-like in appearance and, like hyphae, have indeterminate growth but are nevertheless distinct in one way or another. The septate cystidia discussed above are clearly hyphocystidia.

Unclassified cystidial types

The cystidia of *Repetobasidium mirificum* and *Peniophora longispora* do not fall into any of the categories of cystidia discussed so far.

Repetobasidium mirificum has a simple, almost invisible effused fructification containing septate cystidia. These have a specialized capitate apex surrounded by a membrane and crystals; it would seem that their apical growth is determinate but that they are able to lengthen basally with the addition of more septa. Basidia are able to develop as lateral branches of proximal cells forming the cystidial pedicel. These cystidia are not strictly hypha-like in appearance and also differ from hyphocystidia in apparently growing basauxically.

Peniophora longispora has aseptate hypha-like cystidia of the same width as the generative hyphae and with only very slightly thickened walls. They have a distinctive pattern of crystal-encrustation, but in their young stages are not easy to differentiate from encrusted context hyphae. In the growing edge a thin byssoid context develops on the basal layer. Many of the context hyphae terminate in a cystidium, while side-branches of the cystidial pedicels add to the context and may in turn be terminated by a cystidium. After the hymenium has formed, the cystidia develop from apices of hymenial hyphae or from the apex of two anastomosed hymenial cells (see fig. 30). In the latter case the cystidia appear to be bi-radicate but it is not unusual for cystidia in the context and hymenium also to have a lateral heel near their bases. Because these cystidia are often radicate and are determinate in growth, they cannot be classed with hyphocystidia.

The cystidia of Peniophora cremea are also an unclassified type as although they resemble metuloids they are not true metuloids.

"Tramal" and "Hymenial" cystidia

In the past cystidia have sometimes been classified as either tramal or hymenial (Lentz, 1954; Donk, 1964). However, from the foregoing discussion (and see next section V.B) it is obvious that these terms are difficult to apply rationally. They are not mutually exclusive; the cystidia of a species may be tramal in an early phase of development of the fructification and hymenial in a later phase, as is the case with many skeletocystidia. Other cystidia, which develop in the hymenial region and are embedded by thickening of the hymenium, may appear to have originatedin the context. It is misleading to interpret the origin of cystidia and their relationship to basidia by studying drawings or specimens of mature portions of the fructification. The development of a fructification to maturity is a gradual process; to elucidate the relationships of structures in the fruit-body a study of its development from the growing edge to mature portions is necessary. From this study it is evident that the terms "hymenial" and "tramal" are misleading and not really applicable to the development of cystidia nor of any practical use in the terminology of cystidia. It is suggested that the use of these terms should be discontinued.

Relationship between cystidia and basidia

Corner (1947) introduced a mathematical expression to relate length and width of basidia, namely $L = W(a + bL)$, where L is the length of the basidium, W is its width, and a and b are constants for the species. He showed that "the cystidia of *Clavaria* and *Oedemansiella* conform to the same equations as their basidia and are to be regarded as sterile, and mostly precocious and overgrown basidia". In cases where this applies, the cystidial values of L and W should supply the upper limits for the graph of the basidial values (basidiograph).

It was felt that it would be interesting to test this hypothesis with three species for which adequate measurements were obtained during the course of this study. *Tubulicrinis calothrix* has radicate cystidia which are quite unlike basidia in shape and origin. In *Hyphoderma setigerum* the septate hyphocystidia often develop in the same fascicle as basidia, but do not resemble them at any stage; thus it is unlikely that they are modified sterile basidia. In *Hyphoderma tenue*, however, the leptocystidia and gloeocystidia cannot be distinguished in early development from one another or from basidia; thus there is probably a close relationship between cystidia and basidia in this species.

Corner fitted the equation in the form $L = W(a+bL)$, but this is not the best way as the variables are not independent. For this study the variables were made independent by adopting the form $W = \frac{(\frac{1}{b})\, L}{(\frac{a}{b}) + L}$; where $\frac{1}{b}$ is is the maximum theoretical width attained using the given values, and $\frac{a}{b}$ is a constant which in the context of this work is the width at which half the maximum length is attained. The equation was fitted using the method of least squares (Wilkinson, 1961).

If the cystidia are sterile, overgrown basidia, then the graphs for the cystidia and basidia of a species should not be significantly different. To test this, the theoretical maximum widths were compared in each species (Table 1, p.67).

In Hyphoderma setigerum, the graph for young cystidia was significantly different from that for mature cystidia, but not from that for basidia. This anomaly can be resolved if instead of supposing that the cystidia are sterile basidia the view is taken that the hymenial cells of the fructification have the potential of developing into either basidia or cystidia; thus the cystidia and basidia are separate entities right from the start. In their young stages they will be morphologically similar, but they will become differentiated as they mature. At maturity there is a significant difference in the graphs for cystidia and basidia. The amount of morphological divergence between the cystidia and basidia affects the relationship between their graphs. Accordingly, in H.setigerum and T.calothrix, where the mature cystidia are quite unlike the basidia, there is a significant difference in their graphs; but in H. tenue, where the cystidia are morphologically similar to basidia, there is no significant difference.

The fact that there was a significant difference between the cystidial and basidial graphs in two of the three species (T.calothrix and H.setigerum) confirms the predictions made in regard to these species on morphological grounds, and shows that not all cystidia can be interpreted as sterile basidia.

TABLE 1

Statistical comparisons between cystidia and basidia in three species

	max.width	s.e.	n*	probability	significance
Hyphoderma setigerum					
1. Mature cystidia	10.2811	0.6386	21		
2. Young cystidia	6.3566	1.2495	14		
3. Basidia	6.1132	0.3961	12		
comparing 1 & 2				<.001	sig.
comparing 1 & 3				<.001	sig.
comparing 2 & 3				<.9, >.8	n.s.
Tubulicrinis calothrix					
1. Cystidia	6.0840	0.4945	25		
2. Basidia	4.4754	0.3807	25		
comparing 1 & 2				<.001	sig.
Hyphoderma tenue					
1. Cystidia	8.0824	0.8098	23		
2. Gloeocystidia	8.7783	0.8765	11		
3. Basidia	7.7087	0.6947	14		
comparing 1 & 2				<.2, >.1	n.s.
comparing 1 & 3				<.5, >.4	n.s.
comparing 2 & 3				<.2, >.1	n.s.

* n = number of points to which the equation was fitted

Composition of crystals on some cystidia

DeBary (1887) noted the very general occurrence of calcium oxalate crystals in fungi, giving many examples. Since that time it has often been assumed, usually without analysis, that the crystals which encrust cystidia are composed of calcium oxalate. It was considered desirable to test this by using the technique of X-ray diffraction to analyse the crystals in a few species which did not present great problems in harvesting sufficient material.

A vaseline-coated scrap of razor blade was used to scrape crystal-encrusted cystidia from the surface of fructifications of *Peniophora cinerea* and *Lopharia crassa*. The mixture of cystidia and vaseline was spread over a thin glass road and used as the sample. Cultures of *Amylostereum areolatum* with crystal-encrusted skeletal hyphae were available; undoubtedly these hyphae are the precursors of the encrusted skeletocystidia of the fruit-body. The crystal-encrusted hyphae could not be separated readily from the rest of the culture and so the agar was cut into narrow strips which were piled one above the other and allowed to dry. In this way a thin rod was formed, which could be used instead of a glass sample rod.

With all three species the X-ray diffraction patterns showed that the crystals were composed of the di-hydrate of calcium oxalate; no diffraction patterns of any other compounds were detected. It is not suggested that the crystals in other species necessarily have the same composition.

The categories of cystidia recognised in the foregoing comparative studies are, on the whole, easy to determine and lend themselves to taxonomic use, especially for descriptive purposes. These categories are usefully applied at the species level but are too broadly conceived as they now stand to be an aid in defining genera. Each category of cystidium represents a modified hypha which has been recognised and named because its final form is distinctive in one way or another; but the final form can be reached in various ways, and the basis of its recognition or distinctiveness varies from one category to another. Gloeocystidia, for example, are recognised largely by their contents, and skeletocystidia largely by their origin from skeletal hyphae. Moreover a single type of cystidium may be distributed over several genera, which means that species possessing this type are not necessarily congeneric; genera are based on a composite of many features, of which the cystidial type is only one. On further analysis, however, it is found that more weight can be given to cystidia as a generic character if emphasis is placed not so much on the final form of the cystidium (i.e. its "category") alone, but on its precise way of initiation and development with respect to the development of the whole fructification. The following features therefore assist in defining subtypes of cystidia which are meaningful for generic delimitation but are too numerous to be assigned names:

1. The hyphal system from which the cystidia originate;
2. The development of the cystidia in relation to development of the entire fructification;
3. The final morphology of the cystidia;
4. Reactions of the cystidia with chemicals such as Melzer's solution, sulfo-aldehyde, and KOH solution.

These features do not carry equal weight, nor the same weight in all circumstances, and the taxonomist must judge for himself which factors are more important in a particular situation.

Although this thesis emphasizes cystidia, it is naturally realized that by themselves they are not to be regarded as primary characters in deciding taxonomic relationships; the form and habit of the fructification, the hyphal types and systems, and the basidial and sporal characters are all important and must be assessed together. However, many of these sorts of taxonomic information are often applied separately in generic differentiation and if it is possible to link some of them through a study of the cystidia a more unified basis for the differentiation of genera is likely to emerge. One of the main conclusions arising out of this work is that, at least in the species studied, it is indeed possible to correlate the type and development of cystidium with the type of hypha giving rise to the cystidium and with the manner in which the fructification as a whole develops.

B. FRUCTIFICATIONS AND THEIR DEVELOPMENTAL TYPES.

To a large extent taxonomists have neglected the development of the fructification in their search to find new features for classifying the effused Aphyllophorales. But this aspect of micromorphology is important for a clearer understanding of the relationship between species and is essential for an understanding of the relationship of cystidia to the rest of the fructification. Cystidia are an integral part of the fructification, therefore it is to be expected that their development should be closely allied to that of the fructification. In this study it was found that the pattern of fruit-body development was characteristic for each species and that for the species studied there were only three main types of development, as follows:

Type 1

The stereoid fructification, typified by Stereum s.str., is effuso-reflexed, with a distinctive internal structure; a substantial basal layer of parallel, slightly colored, generative and skeletal hyphae forms the cortex from which the trichoderm develops in reflexed portions. Hyphae from the cortex gradually curve down to the vertical, forming a broad and usually dense context on which the hymenium develops. The fructification grows laterally faster than vertically, so that the hymenium is eventually formed well back from the growing edge. Cystidia developing in fructifications of this type are first found in the growing edge as modifications of the downward-turning skeletal hyphae. It was found that effused species with a dimitic hyphal system always developed a stereoid fructification, but also that some monomitic species could be stereoid in form if their generative hyphae in the cortex and context were thick-walled and simulated skeletal hyphae. It would appear that the stereoid type is correlated with the presence of thick-walled hyphae, either skeletal or generative. In the monomitic stereoid fructification cystidia first develop in the growing edge as modifications of some of the downwardly-turning generative hyphae. In both the dimitic and monomitic fructifications cystidia continue to form after the hymenium is established.

Dimitic species with the stereoid type of development include:

Stereum hirsutum
Stereum fasciatum
Stereum vellereum
Amylostereum chailletii
Amylostereum areolatum
Lopharia cinerascens
Stereum sanguinolentum
Duportella tristicula
Duportella fulva
Xylobolus illudens

Monomitic species whose fructifications resemble *Stereum* s.str. in form, but not identically in construction, are the following:

Laxitextum bicolor
Lopharia crassa
Chondrostereum purpureum
Punctularia strigoso-zonata
Punctularia species indet.

Lopharia crassa is usually regarded as having a monomitic hyphal system but its cystidia are like skeletocystidia and develop in the growing edge in the same manner as those in the dimitic species; this is an instance in which it is very difficult to determine the hyphal systems, but it appears to bear out the observation of Lemke (1964) in regard to species of *Aleurodiscus*, that effused species with a sub-dimitic hyphal system are sub-stereoid in habit.

In species of *Punctularia* and in *Chondrostereum purpureum* the generative hyphae may become thick-walled and, in fact, thick-walled, clamped, generative hyphae compose the trichoderm. The construction of *Laxitextum bicolor* does not resemble that of *Stereum* s. str. very closely but seems to be intermediate between developmental types 1 and 3.

Xylobolus frustulatus is considered to have a dimitic hyphal system but its fructifications are not effused or stereoid; they are obconical and gregarious in such a manner that a number of fructifications together simulate an effused, deeply-cracked fruit-body. *Xylobolus illudens* is clearly not congeneric with this species.

Type 2

Fructifications with the second type of development are effused, with a monomitic hyphal system. They have a basal layer of horizontal hyphae which is only a few hyphae in thickness in some species, or a dense mat in others; its thickness is usually characteristic for a particular species. Vertical hyphae grow directly down from the horizontal hyphae without the gradual curvature that occurs typically in the stereoid fructifications. The hymenium develops directly from branches of the basal layer and is usually initiated very close to the growing margin. The depth of the fructification is built up by thickening of the hymenium, thus the so-called context of these fungi is really the subhymenium of the hymenial layer and is not equivalent to the context in fructifications of Type 1 or of Type 3 (see below). Fructifications in which the hymenium thickens considerably, have a dense texture.

This second type of development can be further subdivided into two groups differentiated mainly by the way vertical elements develop from the basal hyphae.

2 a

The delicate fructifications of the so-called "primitive basidiomycetes" (Oberwinkler, 1965) are included in this group. The cystidia, and in some cases the basidia, develop from downwardly-directed lateral outgrowths of the basal hyphae or from downturned apices of the basal hyphae, both of which are broader than the hyphae from which they originate. These young vertical structures are not septate and are continuous with the parent basal hypha. In most instances the first vertical elements developed into cystidia which were usually nature before the initiation of basidia. Mostly the basidia developed from septate vertical branches of the same width as the parent basal hyphae and further back from the growing edge than the zone giving rise to cystidia. Cystidia continued to be produced after formation of the hymenium, originating from subhymenial hyphae and not from the basidial fascicles; normally they are not closely related to young basidia.

Radicate cystidia are associated with fructifications having this type of development. The species with this type of development are:

Peniophora nuda
Peniophora cinerea
Peniophora incarnata
Phlebia gigantea
Phlebia hydnoides
Aleurodiscus species indet.
Gloeocystidiellum lactescens
Gloeocystidiellum leucoxanthum
Litschauerella abietis
Tubulicium vermiferum
Tubulicrinis calothrix
Tubulicrinis umbracula
Xenasma rimicolum
Xenasma pulverulentum
Oliveonia pauxilla
Repetobasidium mirificum

<u>2 b</u>

The second subdivision is for those fructifications in which the downwardly directed lateral outgrowths are the same width as the basal hyphae and usually develop one or more septa before any cystidia or basidia are formed from their apices. The cystidia and basidia develop from homologous apical cells almost simultaneously, the cystidia being formed just prior to the basidia. The cystidia are hymenial but appear tramal in origin when they become embedded by the thickening hymenium. This was the only type of fructification in which leptocystidia were found. The species with this type of development are:

Hyphoderma tenue	Corticium patricium
Hyphoderma pubera	Hypochnicium punctulatum
Hyphoderma species indet.	

Hyphoderma setigerum is intermediate between types 2b and 3.

Type 3

The third type of development occurs in effused, monomitic fructifications with a relatively thin basal layer from which vertical hyphae grow directly downwards as in Type 2; but instead of the hymenium developing immediately on the basal layer as in Type 2, the vertical hyphae in the growing edge form a loosely-branched context and the hymenium develops over its surface. Lateral growth of the fructification continues while the context is being formed, therefore the hymenium is initiated further back from the growing edge than in fructifications with the second type of development.

The hymenium thickens, but generally not to the extent found in fructifications of the second type. This method of development was characteristic of loose-textured, more byssoid fructifications. Cystidia develop as the modified apices of surface context hyphae. After their initiation, the cystidial pedicels and unmodified context hyphae branch and produce basidiferous tissue. Cystidia continue to form in the hymenium but bear the same relationship to the basidia then as they did in the growing edge. Species with this type of development are:

Amphinema byssoides
Amphinema tomentellum
Coniophorella olivacea
Hyphodontia alutaria
Peniophora cremea
Peniophora longispora

The way in which a fructification develops is a useful taxonomic character. Species placed close together on other grounds were usually found to have the same kind of fructification development; and if species which had previously been placed close together differed notably in the development of their fructifications, then a more intensive study indicated that they were perhaps not as closely related as had been thought. However, there are some species with a similar type of development and similar cystidia, which are not considered to be closely related on other taxonomic features. Therefore, the development of a fructification, as with all taxonomic characters, must be used with discretion and in conjunction with as many other taxonomic features as possible.

C. THICKENING OF FRUCTIFICATIONS

Fructifications may increase in thickness by thickening of the hymenium, by repetition of the basal layer, or by repetition of the context. Repetition of the basal layer or context was found in only a few species.

Repetitive basal layer

By this process a new layer of horizontal hyphae grows over an old hymenium and then produces a new hymenium.

The fructifications of Xenasma rimicolum and X.pulverulentum contain virtually no vertical hyphae; cystidia and basidia arising from the basal layer are overgrown and replaced by new horizontal hyphae which, in effect, thicken the basal layer (without stratifying it) before producing further basidia and cystidia. The process is somewhat similar in Litschauerella abietis, but because vertical and horizontal layers of hyphae alternate the fructifications appear stratified in section. The basal layer gives rise to vertical hyphae which grow down between the basidia and cystidia then diverge laterally to form a new layer of horizontal hyphae which in turn gives rise to a new hymenium; this may be repeated several times. Repetition of the basal layer in these Xenasma species and L.abietis implies that their radicate cystidia and pleurobasidia will be formed throughout the fructification. This would not be so with the usual method of hymenial thickening where vertical hyphae grow down between the basidia and produce further basidia from their apices.

In Repetobasidium mirificum the fructification becomes thickened and stratified in a manner resembling that of L.abietis, except that the new layers of horizontal hyphae develop from the apices of basidial stems which cease proliferating to form basidia and instead give rise to hyphal branches which spread out laterally.

Donk (1957a) recognized that the type of thickening in Xenasma species was not referable to any of his categories of thickening hymenia but the other examples mentioned above have apparently not been noticed previously. A repetitive basal layer has now been described for a number of examples, therefore it should be acknowledged as a distinct type of fructification thickening. It probably occurs more frequently than has been recognized, as Cunningham (1963) has illustrations of Corticium perenne, C. kauri, Peniophora inconstans and P.totara with what appear to be repetitive basal layers.

Repetitive context

This was found occasionally in Amphinema byssoides, but does not appear to have been mentioned by other authors. Normally a fructification of this species consists of a basal layer, a substantial loosely-interwoven context and a hymenial layer. The hymenium thickens to a certain extent by the usual process of hymenial thickening. In a few collections of this species, however, hyphae had grown through the layer of basidia and formed a loosely interwoven layer over the hymenium. This layer was a second context which had produced another hymenial layer.

This type of development may be normal for this particular species, or for this type of texture, or it may be induced by abnormal growing conditions. I have observed with many species that if fresh fruit-bodies are kept in plastic bags for a few days after collection, sterile context hyphae often grow through the hymenium. With polyporoid fructifications the pores may become almost obliterated by a floccose regrowth. Thus in the collections of A.byssoides just described, the fructifications may have been subjected to very damp conditions which resulted in the floccose overgrowth of context hyphae above the hymenium, and when conditions became drier a hymenium developed on what had become a second context. Bose (1940) found that under dry conditions basidia of many Polyporaceae became transformed into hyphal elongations with terminal spores identical to basidiospores; on return to moist conditions the hyphal elongations soon became converted again into regular basidia. Therefore the suggestion that excess moisture is the cause of the atypical fructifications of A.byssoides is perhaps not unreasonable.

As only one example of a repetitive context was found, it may not be a significant method of fructification thickening. But it deserves further investigation, as an illustration of *Hymenochaete cinnamomea* by Cunningham (1963) shows what looks like a repetitive context.

Stratification

Stratification or horizontal zoning of fructifications is frequently seen and can be brought about in various ways. Alternation of horizontal and vertical hyphae, as in *Litschauerella abietis*, will result in stratification; so also will regular changes in texture such as repetition of a loose context with a denser hymenial layer, as in *Amphinema byssoides*. But probably the most frequent cause of stratification would be changes in growth rate of the fructification.

Xylobolus frustulatus has clearly defined stratification, which is seen even in very small frustules without the aid of magnification. Microscopically the strata are seen as zones where the apices of acanthohyphidia are at the same level, probably marking the position of a previous active hymenium; these alternate with zones of lighter color which contain the proximal portions of other layers of acanthohyphidia whose walls are thinner, lighter in color and have fewer aculeate processes than the apices. The crystal-encrusted apices of skeletocystidia in *Amylostereum chailletii*, and metuloids in many species of Peniophora s.str., tend to be in zones and not scattered evenly through the fructification. The zoning in all these species can be interpreted as caused by changes in growth rate. When suitable conditions prevail a hymenium develops and produces sterile elements and basidia; but if conditions do not remain suitable the hymenium ceases activity. The return of favourable conditions initiates a burst of renewed growth which separates the new sterile elements and basidia from the previous ones. Hence the hymenium does not thicken continuously and evenly. The differential growth rate in these examples is probably related to the xerophytic nature of the fruit-bodies which allows them to withstand fluctuations in water-supply. Factors which contribute to the strata being plainly visible are the dense texture of the fruit-bodies and the distinctness of the subhymenial hyphae, whose rigid walls do not easily collapse.

D. TAXONOMIC USE OF THE DATA.

.1. HIGHER TAXONOMIC LEVELS

Table 2* was prepared to summarize the developmental and microscopic features of all the species studied, and to show their current classification in families (Donk, 1964) and sub-family groupings (Eriksson, 1958b). The genera shown are mostly segregates from Stereum s.lat. and Peniophora s.lat., since these were chosen because they contain a large number of cystidiate

* Appendix II

species; these generic segregates are accepted by most mycologists nowadays.

When one examines the Table, and more especially family and subfamily groupings, very few correlations can be observed, since the basis of separation varies from one family to another. Where basidia or spores are highly characteristic they may be made the prime character of the family, similarly with highly characteristic types of fruitbody construction or hymenial configuration.

The Ceratobasidiaceae and Xenasmataceae are founded largely on basidial morphology; the Coniophoraceae on spore cyanophily; the Hericiaceae on gloeocystidia and rough amyloid spores; the Punctulariaceae on a catahymenium spread over small areas separated by sterile fissures; the Stereaceae on construction of the fruitbodies. This is not to say that these prime features are not in each case associated with other features adding up to a family diagnosis, but it is doubtful whether such families would have been recognized without the regular occurrence of these pointers to affinity. The remainder of the genera dealt with are placed in the artificial family Corticiaceae since no features correlate sufficiently well for more natural groupings to be suggested.

The question is therefore: what taxonomic value can be attributed to the developmental type, cystidial type and hyphal system when these are taken together? By examination of the Table it would seem that these features do not correlate sufficiently with others to be of definitive value at subfamily or family level. They do, however, correspond roughly with current subfamily and family groupings and if used by themselves would not cause any major rearrangement of the classification. This work has clarified cystidial types and emphasized fruit-body development, but concludes that neither is usually important as a taxonomic feature above the rank of genus. At the generic level, however, they are extremely useful, especially in combination. They then correlate very well with a number of other features and with current concepts of which genera or species-groups are "good", and which are heterogeneous. For example species assigned to Stereum s.str., Punctularia, Tubulicrinis and Amphinema, showed correlation in all the tabulated features within their respective genera; and those of Xenasma, Phlebia, Peniophora s.str., and Duportella differed in only minor details within their respective genera, e.g. in the presence or absence of clamps, or in the combination of cystidial types when more than one type was present. Where more than one type of cystidium was present in a fructification it was found that they were usually initiated in the same way even though they had to be placed in different cystidial categories through differing in mature morphology.

The species of *Lopharia*, *Xylobolus*, *Gloeocystidiellum* and *Hyphoderma*, do not correlate, within their respective genera, in enough features to warrant their being associated together in one genus. In other words, these genera are not homogeneous in species composition, although in *Hyphoderma* there is a homogeneous subgroup.

Most of the genera in which only one species was studied do not correlate with any other genus. Many of them are controversial genera, but this work would suggest that they are relevant segregates.

It is interesting to observe that some of the best correlations are seen in the stereoid genera and in the Xenasmataceae-Tubulicrinoideae groups which respectively show the best-developed and least-developed fructifications and perhaps indicate the greatest and least number of form-factors involved in the development of the fructifications. The intermediate groups in these respects are those in which correlations are most difficult to find.

2. NOTES ON THE GENERA

In the following notes I propose to dwell on areas of taxonomic controversy rather than on those of general agreement, attempting to contribute to a solution of some of the problems from the results of my own studies.

STEREACEAE (Pilát, 1930; Donk, 1964)

HAEMATOSTEREUM Pouzar (1959): Type species Stereum sanguinolentum.

Pouzar separated this genus from Stereum because the contents of the "vascular hyphae" (skeletocystidia) become red on contact with air and because he considered that the hyphal system is monomitic. Boidin (1958d) contends that Stereum section Luteola (Bourdot & Galzin, 1928; typified by S.hirsutum) and Stereum section Cruentata (typified by S.sanguinolentum) differ only in quantitative features such as wall thickness and the degree of differentiation of the cystidial contents. Consequently Boidin (1960) rejects Haematostereum.

An examination of S.sanguinolentum showed that its development and construction, and its basidia and spores, were like those of Stereum hirsutum, the type species of Stereum s.str. These species also correspond in their pattern of clamp-distribution (Boidin, 1958a). The skeletocystidia of S.sanguinolentum and S.hirsutum differ in wall thickness and intensity of staining of their contents. These differences are not considered sufficient to maintain Haematostereum as a distinct genus.

AMYLOSTEREUM (Boidin, 1958d): Type species Stereum chailletii.

The genus Lloydellopsis Pouzar (1959) is an obligate synonym of Amylostereum.

By reference to Table 2* it will be seen that *Amylostereum* corresponds with *Stereum* in all the listed features except the site of clamps; some workers have therefore doubted whether it should be segregated from *Stereum*. While both genera possess skeletocystidia these differ considerably in form. In *Amylostereum* the skeletocystidia are brown, with thick-walled, acute, crystal-encrusted apices ending at or beyond the hymenial level; in *Stereum* they are lightly colored or hyaline and smooth. In young stages the skeletocystidia of *Amylostereum* may branch (Talbot, 1964) and are not unlike those of *Lopharia crassa*, while in old fructifications their pedicels are obscured and they then appear not unlike short metuloids. They do not appear to have the tannin-like contents which Boidin (1958d) attributes to those of *Stereum*. In addition, Boidin (cited in Lentz, 1960) has found differences between these genera in their reaction on gallic acid medium and in the number of nuclei in their spores. My conclusion is that the genus *Amylostereum* is well distinguished from *Stereum*.

CHONDROSTEREUM Pouzar (1959): Type species *Stereum purpureum*.

According to Pouzar the type species differs from *Stereum* in texture, non-amyloid spores, presence of vesicular bodies, arrangement of the dimitic hyphal system, and in having hygroscopic fructifications.

*Appendix II

Pouzar states that generative hyphae are present only in the part of the context next to the hymenium and in the hymenium, the remainder of the fructification being composed of skeletal hyphae.

A detailed study of Stereum purpureum revealed that although it has a stereoid tissue-construction, the hyphal system is in fact monomitic with clamped generative hyphae; this was also found by Boidin (1959). Hyphae in the base of the context and the cortex become very thick-walled but still possess clamp connexions despite their resemblance to skeletal hyphae. The vesicles of this species are gloeocystidia of an unusual shape, and their development is unlike that of gloeocystidia in the other gloeocystidiate species that were studied. Stereum purpureum therefore differs from Stereum in a number of important features and the genus Chondrostereum is considered to be worthy of recognition.

XYLOBOLUS Boidin (1958d): Type species Stereum frustulatum.

It is curious that the unusual type of fructification in the type species of this genus has received so little comment. It is an obconical frustule, and since the fruit-bodies are gregarious the adjacent frustules eventually make contact at about the level of their hymenia and thus form an apparently resupinate plaque, with deep fissures reaching the substratum between the frustules. The hyphae are short-celled and without clamps in the fructifications. Thick-walled acanthohyphidia are a dominant feature of this species; most are relatively short, but some are very long and can be linked through intermediates with long, naked, thick-walled hyphae resembling skeletal hyphae, which are possibly not homologous with the skeletal hyphae in species of *Stereum*. *X.frustulatus* is usually regarded as dimitic; I was unable to decide its hyphal system with any confidence but would describe it as monomitic to weakly dimitic.

The type species of *Xylobolus* clearly differs from *Stereum* and represents a good genus; but the position is not so clear with *Stereum illudens* which Boidin (1958d) also assigned to *Xylobolus*. The fructification of *S.illudens* is effuso-reflexed and stereoid, quite unlike that of *X.frustulatus*. Its hyphal system is again difficult to interpret. The hyphae in the context and cortex are thick-walled but they become thin-walled towards the hymenium. Superficially the hyphal system appears to be dimitic. The situation was similar in the monomitic stereoid fructifications studied, but in those the septa were clamped and gave a definite indication that all the hyphae were generative. In *S.illudens* there are no clamps in the fruit-body to use as a guide for distinguishing hyphal types. If *S.illudens* is taken to be monomitic this precludes its being placed in *Stereum* and it would be better left in *Xylobolus*; my impression, however, is that it is dimitic and therefore a *Stereum*.

Another controversial point is the weight to be attached to acanthohyphidia in separating *Xylobolus* from *Stereum*. Boidin (1958d) recorded aculeate-tipped basidioles in *Stereum lobatum* and Lentz (1955, pl.16) in *S.ostrea* and *S.sanguinolentum*; these are all species of *Stereum* s.str. Lentz states in his discussion of *Xylobolus*: "Aculeate protuberances may appear on almost any hyphal endings in the hymenium, possibly excepting fertile basidia. The most scantily beset of these elements may resemble the aculeate-tipped basidioles found in some species of *Stereum*, but the more profuse development of protuberances results in the formation of acanthophyses". Therefore because of similarities in development and morphology it seems preferable for the time being to retain *Xylobolus illudens* in *Stereum*.

LOPHARIA Kalchbrenner & MacOwan (Kalchbrenner, 1881):
Type species *L.lirellosa*.

Talbot (1951, 1954b) regarded the type species of *Lopharia* as synonymous with *Lopharia mirabilis* and contended that the latter was also a synonym of *Stereum cinerascens*, though this has been disputed by Boidin (1959). Cunningham (1956a) emended *Lopharia* to include *L.vinosa* (*L.crassa*; = *Stereum umbrinum*), accepted *L.mirabilis* as synonymous with *S.cinerascens*, but placed the latter in *Lopharia* rather than *Stereum*. Lentz (1960) realized that Lopharia as emended by Cunningham and by Boidin (1959) had become very heterogeneous.

In Stereum cinerascens the cystidia are modified skeletal hyphae, although this is not obvious in those cystidia which develop in the hymenium; the latter have a metuloid appearance and are unlike the crystal-encrusted cystidia of other Stereum species. The combined characteristics of S.cinerascens indicate that it is unlike Stereum, but that it is suitably placed in the genus Lopharia.

Lopharia crassa (Cunningham, 1956a, 1963; Boidin, 1959) resembles L.cinerascens in having smooth, hyaline, non-amyloid spores and the possession of crystal-encrusted cystidia. However, the texture of the two species is dissimilar. L.crassa has a loosely-constructed fructification which is monomitic save for the long thick-walled, colored pedicels of the cystidia. As explained earlier these pedicels are best regarded as skeletal hyphae, a view also held by Talbot (1954b), Boidin (1959) and Lentz (1960). The generative hyphae lack clamps, and the basidia and spores are much smaller than in L.cinerascens. In addition the cystidia of L.crassa are quite unlike those of L.cinerascens. They have colored walls, and the pedicels of cystidia formed near the base are long and curved, but shorter and more vertical in those formed near the hymenium. Often a pedicel branches, forming a number of cystidia of varying lengths. This characteristic was found only in one other species, the totally unrelated *Coniophorella olivacea*. If the crystal-encrustation is particularly heavy then the cystidial apices may be metuloid in appearance; but this occurs sporadically in some collections and never in others. It is concluded from these observations that *L.crassa* is unlike *L.cinerascens* and should be removed from the genus *Lopharia*. Lentz (1960) and Talbot (personal communication) are also of this opinion. The question is which genus would be suitable to receive this species. The cystidia of *L.crassa* have some resemblance to those of *Amylostereum chailletii* and, in some collections, to those of *Duportella fulva*, but neither of these genera correspond in other features with *L.crassa*.

It would appear that *Lopharia* is heterogeneous and that *L.crassa* might well be made the type species of a new genus which could probably include *Lopharia papyracea* (Lentz, 1960) as well.

HERICIACEAE (Donk, 1964)

LAXITEXTUM Lentz (1955): Type species *Stereum bicolor*.

This genus is accepted as being a well-defined segregate from *Stereum*, although the fructification in *L.bicolor* is effuso-reflexed and tends to be stereoid. In addition to being monomitic with clamped generative hyphae in the fructification, *L.bicolor* differs from *Stereum* in its duplex context of brown, moderately thickened hyphae sharply differentiated from the hyaline layer of thickened hymenium. The presence of gloeocystidia and small, ellipsoid, amyloid and spiny spores are additional features differentiating this species from a *Stereum*. Although hyphae in the growing edge of the fructification curve down to the vertical in the same manner as in *Stereum*, the development of the gloeocystidia and their relation to the basidia is the same as in those resupinate species in which a context is formed before the hymenium develops. Donk (1964) places the genus *Laxitextum* in the Hericiaceae but no comment can be made on this disposition as species of the type genus, *Hericium*, were not studied in the course of this work.

PUNCTULARIACEAE (Donk, 1964)

PUNCTULARIA Patouillard (Patouillard & Lagerheim, 1895): Type species *P.tuberculosa*.

The type species of this genus is *P.tuberculosa*, notable for the manner in which the hymenium forms over small cushions of tissue seated on a common resupinate foundation but separated by sterile fissures (Talbot, 1958).

Cunningham (1956b) placed *Phlebia strigoso-zonata* in the genus *Stereum*, but it was placed in *Phaeophlebia* by W.B. Cooke (1956) and in *Punctularia* by Talbot (1958). This species and an undescribed species of *Punctularia* were studied. As in other monomitic stereoid fructifications, hyphae in the base of the context and the cortex are thick-walled and resemble skeletal hyphae. Cystidia were not present in either of the species but there was a marked tendency for the apices of the vertical hyphae to branch profusely and thus form a layer of fine dendrohyphidia over the surface of the fructification; the catahymenium is an important generic character. Spores of both species were large, ellipsoid and non-amyloid.

These species cannot be considered as members of *Stereum* since their hyphal systems, spores and hymenium are all quite different in character from those of *Stereum*. The genus *Phaeophlebia* was erected by W.B. Cooke (1956) to accommodate *Phlebia strigoso-zonata*; however, Talbot (1958) allied this species with *Punctularia* and regarded *Phaeophlebia* as a redundant genus. I am unable to comment on this since I have not studied *P.tuberculosa*, the type species of *Punctularia*.

CORTICIACEAE (Herter, 1910, Donk, 1964)

Eriksson (1958b) introduced a number of provisional subfamilies for the Corticiaceae; they are not nomenclaturally valid but are used below for grouping related genera in this large artificial family.

PENIOPHOROIDEAE

PENIOPHORA s.str. Eriksson (1950): Type species Peniophora quercina.

There is general agreement with Eriksson's (1950) restriction of Peniophora to a group of species formerly placed in Peniophora section Coloratae (Bourdot & Galzin, 1928). Three of these species were studied: P.cinerea, P.nuda and P.incarnata. The first two of these are placed by Eriksson in the same group as the type species; it was therefore considered that they would be adequate to define the construction and cystidial type of Peniophora.

The development and morphology of the fruit-body and cystidia may be used to supplement the other distinguishing features of Peniophora which were noted by Eriksson (1950). However, when it comes to deciding the affinities of Peniophora with other genera (e.g. Duportella, Lopharia and Stereum) difficulty arises in the interpretation of hyphal systems. Lopharia cinerascens is clearly dimitic, with hymenial metuloid cystidia which can be traced through intermediate stages to metuloids formed as the modified apices of skeletal hyphae in the growing edge. In Peniophora there are no skeletal hyphae and the fructification is apparently monomitic; but by analogy with Lopharia cinerascens the metuloids in Peniophora might be regarded as modified skeletal hyphae, constituting a reduced skeletal system. Further suggestion of a reduced skeletal system comes from *Peniophora cinerea*, in which long thick-walled hyphae develop from generative hyphae in the basal layer, and turn down to grow at the same rate as the thickening hymenium; they also form from generative hyphae throughout the vertical tissues. Metuloids in the growing edge of *P.cinerea* develop in a manner similar to the thick-walled hyphae and may be homologous with them. Thus *P.cinerea* should, perhaps, be interpreted as having a reduced skeletal hyphal system.

The length of thick-walled hyphae is no criterion as to whether they are skeletal hyphae or not. In the growing edge of dimitic fructifications, the skeletal hyphae become very long, especially if they curve down towards the vertical and end as skeletocystidia in the hymenium. But they can also form during vertical growth of the fructification and in this situation are quite short at first, but lengthen as the hymenium thickens. Short metuloid cystidia in *Lopharia cinerascens* and short skeletocystidia in *Duportella* species were respectively homologous with their longer counterparts in the growing edge. While Corner's (1932 a, b) work on hyphal types and systems introduced new and important taxonomic characters, one would agree with Donk (1964) and A.H. Smith (1966) that their interpretation needs great care and that the present terminology is perhaps inadequate.

DUPORTELLA Patouillard (1915): Type species *D.velutina*.

The lectotype species, *D.velutina* (Donk, 1957b), is considered a synonym of *Duportella tristicula* (Talbot, 1951). Specimens of the latter were studied.

Duportella was separated originally from *Hymenochaete* for species with structures that were setoid in appearance but were not true setae. These structures are the apices of dark-colored skeletal hyphae which end in the hymenium; they are skeletocystidia of a distinctive form, narrower than most and often rough-walled towards their apices. *Duportella* is undoubtedly a genus distinct from *Hymenochaete*, and also from *Stereum*, but Boidin & Ahmad (1963) have raised the question of its affinity with *Peniophora*. They drew attention to the fact that *Duportella tristicula* corresponds with *Peniophora* in having sulfocystidia (gloeocystidia reacting positively with sulfo-aldehyde) pink amyloid spores, clamps and tetrapolarity. The considered it possible to place *D.tristicula* in *Peniophora* but did not formally do so because *Duportella* is a well-known genus and because they wished to avoid lumping. Reference to Table 2* shows that *Duportella* and *Peniophora* differ in development of their fructifications, and in development and morphology of their cystidia; thus I conclude that Duportella should be maintained as a distinct genus.

Duportella fulva was also studied. While Boidin &

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Ahmad (1963) do not regard this species as belonging in Duportella because it lacks cystidia and has colorless basidiospores, it nevertheless correlates with Duportella tristicula (see Table 2*) in all the other features that were recorded. I therefore prefer to maintain D.fulva as a species of Duportella.

PHLEBIOIDEAE

PHANEROCHAETE Karsten em. Donk (1962): Lectotype species Stereum alneum.

Donk (1962) states that there is no published description of the genus, "the limits of the genus being as yet insufficiently established". His purpose in discussing Phanerochaete, and in tentatively grouping species under this name without formally transferring them, was apparently to "draw attention to it and to invoke critical consideration". Phanerochaete comprises many species, some of which had been placed in the provisional (invalid) genus Membranicium (Eriksson, 1958a; Christiansen, 1960), and earlier in Peniophora section Membranacea A and Peniophora section Radicatae (Bourdot & Galzin, 1928). Christiansen regarded Peniophora cremea as typifying Membranicium. The species studied in the course of this work were P.cremea, Peniophore gigantea and Odontia hydnoides, all of which were tentatively included by Donk in Phanerochaete. At this stage I am unable to

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say whether any of these three species should be placed in *Phanerochaete*, but I have considered whether they should be regarded as congeneric.

Peniophora cremea has a loosely-constructed membranous effused fructification composed of moderately thick-walled hyphae lacking clamp connexions; however, clamps are produced in culture (Boidin, 1958a). The development of the fructification and of cystidia in this species is similar to that found in the septate-cystidiate species of the Hyphodermoideae; but in other respects *P.cremea* differs from the Hyphodermoideae since its cystidia are non-septate, moderately thick-walled and crystal-encrusted, while the basidia are clavate and of medium size. It is probable that *P.cremea* is congeneric with *Peniophora velutina* (Eriksson, 1958a; Donk, 1962) which has been regarded as closely related to *Stereum alneum* (Donk,1957b), the lectotype species of *Phanerochaete*.

My studies of *P.gigantea* and *O.hydnoides* show that their fructifications and cystidia develop in the same way and I regard these species as congeneric; but I do not consider that they are also congeneric with *P.cremea*. The cystidia in *P.cremea*, although crystal-encrusted, never attain a true metuloid morphology as do those of *P.gigantea* and *O.hydnoides*. There is also a great difference in texture, intimately related to the different modes of development of the fructifications. The small basidia and spores found in *P.gigantea* and *O.hydnoides* are suggestive of *Phlebia*, in which these two species had previously been placed by Donk (1957a) and Christiansen (1960). On the other hand, *Odontia hydnoides* may be synonymous with *Grandiniella livescens* (Donk, 1957b, 1962) the type species of *Grandiniella* P.Karst. Thus *Grandiniella* might be a suitable genus for *O.hydnoides* and *P.gigantea*.

HYPHODERMOIDEAE

Eriksson (1958a) proposed the genera *Hyphoderma*, *Hypochnicium* and *Hyphodontia*, drawing their members from *Peniophora* s.lat., *Corticium*, *Odontia* and *Radulum* and relating them in particular by basidial morphology. The basidia are clavate but conspicuously constricted (utriform), which results from their development in two phases. Similar development is found in *Coniophora* (Lentz, 1957) and several other genera (Donk, 1964) with urniform or utriform basidia. While it is apparent that these genera proposed by Eriksson are potentially useful groupings, they are not easy to apply because the generic diagnoses given by Eriksson were rather inadequate. In *Hyphoderma* the basidia were described as large, utriform, and the spores as smooth and thin-walled; in *Hypochnicium* the basidia were similar but the spores relatively thick-walled and sculptured; in *Hyphodontia* the basidia were smaller, the hyphae narrower, and the fruitbodies more fibrous. In each of the three genera, cystidia of various sorts may be present or absent. This would appear, then, to be an area in which the type of work described in this thesis might be expected to contribute to a solution of some of the difficulties.

Table 2* shows that members of the Hyphodermoideae correlate well in all characters except the cystidial types, in which there is a wide scatter, and fructification developmental type (Types 2b and 3).

HYPHODERMA Eriksson em.Donk (1957a): Type species H.setigerum.

The type species of Hyphoderma possesses septocystidia which are at first about the same width as the context hyphae but become wider, thicker-walled, and more septate as they lengthen with the thickening of the hymenium. Young basidia and cystidia are closely associated, often in the same fascicle, but they are not easily confused with each other. The cystidia retain their hyphal nature at all times. None of the other species of Hyphoderma studied had this cystidial type, although it occurred in certain other Hyphodermoideae (Hyphodontia alutaria and Amphinema).

A second group of Hyphoderma species is represented by H.tenue, which was transferred to Hyphoderma from Peniophora by Donk (1957a). In H.tenue there are two types of cystidia, leptocystidia and gloeocystidia;

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these and the basidia develop from homologous cells which are virtually indistinguishable in young stages. In addition, H.tenue possesses pyriform, 2-celled stephanocysts.

Stephanocysts are distinctive and unusual structures which have been found in only a few species (Boidin, 1958a) and particularly in cultures. Boidin found them in the Gloeocystidium tenue - praetermissum complex, G.pallidum, Peniophora pubera, Corticium gemmiferum and an unidentified Corticium species. In addition they are present in Corticium torquatum (Cunningham, 1954b), which by its general description is likely to be a synonym of Hyphoderma tenue.

Hyphoderma pubera corresponds in development and structure with H.tenue and also possesses stephanocysts, but differs in forming metuloids instead of leptocystidia, It has the Hyphoderma-type of basidium and may be regarded as a member of the distinctive group of Hyphoderma species with stephanocysts. This is certainly preferable to its being placed in Phlebia (as by Christiansen, 1960) since it differs from the species of Phlebia studied (P.gigantea and P.hydnoides) not only in developmental type but also in having basidia and spores larger and different from the types which characterize Phlebia (Table 2*).

H.tenue and H.pubera are thus seen to differ from the type of the genus (H.setigerum) in the morphology of their cystidia and the relationship between the cystidia

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and the basidia. They also differ in texture, *H.tenue* and *H.pubera* being fleshy-membranous whereas *H.setigerum* has a drier membranous fructification often with a narrow loosely-branched hyphal system at the base of the context. Boidin (1958a) proposed a section Stephanocystis in the genus *Corticium* for a group of several species possessing stephanocysts (Type: *C.(Stephanocystis)tenue*). While some of these species have already been transferred to other genera, others currently placed in *Hyphoderma* would evidently form the nucleus of a group which could well be segregated from *Hyphoderma* s.str.

There is also a third apparently distinct group of species within *Hyphoderma*, as revealed by McKeen's (1952) studies of *H.heterocystidium*, *H.populneum* and *H.mutatum*, which all form *Oedocephalum* imperfect states in culture and whose natural fructifications all have crystal-encrusted cystidia and gloeocystidia. Neither stephanocysts nor *Oedocephalum* states have been recorded for *Hyphoderma setigerum*, the type of *Hyphoderma*, and as they are mutually exclusive Donk (1962) suggests that they could be used to characterize sections within *Hyphoderma*.

This study shows that the stephanocyst-group differs in a number of aspects from *Hyphoderma* s.str. and could well form a new genus which would be suitably named *Stephanocystis*; the group producing conidiophores might well be segregated into another new genus; *Hyphoderma* should be restricted to species similar to *H. setigerum*. However, relatively few species were studied and further investigation is essential before such suggestions are confirmed.

This may be a suitable place to discuss the nature of septate hyphocystidia in further detail.

Septate hyphocystidia retain hyphal characteristics. They are hypha-like in morphology and in their indeterminate growth. Also they were capable of branching, the lateral branches becoming cystidia in *Hyphoderma setigerum*, *Hyphodontia alutaria* and *Coniophorella olivacea*; in *Repetobasidium mirificum* and *Pellicularia fodinarum* (Talbot, 1958) basidiferous side-branches developed from mature cells of the cystidia.

In a mature fructification long multi-septate cystidia, especially if branched, can give the impression of a giant hyphal system within the fructification. It is feasible to postulate that the septate hyphocystidia are a polyploid hyphal system. A significant size difference has been used as circumstantial evidence for polyploidy in fungi (Bauch, cited in Sansome, 1953; Boidin, 1958b). Pontecorvo & Roper (Pontecorvo, 1953) found that among other properties the diploid of *Aspergillus nidulans* could be unequivocally identified from the haploid on the basis of diameter of conidia; the diploid being larger than the haploid. Thus polyploidy is a possible explanation of how septate hyphocystidia might arise, but the mechanism of the change and why it might happen are unknown. No satisfactory way could be devised to test this hypothesis.

If septate hyphocystidia represent a polyploid hyphal system, for some reason they do not produce giant basidia but remain sterile. Of the rare instances where basidiferous tissue has arisen from a cystidium the basidia appear to be the same size as in the rest of the fructification. Possibly they arise from one of the cystidial cells in which the nuclei have reverted to the normal ploidy of the fructification.

HYPOCHNICIUM Eriksson (1958a): Type *H.bombycinum*

According to Eriksson (1958a) this genus is very close to *Hyphoderma* and distinguished from it mainly by the spores which are somewhat thick-walled and often externally sculptured. The type species is *Hypochnicium bombycinum*.

Hypochnicium punctulatum, a species placed in this genus by Eriksson, was studied. The cystidia are leptocystidia which eventually become somewhat thick-walled and long, although they have determinate growth. The basidia are more clavate than the utriform *Hyphoderma* basidia and the spores are round, thick-walled and sculptured. A mature fructification of *H.punctulatum* is densely membranous and arid, eventually becoming creviced. In the base of the context wide bands of tightly packed thick-walled hyphae are present.

Apart from the differences mentioned with regard to spores and basidia, Hypochnicium punctulatum differs from Hyphoderma setigerum also in cystidial type, and from Hyphoderma tenue in lack of stephanocysts. Hypochnicium can thus be maintained as a distinct genus.

HYPHODONTIA Eriksson (1958a): Type species H.pallidula.

This genus contains species formerly placed in Corticium, Peniophora, Odontia and Radulum, and is related to Hyphoderma (Eriksson, 1958a). The type species is Hyphodontia pallidula which is closely related to the species studied, H.alutaria (Eriksson, 1958a). Both species formerly belonged in Peniophora.

The fructification of H.alutaria is loosely membranaceous, with two kinds of cystidia, both developing soon after vertical growth is established. Septate hyphocystidia appear just before the initiation of basidia and bear the same relationship to the basidia as do those of Hyphoderma setigerum. Subulate cystidia, with crystal-encrusted apices, develop terminally from hyphae anywhere in the fructification, i.e. from basal hyphae in the growing edge to basidium-like cells in the hymenium.

Apart from noting the presence of these subulate cystidia, which may be merely a specific character in H.alutaria, this study has not brought out any better means of distinguishing *Hyphodontia* from *Hyphoderma* than those suggested by Eriksson originally. It did confirm, however, that the fruitbody of *H.alutaria* is more fibrous, and its basidia and spores smaller, than in a *Hyphoderma*; also, as noted by Eriksson, that the hyphae branch characteristically. Two equal lateral branches develop at about the same level from a parent hypha, giving three equal hyphae diverging from the same point.

AMPHINEMA Karsten (1892): Type species *A.byssoides*.

Amphinema byssoides, the type species of this genus, has a long synonymy (Rogers & Jackson, 1943: Donk, 1957b) and is perhaps best known as *Peniophora byssoides* or *Coniophorella byssoides*. The main areas of difficulty in regard to this species are firstly its generic disposition, and secondly whether it can be distinguished from *Amphinema tomentellum*.

The fructification of *A.byssoides* is byssoid, with septate hyphocystidia. The basidia are small, more or less clavate but usually with an inflated apex which is most noticeable just before formation of the sterigmata. The spores are small and oval; they do not appear to be cyanophilous but were too small and too thin-walled for this to be determined accurately. None of these features is typical of a *Peniophora*; nor should this species be placed in *Coniophorella* as, apart from the fact that both possess septate hyphocystidia, there is little in common between them. *A.byssoides* does not have the typical large utriform basidia of a *Coniophorella*, nor the obviously cyanophilous spores, and there are also differences in the way in which their hyphocystidia develop.

Following the work of Rogers & Jackson (1943), *Amphinema tomentella* has usually been treated as a synonym of *A.byssoides*; but Christiansen (1960) was able to separate them on grounds which have been confirmed in this work; the spores of *A.tomentella* are obovate and smaller than the oblong spores of *A.byssoides*. In *A.byssoides* the cystidia are usually minutely roughened, while those of *A.tomentella* are usually smooth. The fructifications of *A.tomentella* are also less byssoid.

A close relationship between *Amphinema* and *Hyphodontia* is shown especially in *Amphinema tomentellum*, which in many respects parallels *Hyphodontia pallidula* (Eriksson, 1958a). In both these species the septate cystidia are similar, the spores small and subglobose to obovate, and the basidia small and slightly constricted. Eriksson (1958a) considered placing *Amphinema byssoides* in *Hyphodontia* but felt that it would destroy the naturalness of the latter genus to do so. Since *Amphinema* is a prior generic name, *A.byssoides* would have become the type species of a group of *Hyphodontia* species for which it is not typical.

Amphinema species also show similarity with

Hyphoderma setigerum. The texture in young portions of *H.setigerum* and the tendency to form a byssoid layer on which the hymenium develops is very like that of *Amphinema* species; the septate hyphocystidia in all species have the same relationship to the basidia and develop in the same manner. However, the large utriform basidia and large spores of *H.setigerum* are distinctive and it is thus better to retain two distinct genera. Nevertheless, the conclusions from this study support Eriksson's (1958b) grouping of the genus *Amphinema* in the subfamily Hyphodermoideae.

ALEURODISCOIDEAE

GLOEOCYSTIDIELLUM Donk (1956): Type species *G.porosum*.

Two species of *Gloeocystidiellum* were studied: *G.lactescens* and *G.leucoxanthum*. They appear to correlate well in the major features recorded in Table 2*, but differ in the presence or absence of clamp connexions and hyphidia, and in basidial shape. While the developmental type of the fruit-body is the same in both species, they differ in details. The fruit-body of *G.lactescens* has a thick basal layer from which develop the gloeocystidia and then the hymenium. Hyphae in the context usually branch at a very acute angle to the vertical, resulting in a closely packed tissue. The gloeocystidia of *G.lactescens* are unusual in that there appears to be a maximum volume for the cytoplasm; when the gloeocystidia

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become longer than is needed to contain this volume, secondary septa are laid down at intervals in the proximal portion of the gloeocystidia while the cytoplasm remains in the distal portion. The basidia are very long and narrowly clavate; the spores are oval with smooth walls and only very faintly amyloid.

G. leucoxanthum has a thin basal layer on which the hymenium develops directly. The elongating gloeocystidia retain cytoplasm throughout their length. The basidia are broadly clavate and slightly constricted in places but do not develop in two phases as utriform basidia do; the spores are large, elliptical, smooth-walled and strongly amyloid. This species also has simple hyphidia and sparingly branched dendrohyphidia in the hymenium. It appears to be closely allied to the single species of *Aleurodiscus* that was studied.

Unfortunately specimens of *Gloeocystidiellum porosum*, the type species of the genus, were not available for study. From its description this species is unlike the two species of *Gloeocystidiellum* studied, particularly in its possession of small, ellipsoid and finely warted spores which resemble those of *Laxitextum bicolor*. Indeed Donk (1956, 1962, 1964) regards the microstructure of *Gloeocystidiellum* as being closely allied to that of the Hericiaceae, where he placed *Laxitextum*.

Boidin (1966) suggested that *Gloeocystidiellum* is heterogeneous and constructed a table in which he arranged several species according to cytological features and to whether the clamps were present, whorled, or absent. In this table *G.porosum*, *G.lactescens* and *G.leucoxanthum* fall into different categories. Essentially the same conclusion is reached in this study, but through a consideration of other anatomical features. A thorough study of *Gloeocystidiellum* species is needed; some will probably find a place in the Hericiaceae and others in *Aleurodiscus* (Eriksson, 1954; Lemke, 1964; Boidin, 1966). *Gloeocystidiellum leucoxanthum* has definite affinities with *Aleurodiscus* and if *Gloeocystidiellum* is to be split up the transfer of this species fo *Aleurodiscus* should be considered.

REPETOBASIDIOIDEAE

REPETOBASIDIUM Eriksson (1958a): Type species *R.vile*

The distinguishing feature of this genus is the method of basidial proliferation, whereby a new basidium develops from the apex of the pedicel of an exhausted basidium (Eriksson, 1958a; Oberwinkler, 1965); this type of basidial proliferation is known to occur also in some species of *Galzinia* (Eriksson, 1958a). In *Galzinia*, however, the basidia are long and constricted in the median portion; those of *Repetobasidium* are short and ovate to clavate. The cystidia present in *Repetobasidium mirificum* are of a unique form (see AppendixI), and the fructification is able to thicken by means of horizontal hyphae which develop from the apices of basidial stems which have ceased proliferating (see p. 79). This study therefore provides additional evidence of the fact that *Repetobasidium* is a "good" and easily-recognised genus.

TUBULICRINOIDEAE

The genera *Tubulicrinis*, *Tubulicium*, *Xenasma* and *Litschauerella* are well differentiated from *Peniophora* by their radicate cystidia. These genera appear to form a highly correlated group (Table 2*), but for the fact noted by Oberwinkler (1965) that *Xenasma* and *Litschauerella* have pleurobasidia, while *Tubulicium* has podobasidia. Oberwinkler did not deal with *Tubulicrinis*, in which the basidia appear to be subclavate. Oberwinkler erected a new family, Xenasmataceae, for *Xenasma* and *Litschauerella*. For the present *Tubulicrinis* and *Tubulicium* will be retained in the Corticiaceae, subfamily Tubulicrinoideae.

TUBULICRINIS Donk (1956): Type species *Peniophora glebulosa*.

This genus was proposed to accommodate species of *Peniophora* section Tubuliferae group 3 (Bourdot & Galzin, 1928), and was characterized particularly by its lyocystidia. However, as not all lyocystidiate species fit into the genus *Tubulicrinis* it is necessary to give a more precise description of the cystidia which characterize

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this genus.

The cystidia are biradicate, at least in the base of the fructification, and have smooth, unencrusted walls which dissolve in KOH solution. The apex may be capped with crystals. The lumen of the cystidium is capillary for the greater part of its length, but expands into a bulb at the apex, which often becomes thin-walled; this feature of the apex differentiates cystidia of *Tubulicrinis* from those of *Tubulicium* (see below).

The basidia of *Tubulicrinis* appear to be neither pleurobasidial nor podobasidial but instead are usually subclavate.

TUBULICIUM Oberwinkler (1965): Type species *Peniophora vermifera*.

Oberwinkler characterized this genus by the gelatinous fructifications, the podobasidia, and the conical multi-radicate cystidia. Almost simultaneously, but a month later, Parmasto (1965) erected the monotypic genus *Tubulixenasma* which is based on the same type species and is therefore an obligate synonym of *Tubulicium*. Parmasto considered *Tubulixenasma* to be intermediate between *Xenasma* and *Tubulicrinis*; it was regarded as having the basidial structure of a *Xenasma* (i.e. "pleurobasidia") and cystidial structure and amyloidity like a *Tubulicrinis*. There is obviously a difference of opinion between Oberwinkler and Parmasto on the cystidial and basidial morphology in this genus. These aspects were concentrated upon in the present study of *Tubulicium vermiferum*.

The cystidia of *T.vermifera* are similar to those of *Tubulicrinis* only in their amyloidity and in disintegrating in KOH solution; they differ in being multi-radicate, conical in shape, and possessing a capillary lumen which does not expand at the apex. In the specimens studied, the basidia were podobasidia as noted by Oberwinkler, not pleurobasidia as stated by Liberta (1960), Weresub (1961) and Parmasto (1965).

Christiansen (1960) and Cunningham (1963) placed *P.vermifera* in *Tubulicrinis* on account of its lyocystidia; Weresub (1961) thought that it belonged in *Xenasma*, placing more emphasis on its supposed pleurobasidia than on the lyocystidia.

This study confirms that *P.vermifera* does not fit either *Tubulicrinis* or *Xenasma*, and supports Oberwinkler's erection of the genus *Tubulicium* to accommodate it.

CORTICIOIDEAE

CORTICIUM.

Corticium is here used as an artificial genus after the manner of Eriksson (1958a), for two species which could not be placed in any known genera: *Peniophora longispora* and *Corticium patricium*.

Peniophora longispora

The fructification has a scanty basal layer on which develops a loose interwoven context before the basidia begin to form. The cystidia are non-septate, swollen or of the same width as the hyphae at the base, but tapering to a narrow apex; they are long and have a characteristic pattern of crystal-encrustation. The cystidia develop from the apices of context hyphae and contribute towards the formation of the context before basidia are initiated. This relationship between the cystidia and basidia is found also in *Amphinema byssoides*, which, however, differs in cystidial and basidial morphology. *P.longispora* and *A.byssoides* are not congeneric, but possibly the similarities are great enough for *P.longispora* to be placed with *Amphinema* in the Hyphodermoideae. My conclusion is that *P.longispora* should be the basis for a new genus which would probably include *Peniophora nikau* (Cunningham, 1963); however, I have seen no specimens of the latter.

Corticium patricium

The cystidia of this species are not gloeocystidia as stated by Cunningham (1954b), but instead are leptocystidia. They are large, cylindrical, with rounded apices and slightly thickened walls, are unencrusted and develop from cells homologous with basidia. They project well beyond the level of the hymenium and their homogeneous contents do not stain any more deeply than hymenial cells. In young stages the basidia and cystidia look alike and cannot be differentiated. The basidia are large, clavate to utriform; the sterigmata are large, developing in two stages, as described for some other species by Oberwinkler (1965).

The general features of *Corticium patricium*, except its large basidia and spores, ally it with leptocystidiate species placed in *Hyphoderma*. This however, is already a heterogeneous genus and I prefer not to transfer species to it. For the present *Corticium patricium* is better left in the artificial genus *Corticium*.

XENASMATACEAE Oberwinkler (1965)

XENASMA Donk (1957a): Type species *Peniophora rimicola*.

This genus was erected for the *Peniophora rimicola* group of species (Jackson, 1950b).

Species of this genus have soft-waxy to gelatinous fructifications which become vernicose on drying. The basidia are pleurobasidia and the spores of the two species studied were ornamented in Melzer's solution; the ornamentation disappeared in KOH solution. The cystidia were bi-radicate but did not dissolve in KOH solution. The walls of the large cystidia in *Xenasma rimicolum* were thickened, but not to the extent seen in *Tubulicrinis* cystidia. The fructification was composed entirely of horizontal hyphae, except for the vertical cystidia and basidia. The fructification became thickened by repetition of the basal layer of hyphae. These features when taken together make a well-defined genus.

LITSCHAUERELLA Oberwinkler (1965): Type species *Peniophora abietis*.

Peniophora abietis has cystidia almost identical in appearance with those of *Tubulicium vermiferum*. However, they do not disintegrate in KOH solution and are pseudoamyloid. Another difference between the species is that the basidia of *P.abietis* are pleurobasidia.

At present there is confusion about the classification of *P.abietis*. Weresub (1961) placed *P.abietis*, *Peniophora gladiola* (and perhaps *Peniophora hastata*) in synonymy under *Peniophora clematidis*. She regarded this species as belonging in the genus *Xenasma* because the basidia are pleurobasidiate. Liberta (1960) accepted Weresub's synonymy and formally transferred *P.clematidis* to *Xenasma*. However, Oberwinkler (1965) included *P.clematidis* in his new genus *Tubulicium* and did not agree with Weresub, Boidin (1958d) and Liberta that *P.clematidis* and *P.abietis* are idential (except in their ploidal stage). He found that *P.clematidis* differed from *P.abietis* by lacking pleurobasidia and that its basidia and spores are considerably smaller. Thus supposition of polyploidy would be justified on the differences in size of basidia and spores but because of the different basidial formation and morphology such a view could not be supported. Conseqnently he made *P.abietis*, with *P.gladiola* as a synonym, the type of a new genus *Litschauerella*.

The specimens that I studied had pleurobasidia but the morphology of the cystidia and the method of thickening of the fructification, as well as its texture are not the same as those of *Xenasma rimicolum*. *Xenasma*, then, is not a suitable genus for *P.abietis* and as it does not fit into any other genus Oberwinkler's genus *Litschauerella* is necessary. As pleurobasidia were found in the specimens studied, the specific epithet *abietis* is used in preference to *clematidis* until the problem of synonymy is sorted out.

CONIOPHORACEAE (Ulbrich,1928; Donk, 1964)

CONIOPHORELLA Karsten (1889a): Type species *C.olivacea*

The debatable point in regard to this genus is whether it is desirable to segregate it from *Coniophora*. The basidial development (Lentz, 1957; Donk, 1964) and the cyanophily of the spores (Kotlaba & Pouzar, 1964) in *C.olivacea* are, in common with such features in *Coniophora*, characteristics of the family Coniophoraceae. Whether *Coniophorella* is segregated or not depends upon the importance attached to the presence or absence of cystidia at a generic level; there is no general agreement on this point, although cystidiate and non-cystidiate species are nowadays often included in a single genus if there are enough other characters in common to warrant it. It is usually not a good practice to maintain a genus on the basis of a single striking character. Despite the fact that *Coniophorella* is segregated from *Coniophora* only by the possession of septate hyphocystidia (Rogers & Jackson, 1943), these come from a hyphal system with darker and thicker walls than the hyphae of the basidial system, which may possibly be regarded as another generic feature. About five species of *Coniophorella* have been recorded (Ainsworth, 1961). Although it remains a matter of personal preference, it would seem not unreasonable to maintain the genus *Coniophorella*.

CERATOBASIDIACEAE Martin (1948)

The lack of general agreement on the taxonomic position of the Ceratobasidiaceae, Tulasnellaceae, and the genera comprising these families, is reflected in numerous papers (e.g. Martin, 1945, 1948, 1957; Jackson, 1949a; Olive, 1957; Christiansen, 1959, 1960; Donk, 1956, 1958, 1964; Eriksson, 1958a; Talbot, 1965, 1968; Lowy, 1968). This thesis deals with only one of the genera in question, *Oliveonia*, which is commonly thought to be a member of the Ceratobasidiaceae.

OLIVEONIA Donk (1958): Type species *O.fibrillosa*.

The name *Oliveonia* was introduced to replace *Heteromyces* Olive (1957), a preoccupied generic name.

O.fibrillosa and O.pauxilla are both original members of the genus; both are cystidiate species. Talbot (1965) emended the genus to include O.atrata, a non-cystidiate species.

The main point of controversy in this genus, apart from its taxonomic position, is whether the cystidiate organs are gloeocystidia or not. Most authors have regarded them as gloeocystidia; but since they give a negative aldehyde test, do not possess oily or granular contents, are not flexuous in shape and project for the most part above the basidial level, they are not typical gloeocystidia. Although they are thin-walled they are also not leptocystidia, since they are not easily confused with basidia. These structures are in fact bi-radicate cystidia.

Superficially there is some resemblance between Xenasma and Oliveonia; their fructifications are simply constructed with a basal layer of horizontal hyphae from which basidia and cystidia arise directly without interposed vertical hyphae; their cystidia, while differing markedly in wall-thickness, are bi-radicate, and bear the same relationship to the remainder of the fructification in each case. They differ considerably in basidial characters, however. The basidia of Oliveonia have stout finger-like sterigmata and repetitive spores, features which have induced some authors to place Oliveonia among the Heterobasidiomycetes.

V. FUNCTION OF CYSTIDIA

Since the general term 'cystidium' may refer to diverse structures in quite different types of fructification it is difficult to compare the statements of various authors who have speculated upon the possible functions of cystidia ever since Micheli in 1729 first drew attention to these structures in agarics. Even now, the precise function of any type of cystidium is not known.

Micheli thought that cystidia held the gills of agarics apart, thus enabling the spores to fall freely, and this has become a generally accepted interpretation of the function of cystidia in fruit-bodies with lamellae. Buller (1924) published detailed studies of some species of *Coprinus* and concluded that "the cystidia are unicellular organs which function by holding the gills apart and thus maintaining the interlamellar spaces in which the spores can develop without mechanical hindrance". Although this may be an important feature for fungi whose lamellae undergo progressive autodigestion, a recent opinion (A.H. Smith, 1966) is that "the mechanical function of cystidia generally has been greatly overemphasized even for coprini."

Before the process of sexual reproduction in basidiomycetes had been correctly elucidated, a number of mycologists regarded cystidia as the male elements of these fungi (reviewed in Buller, 1909; Lentz, 1954).

Those who held this view supposed that the detached basidiospores were fecundated when they adhered to the moist surface of the cystidia, but De Bary (1873) remarked that this was more like the phenomenon of nutrition than of fecundation. W.G. Smith (1881) discussed cystidia in agarics and illustrated them with granular contents which he considered to be the fertilizing agent; he supposed that the contents escaped when an operculum at the apex of the mature cystidium dropped off. On the other hand, Massee (1887) thought that the developing spores were nourished by the released contents of cystidia, which he considered to be the terminations of laticiferous vessels. Both of these authors were upholding the view of Corda (cited in De Bary, 1873) and other early writers that cystidia discharge their contents through an apical pore, although De Bary (1873), Hoffman (cited in De Bary, 1873) and Brefeld (cited in Buller, 1909) were never satisfied that this occurred spontaneously.

An excretory function has often been attributed to cystidia. Patouillard (1882) thought that the presence of calcium oxalate crystals on some cystidia indicated that they were excretory elements; and others have held this view (Knoll, 1912; Heim, 1931; Langeron, 1945), which stems largely from the assumption that as metabolic products are deposited in or on cystidia then they must be a type of excretory organ (A.H. Smith, 1966).

Boudier (1890), however, believed that this was not necessarily so, as crystals on the cystidial wall could be deposited simply by exosmosis from an actively-growing cell. From personal observation it would seem, at least in some examples, that cystidia are not specifically organs of excretion, since crystals may also be formed on hyphal walls. Species without cystidia may have crystal-encrusted hyphae, e.g. *Corticium byssinum* and *C.bicolor*. It was noted that if cystidia are present in species with crystal-encrusted hyphae, then the cystidia are also encrusted, as in *Peniophora longispora*. Sometimes (e.g. in *Amylostereum chailletii* and *Lopharia crassa*) in species with crystal-encrusted cystidia, the hyphae in the growing edge of the fructification have crystal deposits. It seems likely that crystals are deposited where substances diffuse through hyphal walls and where water can evaporate from a surface; this is likely to occur most in floccose fructifications and also at the exposed apices of cystidia and on exposed hyphae in the growing edge where tissues are not so tightly packed.

In thelephoraceous fungi, Massee (1889) considered that cystidia function as organs of transpiration because, under certain conditions, minute drops of water were to be seen on them. He also found that before the onset of transpiration the cystidia were perfectly smooth, but that after its commencement masses of calcium oxalate were formed externally, and continued to increase in amount owing to the escape of water containing this substance in solution.

The ability of cystidia to transpire has led Watling (cited in A.H. Smith, 1966) to suggest that their function may be to increase the humidity in the area of spore-production, by drawing water from the tissues of the fructification and evaporating it in the hymenial region. A.H. Smith (1966) adds that the presence of cystidia may reduce air movement over the hymenium. These two effects would combine to produce pockets of relatively still, moist air favourable to basidiospore development, and might well be important in thelephoraceous fungi which, unlike the polypores, agarics and hydnums, have a rather smooth hymenium without pores, gills or spines to keep up the relative humidity around the hymenium. Little, however, is known about the microclimate over the hymenium of a fungal fructification. For cystidia to function in keeping up a high relative humidity over the hymenium it might be supposed that they could make no significant contribution except when the fructifications are in a fairly protected environment. Also, in an open habitat, projecting cystidia might actually be a disadvantage as moisture could be evaporated too quickly from their surfaces and thus cause excessive drying of the fructification. It may be significant that the majority of thelephoraceous fungi have relatively thin, fragile fructifications and grow in sheltered places, such as in humus or under fallen logs, and it is in this group of fungi that cystidiform structures appear to be most numerous and most diverse. It is interesting to note in this connexion that cystidia are rare in the Clavariaceae (Corner, 1950) but when they do occur it is usually in the minute, delicate fructifications; this is especially true if the cystidia are of the projecting type. An extension to Watling's hypothesis is that there may be a correlation between dryness of the fructification and the length to which cystidia project beyond the hymenium. In fructifications which are normally floccose and dry in texture, cystidia often project well beyond the hymenium, as in *Peniophora longispora* and *Amphinema byssoides*; but some of the more membranous and moister fructifications do not appear to have such long cystidia, e.g. many species of the Coloratae group of *Peniophora*. The reason may be that the air over the hymenium of a moist fructification is likely to have a higher humidity than that over a drier fructification.

Much more work has been done on the ecology and biology of pileate than of resupinate species, and mycologists have too often extrapolated from results of studies of the former type without realizing that they do not necessarily apply to the latter. The pileate fructification stands above the substratum with its hymenium facing downwards. Basidia and spores are protected from above by the tissues of the pileus, and this prevents free water from damaging the basidia and affecting the spore-discharge mechanism. At the same time there is a lamellar boundary layer of practically still air around the whole fructification, as around any surface (Gregory, 1961), and it may be assumed that this layer is fairly humid from water evaporated from the tissues. Thus the spores are discharged actively, and fall through the boundary layer into the more turbulent air between the pileus and the substratum, from whence they are dispersed. Although some species of resupinate basidiomycetes (mainly effuso-reflexed types) characteristically inhabit stumps, twigs or branches, where similar conditions to those of pileate species would prevail, the majority occur in humus or litter on the ground, or on fallen branches and logs. The hymenium does not necessarily form on the under-surface of these substrata, although in the majority of cases it does. However, no matter whether the hymenium is formed above or below a log, or on or within litter, it is in a very different ecological site compared with the hymenium of a pileate species. Basidiospores are not actively discharged for a distance of more than about 100-200 u (Ingold, 1965); thus with an upward-facing hymenium the spores are quite unlikely to be discharged through the still lamellar boundary layer of air, which is usually about 1 mm in depth at ground level (Gregory, 1961). In fact they are likely to fall back on the hymenium. On the other hand, if a hymenium faces downward (under a log or in litter) the spores may be freely discharged but are unlikely to be air-dispersed because the entire airspace surrounding the fructification is probably of relatively still air. Dispersal by small insects or by water-flow is therefore probable (Talbot, 1952). Under logs or in litter the problem is probably not to maintain humidity around the fructification, or to maintain a still layer of air, but instead to prevent free water from damaging the hymenium. Thus it is possible that the cystidia of resupinate fructifications in such sites are useful in interrupting water-flow and forming air-pockets over the hymenium; the weight of water does not press on the downward-facing hymenium to displace trapped air. Personal observation has shown that thelephoraceous fructifications collected from wet localities often have a film of water stretched over the apices of the cystidia.

An often-expressed idea about the function of cystidia is that they may prevent small animals from damaging fructifications (Lentz, 1954). It was argued that the pointed apices of cystidia and setae deter slugs and other small animals from walking over and eating the fructifications. Buller (1922, 1924), however, observed that slugs frequently eat agarics in which cystidia abound, and in particular that the hook-tipped cystidia of *Pluteus cervinus* were ingested with impunity by three species of slugs and obviously had no protective function. Buller's observations were mainly concerned with the action of slugs on fruitbodies and it is now known that snails and slugs contain powerful digestive enzymes which are able to dissolve fungal cell walls. It is a notable feature of freshly-collected fructifications of thelephoraceous fungi that they usually have a large population of mites or collembola, moving over and feeding on the fungus and apparently unhindered in their movement by the presence of cystidia or setae. Spores of basidiomycetes and other fungi have been recovered from the alimentary tracts and faeces of these animals (Buller, 1909; Talbot, 1952), and in some instances have been shown to be viable. I have observed that those mites and collembola which feed on fungi have quite delicate mouth parts which would probably not allow them to feed on thick-walled cystidia or setae, especially if these structures were covered with crystals. The presence of projecting cystidia or setae had no apparent effect on the depredations of mycetophilid larvae, whose strong jaws set in transparent head capsules were seen on numerous occasions to devour fructifications rapidly.

There have been comparatively few ideas on the function of gloeocystidia. While it is possible that the hymenial endings of laticiferous vessels or gloeocystidia might have unpalatable contents which would deter small animals from eating the fructifications, Buller (1909) found that in Russula, at least, this was not so and that instead the fruit-bodies were particularly palatable to slugs. It is possible that the function of gloeocystidia is concerned with nutrition (Whelden, 1936; Lentz, 1954; Talbot, 1954) and that reserve materials (fats, oils, glycogen) are stored in gloeocystidia and then slowly used by the fungus. This hypothesis receives some support from the observation that the contents of gloeocystidia gradually disappear (Whelden, 1936; my own observations).

This review shows that the possible functions of cystidiform structures are highly speculative and lack supporting experimental data. It is therefore disturbing to find that A.H. Smith (1966) has defined certain types of cystidia on their supposed functions.

APPENDIX I.

Detailed descriptions and illustrations of development of cystidia and fructifications in the species studied.

APPENDIX I.

Aleurodiscus species.

This species is very close to A.cerussatus differing only in the size of the spores.

In this species the fructification has a monomitic hyphal system consisting of clamped, hyaline generative hyphae. Some discontinuous basidia and other hymenial elements are formed directly from repent basal hyphae near the margin at an early stage in growth of the fructification, but later the context thickens and a continuous hymenium is formed. The hymenium contains acanthohyphidia, dendrohyphidia and gloeocystidia, as well as basidia.

Abortive gloeocystidia develop among the basal hyphae at the growing margin, forming as a swelling near the distal end of a hypha and expanding downwards for a short distance but eventually becoming apparently devoid of contents and remaining as a virtually empty shell. The apex of the hypha bearing such a lateral swelling, dies back to the swelling and often leaves a "heel" (fig.1:B). While these abortive gloeocystidia are developing, lateral branches of the basal hyphae, usually clamped at the base, begin to grow vertically downward. Such branched generative hyphae widen and have the potential of developing into functional gloeocystidia, basidia, acanthohyphidia or dendrohyphidia; but the acanthohyphidia and gloeocystidia are formed as specialized branches of the basidiferous hyphae before other types of hyphidia and basidia appear. Basidia are formed only as the hymenium matures, and then in ever-increasing number. It was observed that acanthohyphidia in the growing margin of the fructification are often peculiarly irregular in shape (fig.1:B), while those formed in the mature hymenium are constantly subclavate (fig.1:D,E). Similarly there is a difference in form between abortive gloeocystidia growing in the margin and functional ones associated with the hymenium.

The abortive gloeocystidia are short, broad lateral swellings of horizontal hyphae and grow apically to a limited extent. But the functional gloeocystidia in the hymenium are longer, narrower, apical swellings of erect hyphae; they persist in the mature fructification and lengthen in pace with its increase in thickness. At first they are filled with homogeneous contents, but eventually lose their contents and become overgrown by the thickening hymenium. The change in shape of the gloeocystidia may perhaps be attributed both to directional changes in growth forces and to the change in texture of the fructification from loose at the margin to compact in more central parts. The radiating hyphae, and structures differentiated from them near the margin, are presumably subjected to a diageotropic force; later, the hyphae in the thicker part of the context are subjected to a positive geotropic force which causes their deviation from horizontal to vertical. This would tend to produce relatively longer and narrower gloeocystidia than those in the margin.

Acanthohyphidia undergo somewhat the same change in position, from lateral to terminal with accompanying change in shape, but to a lesser degree than the gloeocystidia. Early in the development of a fructification, aculeate processes may occur on almost all structures except any basidia which may be present; later they appear only as terminal ornamentation of subclavate cells in the hymenium. The change in positioning of aculeate processes, from apparently random to constantly terminal, may well be associated with internal morphogenic factors about which nothing is known, but may also be due partly to changes in directional growth forces. Corner (1948) has shown in Asterodon that asterosetae may have several arms when they occur in context tissues, but are progressively modified in the subhymenial and hymenial tissues; here the number of arms is progressively reduced and those coming within the morphogenic field of the hymenium are considerably elongated. The final expression of this change in form is seen in asterosetae which are reduced to simple setae in the actual hymenium.

Older acanthohyphydia, gloeocystidia, and collapsed basidia are covered by the thickening hymenium, and their contents disappear leaving them apparently empty. The layers in which they occur then appear to be dead and are traversed by only a few living hyphae which give rise to a new hymenium (fig.1:E).

FIG. 1 *Aleurodiscus* species

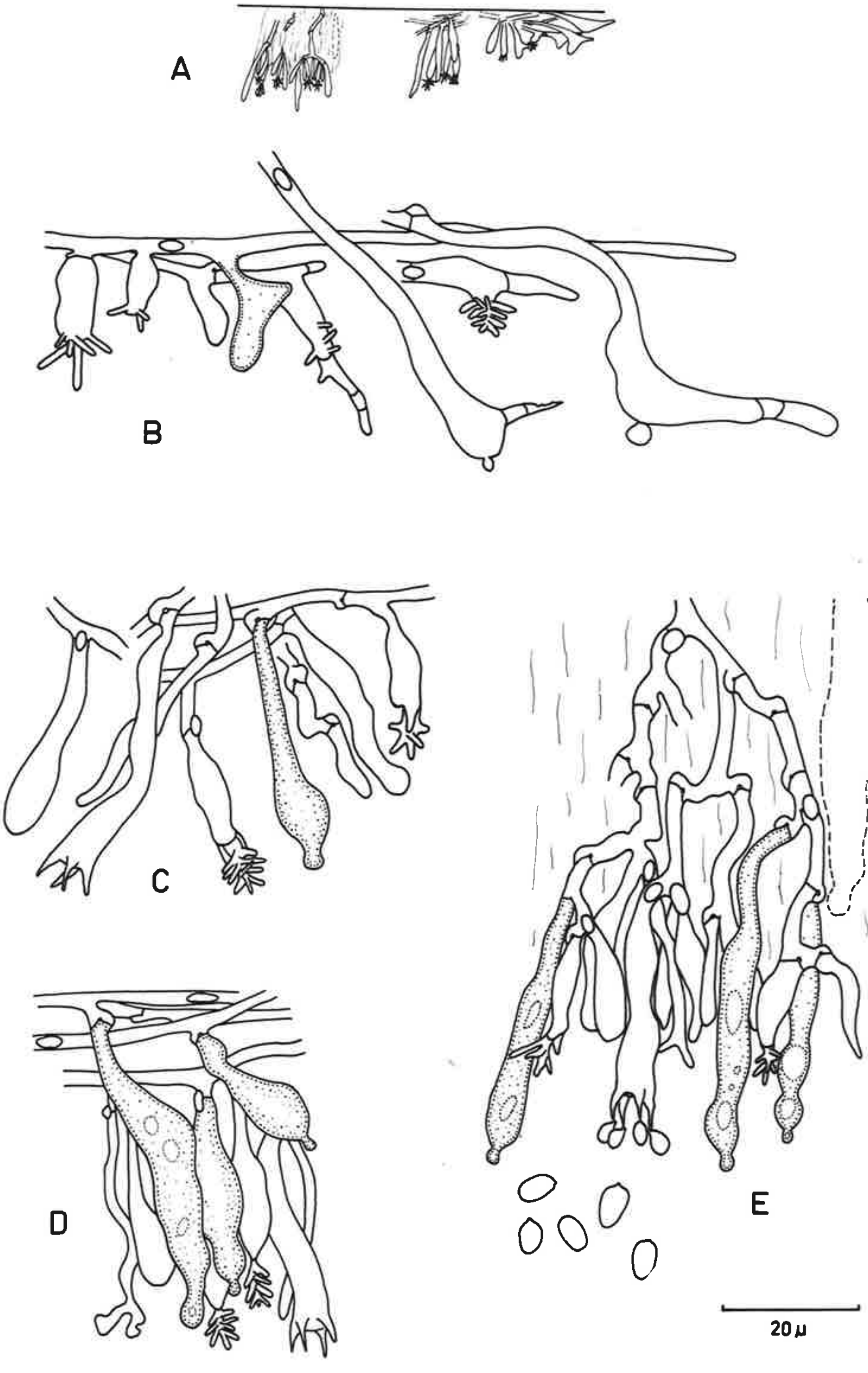
A. Sketch of a section through the fructification showing the relationship of stages B,C,D & E.

B. Growing edge with abortive gloeocystidia and young acanthohyphidia.

C. The growing edge at the stage when basidia are first formed.

D. Well-developed hymenium on the layer of basal hyphae.

E. Mature thickened hymenium.


A
B
C
D
E
20 µ

Amphinema byssoides (Pers. ex Fr.) J.Eriksson (1958a:112)

Syn.: *Thelephora byssoides* Persoon ex Fries (1821:452)
Corticium byssoideum (Pers. ex Fr.) Fries (1874:659)
Hypochnus byssoides (Pers. ex Fr.) Quélet (1879:231)
Coniophora byssoidea (Pers. ex Fr.) Karsten (1882:160)
Tomentella obducens Karsten (1889a:421)
Diplomena sordescens Karsten (1889a:430)
Peniophora byssoides (Pers. ex Fr.) Bresadola apud Brinkmann (1898:130)
Coniophorella byssoidea (Pers. ex Fr.) Bresadola (1903:111)

For further synonyms see Rogers & Jackson (1943).

The fructification of this species is byssoid, with a basal layer of horizontal hyphae and a relatively wide, loosely interwoven context of clamped generative hyphae forming a monomitic system. Context hyphae are hyaline to yellow and covered with crystals, and they branch at a wide angle. Hyphal branches in the context are rarely produced in relation to clamp connexions, but in the hymenium branching is predominantly by proliferation from clamps.

The context hyphae are aligned at an angle to the vertical but in the basidiferous region the distal ends of context hyphae begin to grow vertically downward. Many of these develop into clamped septate hyphocystidia but while young these are difficult to distinguish from basidiferous hyphae as they are hypha-like and unencrusted or only slightly encrusted with crystals (fig.2:B). As the hymenium forms, branching takes place from the ultimate or penultimate clamp connexions of the young cystidia. The lateral branch so produced may develop directly into another cystidium or may proliferate from a clamp connexion to form a fascicle of basidiferous hyphae which have the potentiality of developing further into basidia or perhaps into another cystidium as well as basidia (fig.2:C). The original context hypha continues growing, usually for a length of about three cells, after the clamp connexions have proliferated, developing into a hypha-like cystidium (septate hyphocystidium) which is well defined only because it projects below the general level of the hymenium and is lightly encrusted with crystals. The cystidia are therefore almost undifferentiated terminations of context hyphae in the level of the hymenium, or are entirely hymenial in origin. In either instance they are closely connected with basidial fascicles. The cystidia lengthen as the hymenium thickens, consequently they become obvious, multi-septate structures (fig.2:D).

The hymenium thickens to a limited extent by the addition of new basidia but after this a second context may be developed below the hymenium and in turn may produce another hymenial layer. Thus the fructification may may become stratified in section. Alternatively a second context is not formed and instead young cystidia grow directly from the old hymenium, and branches from these cystidia form a new and more discontinuous hymenium.

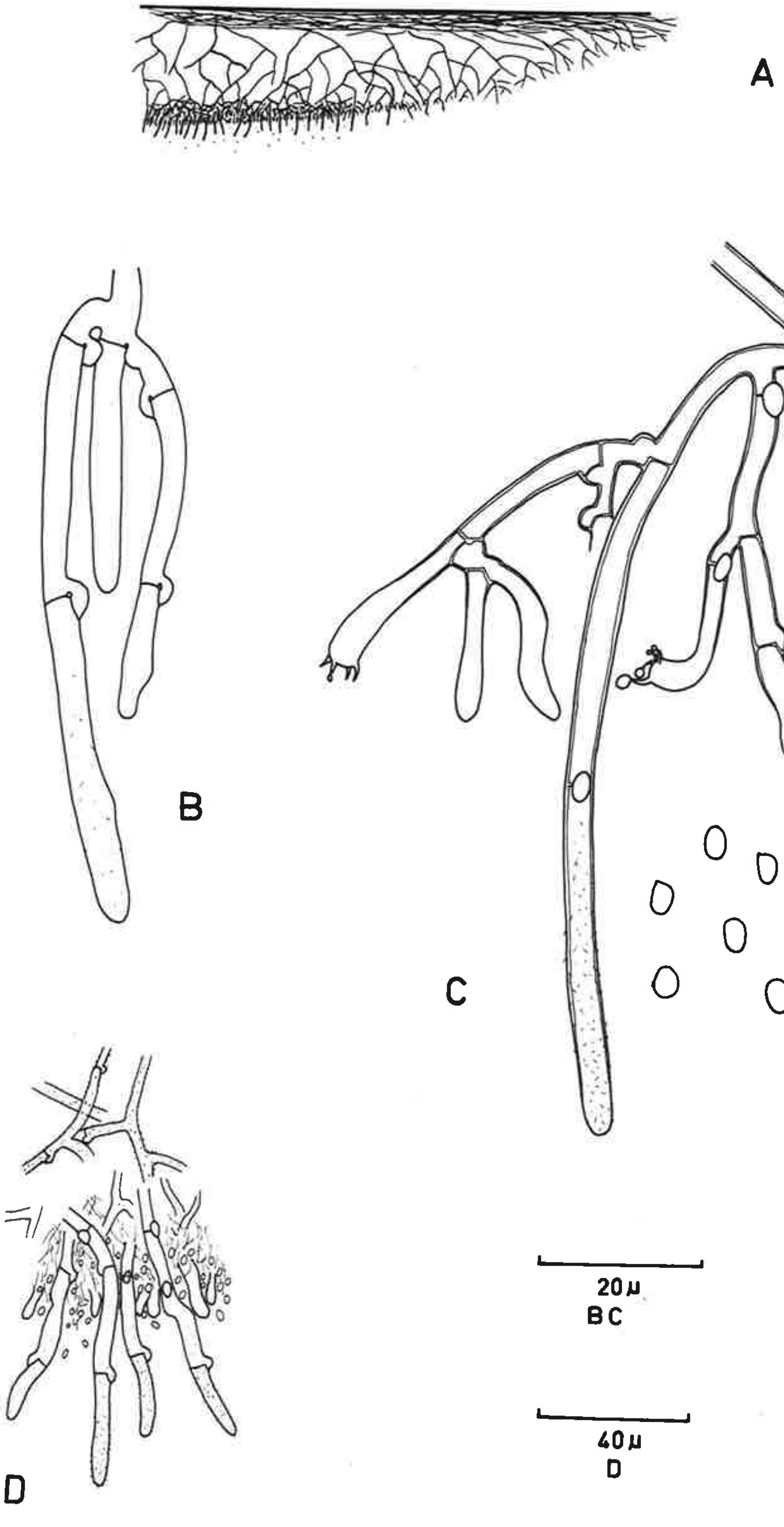
FIG. 2 *Amphinema byssoides*

A. Section of the fructification from the margin to mature portion showing basal layer, context and developing hymenium.

B. Hypha-like young cystidium.

C. Relationship between cystidia and basidial fascicles.

D. Section of mature hymenium showing well-differentiated septate hyphocystidia. Many spores are embedded in the hymenial layer.


A
B
C
D
20µ
B C
40µ
D

Amphinema tomentellum (Bres.) Christiansen (1960:229)

Syn.: _Kneiffia tomentella_ Bresadola (1903:103)
Peniophora byssoides subsp. _tomentella_ (Bres.) Bourdot & Galzin (1912:391)

The general features of the fructification in this species are like those of _A.byssoides_, but the context is not as wide and the context hyphae usually branch more acutely and have few, if any, crystals. As in _A.byssoides_, branching in the context is not in relation to clamp connexions; but, in contrast, proliferation of clamp connexions is rare in the hymenium of _A.tomentellum_.

Young cystidia are formed from lower context hyphae in the manner described for _A.byssoides_ and are not very different from ordinary hyphae (fig.3:A). Lateral branches from the young cystidia contribute to the formation of the hymenium and are usually produced just below a septum on the opposite side to a clamp connexion, not from the clamp connexion as in _A.byssoides_ (fig.3:E). In addition to a lateral branch from below the ultimate or penultimate clamp, other branches may be formed in a more proximal position on the same cystidium, all adding basidiferous hyphae or basidial fascicles to the hymenium (fig.3:B). Such branches either develop directly into a basidium or continue growth and branching to form a basidial fascicle. None was seen to develop into another cystidium as in _A.byssoides_. The cystidium continues to lengthen, eventually becoming multiseptate, with a clamp at each septum, and extending from the original hymenial level to well above the level of any new basidia added by thickening of the hymenium (fig.3:D). In general the cystidia are unencrusted although some are lightly encrusted with crystals. The cystidia in this species are relatively undifferentiated terminations of context hyphae in the level of the hymenium and are septate hyphocystidia. They are recognisable in the young stage only by a somewhat misshapen appearance and by projecting slightly beyond the hymenium (fig.3:C) and are not easily distinguished until they have become longer and multiseptate, usually with the septa close together. A secondary context and hymenium was not formed in the specimens studied.

It is apparent that the two species have the same type of cystidia and fruit-body development. In A.tomentellum the context hyphae are much paler; their walls are thicker, and more unevenly thickened, and are either unencrusted or barely encrusted with crystals. An important difference is in the shape, and to some extent the size, of the spores. In A.byssoides the spores are broadly elliptical, widening towards the apiculus, about 3.5-4.0 x 2.0-3.0 u; in A.tomentellum they are subglobose, attenuated towards the apiculus, 4.0-6.0 x 3.0-4.5 u.

It is apparent that the specimens which I have regarded as representing two species are closely related in structure, but from the limited range of material available it was not possible to say whether they are consistently different in the features mentioned above. If the differences are shown to be consistent this would warrant their separation as two distinct species. Christiansen (1960) has treated them as two species, emphasizing "obovate spores" and "almost smooth cystidia" as differentiating *A.tomentellum*.

FIG. 3 *Amphinema tomentellum*

A. Barely differentiated young cystidia. The cystidia are slightly thicker and more contorted than the ordinary hyphae.

B. Terminal cystidium with lateral basidiferous branches.

C. Young hymenium with barely differentiated cystidia.

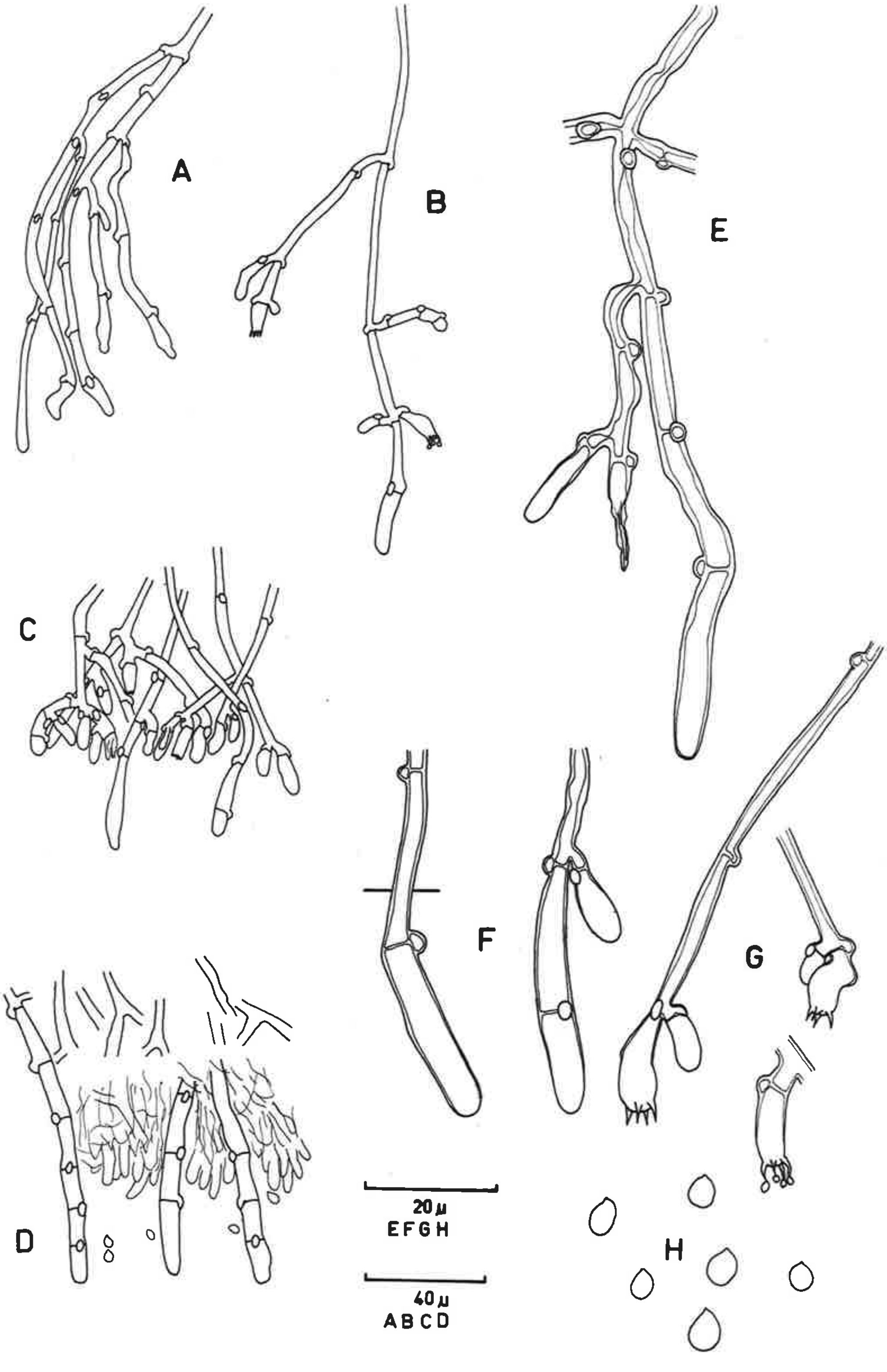
D. Mature hymenium with obvious multi-septate cystidia.

E. Hypha-like cystidium with side-branch on the opposite side to the clamp connexion.

F. Cystidia.

G. Basidia.

H. Spores.


A
B
E
C
F
G
D
20 µ
EFGH
40 µ
ABCD
H

Amylostereum chailletii (Pers. ex Fr.) Boidin (1958b:345)
Syn.: *Thelephora chailletii* Persoon ex Fries (1928:188)
Stereum chailletii (Pers. ex Fr.) Fries (1838:551)
Lloydella chailletii (Pers. ex Fr.) Bresadola (1901:51)
For further synonyms see Lentz (1955).

A.chailletii is predominately resupinate, the margin eventually becoming slightly elevated or narrowly reflexed. The fructification has a stereoid arrangement of tissues and a dimitic hyphal system. The generative hyphae are hyaline, (fig.4:A), mostly thin-walled, with clamped septa. The skeletal hyphae are brown with slightly thickened to much thickened walls and are usually aseptate, although rare septa were seen. The reflexed superior surface has a short, silky, brown tomentum, consisting mainly of skeletal hyphae. There is a deep brown cortex, also mainly of skeletal hyphae. A context of roughly horizontal skeletal and generative hyphae curves down to a more or less vertically arranged hymenial layer. The successive layers of the thickening hymenium are indicated by concentrations of cystidia.

The cystidia are crystal-encrusted apices of skeletal hyphae (fig.4:B,C). In the growing edge, where the texture is looser, the skeletal hyphae are encrusted for most of their length but those in the hymenium have only the apical portion encrusted. Skeletal hyphae are longer in the margin where horizontal growth is not restricted, than in the hymenial region where growth is restricted by the formation of a hymenium. Skeletal hyphae formed near to the hymenium are shorter and more vertical than those formed further away. These shorter skeletal hyphae are easily traced to their basal clamp connexions. The apices of the skeletal hyphae are moderately thick-walled and acute, ending at or beyond the hymenial level. They are not thin--walled and slightly swollen as are the hymenial endings of skeletal hyphae in *Stereum hirsutum* and related species.

In cultures of *Amylostereum areolatum* the apices of skeletal hyphae (fig.4:D) have a tendency to branch. A feature of the skeletocystidia, not seen in any except *Amylostereum* species, was the presence of small nodules along the cystidial walls. These were the same color as the hyphal walls and were probably a local swelling of the walls; they have also been noted by Talbot (1964).

FIG. 4: A, B, C. *Amylostereum chailletii*

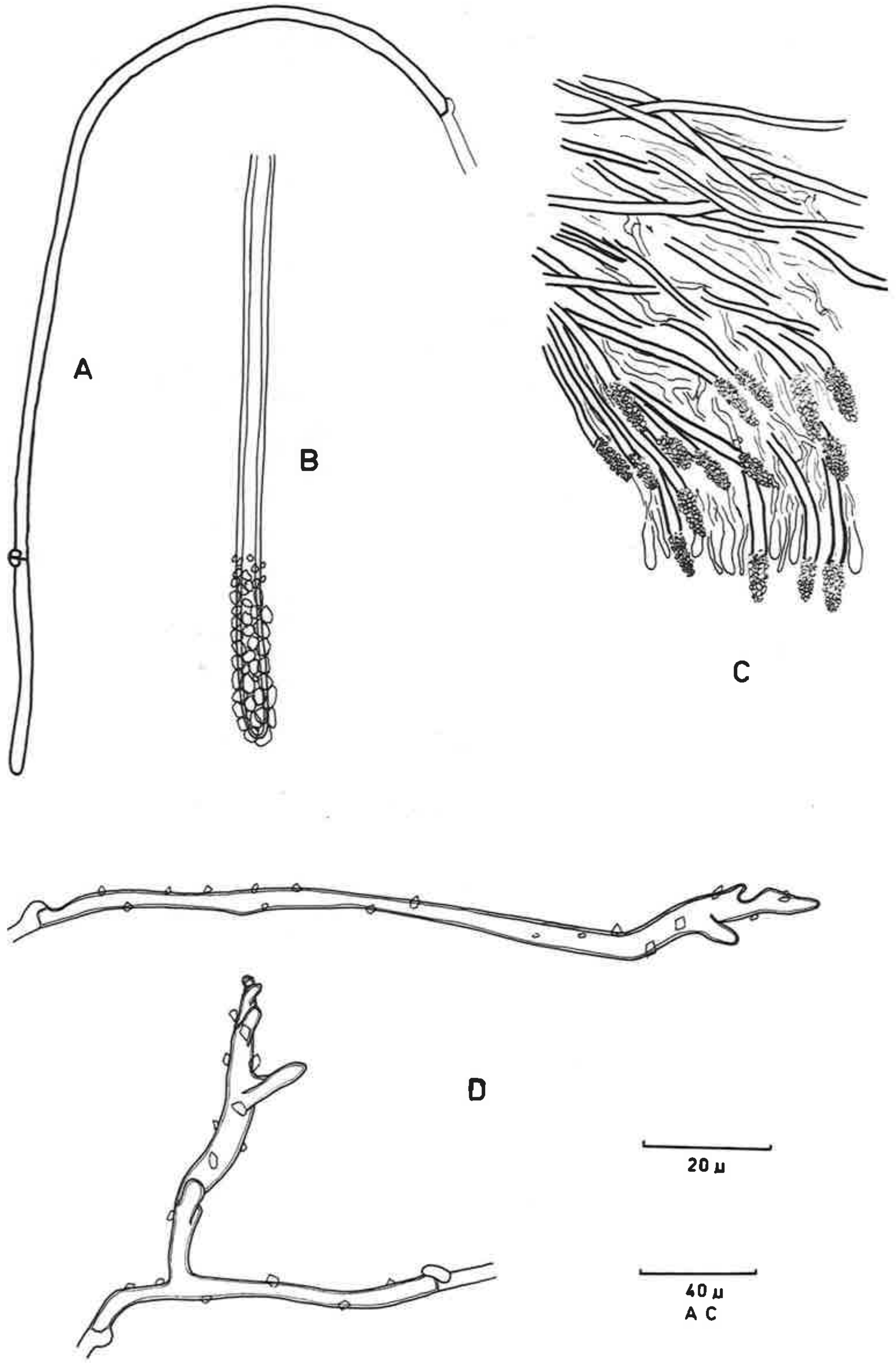
A. Generative hypha with clamped septa, and with partly thickened walls.

B. Crystal-encrusted apex of a skeletal hypha.

C. Section through the fructification showing the slightly layered crystal-encrusted apices of skeletal hyphae ending in the hymenium.

FIG. 4: D. *Amylostereum areolatum*

D. Two skeletal hyphae from a culture of *Amylostereum areolatum*. One is terminal and the other is lateral; both have branched apices. Crystals are scattered over the skeletal hyphae and are absent from the generative hyphae.


A
B
C
D
20 µ
40 µ
A C

Chondrostereum purpureum (Pers. ex Fr.) Pouzar (1959:17)
Syn.: *Thelephora purpurea* Persoon ex Fries (1821:440)
Stereum purpureum (Pers. ex Fr.) Fries (1838:548)
For further synonyms see Lentz (1955).

Macroscopically *C.purpureum* looks like a member of *Stereum* s.str., and microscopically it has a stereoid arrangement of tissues: a cortex and a context of more or less parallel hyphae which curve down to form a hymenial layer. However, the hyphal system is monomitic, composed of clamped generative hyphae. These are hyaline and relatively thin-walled near the hymenium, grading to dark colored and thick-walled at the base. In the thick-walled basal hyphae septa are sometimes few and far between, and occasionally lack clamps, but clamped septa are present (fig.5:F). Therefore these hyphae, although sometimes skeletal in appearance, are generative hyphae.

In a mature fructification vesicular gloeocystidia form a prominent layer just below the sub-hymenial hyphae. They develop as follows:

The growing margin of a young fructification is rather thick. On its distal side some of the context hyphae become bulbous at the apex and the whole apical cell develops dense, homogeneous contents which stain like gloeocystidia. In fact they appear to be merely gloeocystidia of distinctive shape: an inflated apex and a long pedicellate base, arising from a clamped septum (fig.5:A). Being on the distal side of a thickening context, the vesicular gloeocystidia are carried downward and finally form a more or less defined layer below the mass of context hyphae. The hymenium later forms over this layer. As the fructification matures more vesicular gloeocystidia are added to this layer and they also form in the hymenium. Vesicles formed in the context usually have very short pedicels (fig.5:B), while those formed in the hymenium are clavate (fig.5:C). A branch often develops at the base of a vesicular gloeocystidium, either from the clamp or from the gloeocystidial pedicel. This branch either develops as an ordinary hypha or, as frequently happens, into another vesicular gloeocystidium (fig.5:D).

Different growth pressures are probably responsible for differences in pedicel length and shape of the vesicular gloeocystidia. At the growing edge the context is fairly loose and permits freedom of growth to down-turning context hyphae. The gloeocystidium grows in length until the formation of a hymenium restricts horizontal growth; the result is an elongated pedicel and a bulbous apex to the gloeocystidium (fig.5:E). In the more compact parts of the context, however, growth in length is restricted by pressure of surrounding hyphae and by the developing hymenial layer below. The few gloeocystidia that form in the hymenium are more attenuated, probably due to lateral pressure of the developing basidia. All these forms of vesicular gloeocystidia are simply modified apical cells of context or hymenial hyphae.

FIG. 5 *Chondrostereum purpureum*

A. A gloeocystidium from the growing edge.

B. A gloeocystidium that has developed in the context.

C. A gloeocystidium that has developed in the hymenium.

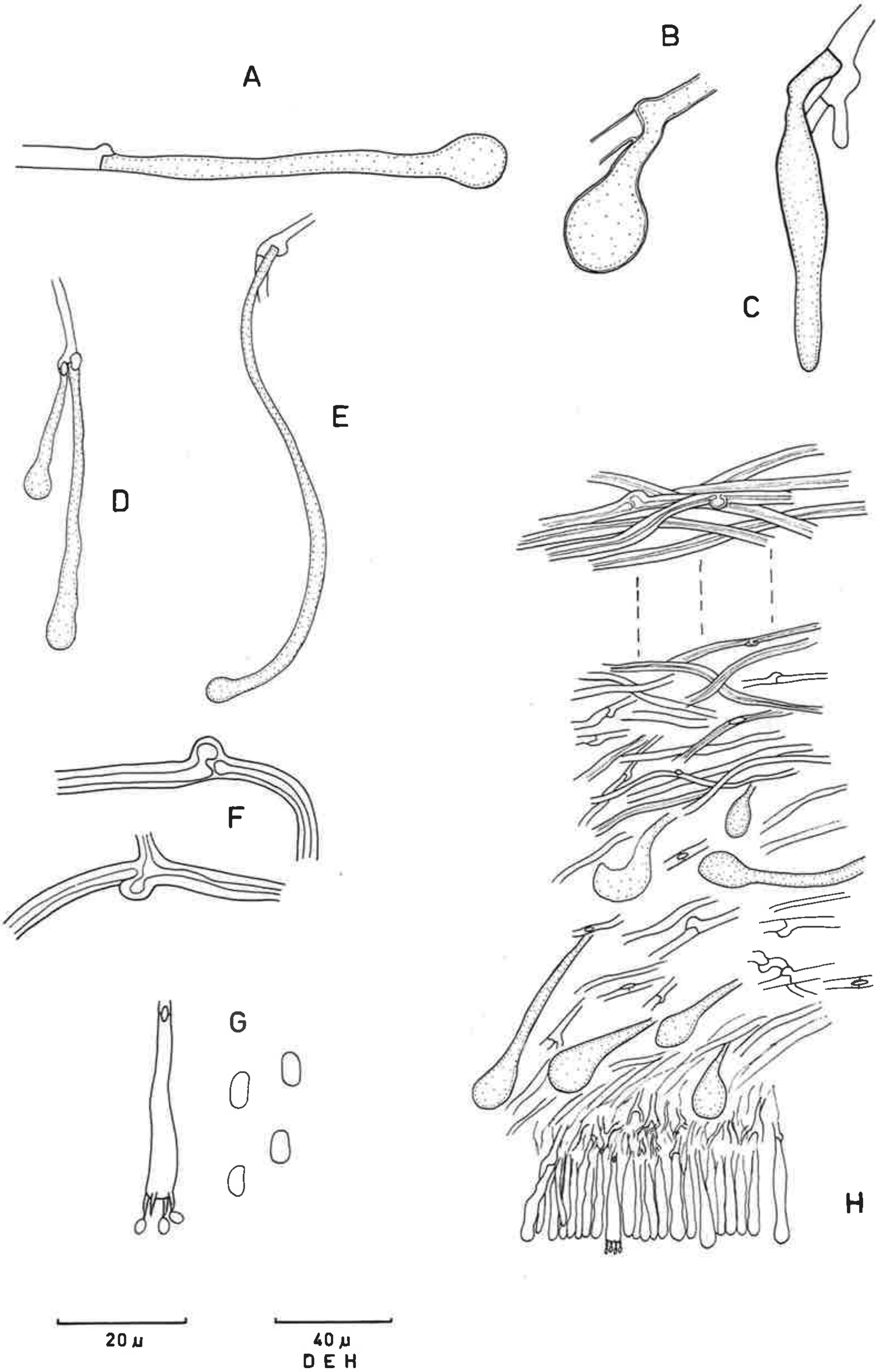
D. A pair of gloeocystidia terminating a hypha.

E. This illustrates the great length to which a gloeocystial pedicel can grow.

F. Thick-walled basal hyphae with clamps.

G. Basidium and spores.

H. Section through a mature part of the fructification showing the hymenium, layer of vesicular gloeocystidia, context and cortex.


A
B
C
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G
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20 µ
40 µ
D E H

Coniophorella olivacea ((Fr.) ex Pers.) Karsten (1889a:438)

Syn.: Thelephora olivacea (Fr.) ex Persoon (1822:143)
Coniophora olivacea ((Fr.) ex Pers.) Karsten
(1882:162)

For further synonyms see Rogers & Jackson (1943).

The fructification is effused, loosely membranous and except in the growing edge is composed of non-clamped generative hyphae. The utriform basidia and cyanophilous spores are typical of the Coniophoraceae.

The growing margin has wide hyphae, the width varying from 7.5u to 25u, with multiple-clamped septa (fig.6:A). The wider hyphae usually have more clamps to a septum than the narrower hyphae. Branches considerably narrower than the parent hypha develop from the clamps, or between the clamps, or even sometimes from the sides of the main hypha and not associated with a septum. The side-branches have frequent non-clamped septa. They either become long and grow parallel to the main hypha, gradually enveloping it in a net of thin hyphae and forming a cordon; or they grow out over the substratum, becoming quite short-celled and much branched, forming an interwoven complex of hyphae which fills the gaps over the substratum between the radiating main hyphae (fig.6:A).

Vertical growth develops from this basal layer of cordons and interweaving hyphae. Although an occasional basidium is formed almost immediately, a hymenium does not become established until much later. First, two types of hyphae become differentiated from the early vertical growth. Both are generative but one has darker walls than the other (fig.6:B). The darker hyphae later give rise to the cystidia and the lighter hyphae to the basidia. Although the cystidial and basidial hyphae appear to be separated at an early stage they are not strictly so, as basidia can develop from cystidial hyphae (fig.6:D).

After a certain amount of vertical growth, by which a loosely interwoven context is formed, the basidial hyphae branch profusely, forming a hymenium. At the same time the cystidial hyphae also branch giving rise to numerous septate hyphocystidia. The cystidia may arise singly or in groups from the branching of the cystidial hyphae. When first differentiated, the cystidia are thin-walled, light-colored and smooth; but they rapidly darken, become encrusted with large granules, and their walls become somewhat thickened. Very little branching of the cystidial hyphae occurs after the initial profuse branching has established the hymenium; thus the majority of cystidia are formed at the initiation of the hymenium.

The cystidia lengthen as the hymenium thickens, becoming very long and multi-septate and eventually projecting for a considerable distance beyond the hymenium (fig.6:E). Hyphae from the hymenium have a tendency to grow down around the cystidia giving the hymenial surface a slightly odontioid appearance.

FIG. 6 Coniophorella olivacea

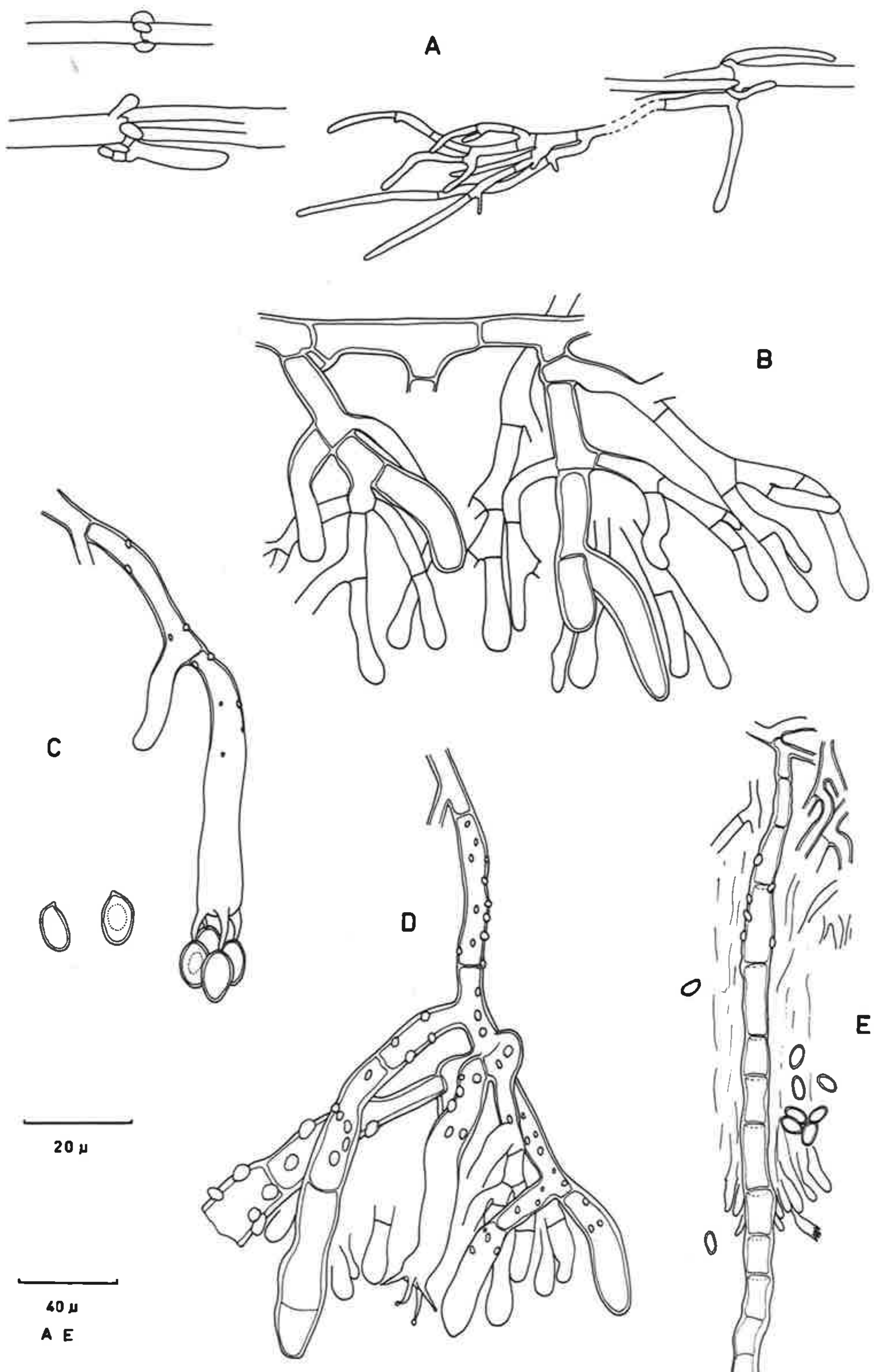
A. Hyphae from the growing edge. Wide hyphae with multiple clamps at the septa; thinner hyphae growing from between the clamps, becoming much branched and interweaving.

B. Young portion of the fructification showing differentiation of the basidial and cystidial hyphae.

C. A basidium and spores.

D. The relationship between the cystidial hyphae and the basidia in the hymenium.

E. A mature portion of the fructification showing a multiseptate hyphocystidium extending from near the base to beyond the hymenium.


A
B
C
D
E
20 µ
40 µ
A E

Corticium patricium Cunningham (1954b:289)

This species has a membranous fructification composed of clamped generative hyphae. The growing edge is a thin layer of basal hyphae. Vertical growth of hyphae commences very close to the advancing edge of the basal layer (fig.7:A). In the early vertical growth some of the hyphal apices become wider and project beyond the general level of the hyphae; these are young cystidia (fig.7:B). Soon after the commencement of cystidial development, basidia are initiated and a hymenium is established. Thereafter basidia and cystidia develop from homologous hymenial cells (fig.7:C) and cannot be differentiated in their young stages. Mature cystidia are long, cylindrical, slightly thick-walled, unencrusted and project well beyond the hymenium. In their manner of origin and their morphology they are leptocystidia.

The hymenium thickens considerably and in the process mature cystidia (fig.7:D) become overgrown. Their contents disappear and they cannot be distinguished from the mass of hyphae surrounding them. In a section through the mature fructification the only obvious cystidia are those projecting from the current hymenium. Slender hyphae often grow down around these projecting cystidia (fig.7:E).

The basidia are large and clavate (fig.7:F,G); the sterigmata are large, developing in two stages, as described for some other species by Oberwinkler (1965) (fig.7:F,G). The spores are large, long-elliptical with rounded ends, and characteristically have a conspicuous guttule (fig.7:H).

FIG. 7 Corticium patricium

A. Near the growing edge showing the basal layer and the early vertical growth.

B. Further back from the growing edge. Cystidial elements becoming differentiated from the vertical hyphae.

C. Basidia (centre) and cystidia (right) develop from homologous cells (left).

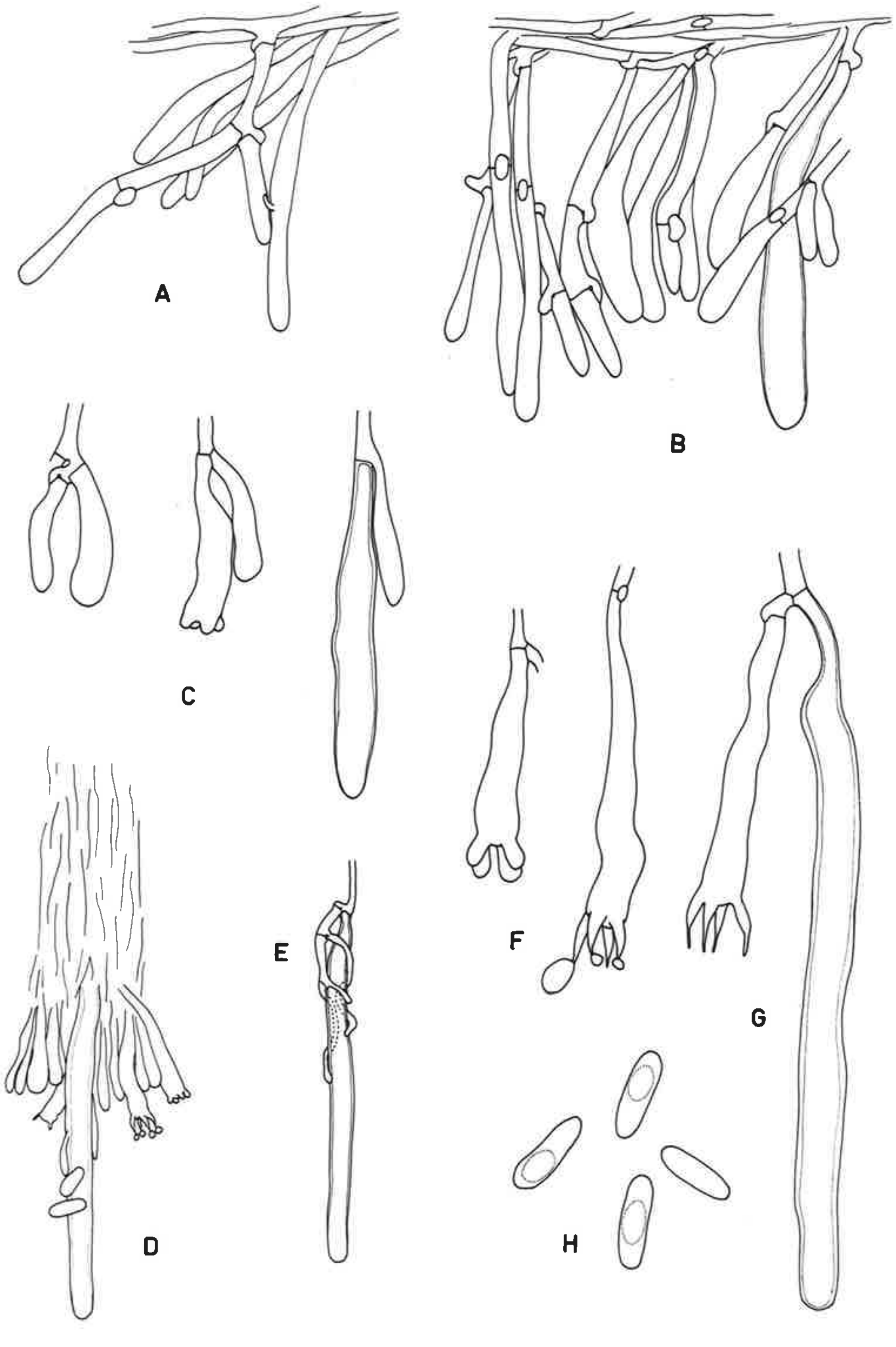
D. Mature cystidia project well beyond the hymenial level.

E. Slender hyphae growing down a cystidium.

F. Basidia.

G. A basidium and cystidium in the same fascicle. This illustrates the close relationship between them.

H. Spores. A conspicuous guttule is usually present.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40 µ
D E

Duportella tristicula (Berk. & Br.) Reinking (1920:364)
Syn.: Corticium tristiculum Berkeley & Broome (1873:71)
Hymenochaete tristicula (Berk. & Br.) Massee (1890:111)
For further synonyms see Talbot (1951).

This species has a thick, effused to effuso-reflexed fructification with an arid membranous texture. The hyphal system is dimitic with hyaline clamped generative hyphae and brown skeletal hyphae. The hymenial surface is brown and finely velutinous.

The margin of the fructification consists of interwoven hyaline, generative hyphae and thick-walled, occasionally septate, brown skeletal hyphae. At an early stage of development some of the skeletal hyphae near the growing margin begin to curve downward and project beyond the basal layer, giving the young growth a velutinate appearance. Generative hyphae grow down among the skeletal hyphae, branching increasingly and eventually forming a basidiferous layer. By this stage the interwoven basal hyphae have formed a fairly thick prosenchymatous base to the fructification (fig.8:B). New skeletal hyphae are differentiated from the generative hyphae during vertical growth, and grow down at a faster rate than the generative hyphae. By the time the basidiferous layer is formed there is a dense palisade of projecting skeletal hyphae (fig.8:B). Their apices are cylindrical but taper to narrow rounded ends and are usually crystal-encrusted to varying degrees but, if not encrusted, are often minutely rugulose near the apex.

Only one specimen, not in very good condition, was available for study and this did not possess a mature hymenium. However, Talbot (personal communication) has shown that a thickening hymenium is built over the palisade of skeletal hyphae, with the apices of scattered skeletal hyphae projecting through it. The length, and degree of curvature, of the skeletal hyphae depends upon their place of origin. Many extend from the basal layer to the hymenium, are markedly curved, and must have originated as some of the first skeletal hyphae to diverge from the basal layer near the margin. The skeletal hyphae produced from the vertically-growing generative hyphae are often easily traced back to a clamp connexion; as they are formed constantly during thickening of the fructification, the closer their point of origin to the hymenium, the shorter and more vertical they are.

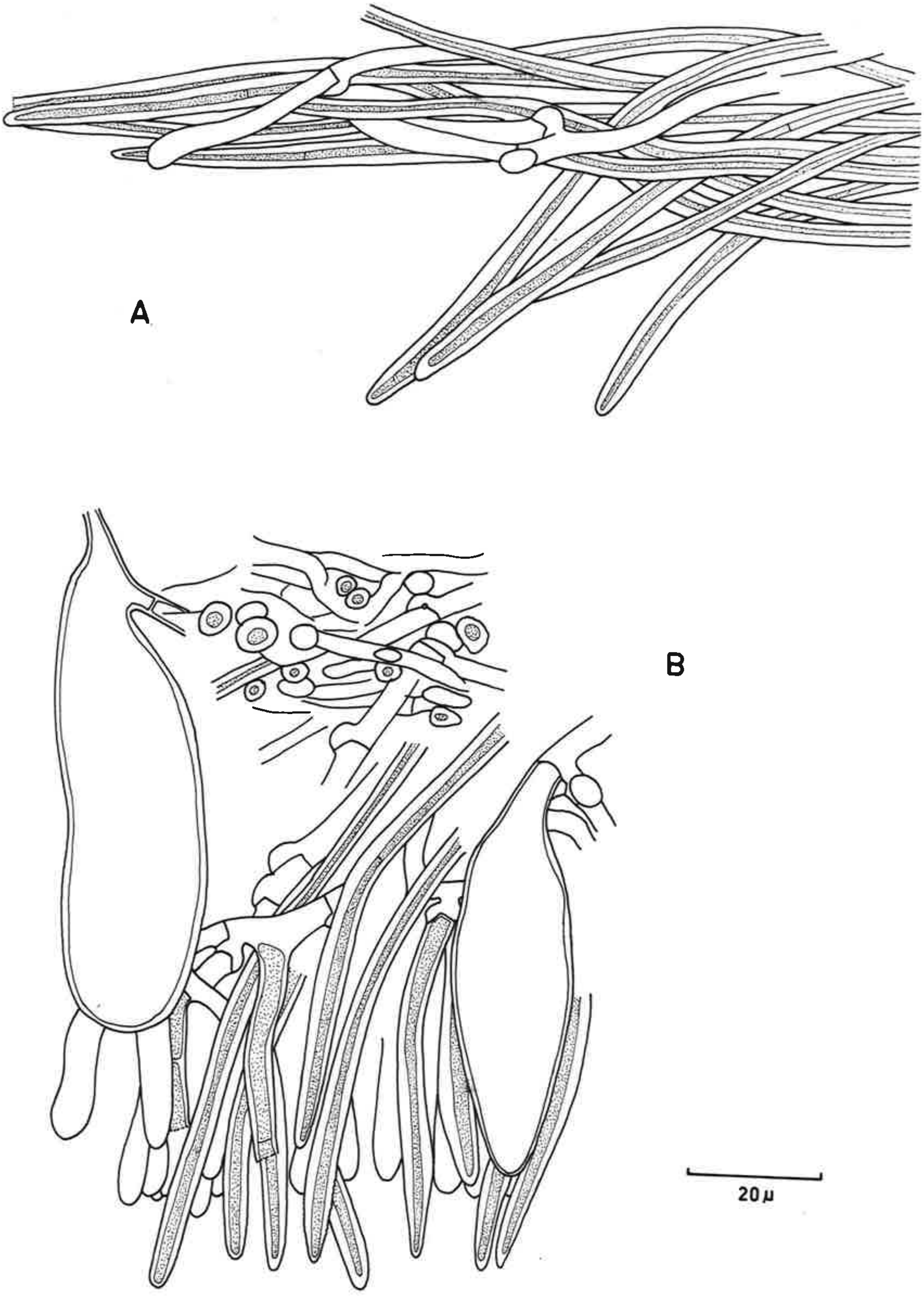
The modified skeletal hyphae, as described above, are distinctive enough to have attracted attention and to merit a morphological term. Although setoid in appearance, they are not true setae and it was for this reason that Patouillard (1915) segregated the genus Duportella from Hymenochaete Lév. Talbot (1951) termed these structures "false setae" and this term was modified to "pseudosetae" by Cunningham (1957). It is a suitable morphological term, but one that does not stress the origin of the structures and has so far been applied only in the genus *Duportella*. It is proposed, therefore, to class these as skeletocystidia, a term which emphasizes their origin and the fact that they are homologous with the skeletocystidia of other genera, e.g. *Lopharia* and *Stereum*.

Gloeocystidia are also a prominent feature of *Duportella tristicula* (fig.8:B). They are formed terminally or laterally from generative hyphae in the basal layer of the fructification, even in primordia, and, being relatively long, they extend from the basal layer to the subhymenium of a mature fructification. They are ovoid to fusoid in shape, deeply-staining, with homogeneous contents, and have been reported (Talbot, 1951) to become 1-2-septate in some instances. Talbot also reported the presence in old fructifications of small hymenial "cystidia", but subsequently he came to the conclusion that these were probably only young gloeocystidia (personal communication). Unfortunately the limited material available for these studies did not show such structures and was also unsuitable for tracing the development of the gloeocystidia in detail.

FIG. 8 *Duportella tristicula*

A. Growing edge composed of hyaline generative hyphae and brown skeletal hyphae.

B. Section of the fructification showing prosenchyma basal layer, gloeocystidia, basidiferous hyphae and skeletocystidia. The skeletocystidia project beyond the basidiferous hyphae.


A
B
20 µ

Duportella fulva (Lév.) Cunningham (1957:93)

Syn.: *Thelephora* (*Stereum*) *fulva* Léveillé (1846:149)
Stereum schomburgkii Berkeley (1873:168)
Hymenochaete olivaceum Cooke (1885:11)
Stereum fulvum (Lev.) Saccardo (1888:570)
Peniophora atrocinerea Massee (1889:141)
Lopharia fulva (Lev.) Boidin (1959:213)

For further synonyms see Cunningham (1963)

The components of the fructification, and their structure, development and arrangement, are very similar in *D.fulva* and *D.tristicula*, the most notable difference being the absence of gloeocystidia in *D.fulva*. In both species, the skeletocystidia develop in the same way. In material examined, secondary septation of the skeletal hyphae was common in *D.fulva* but not in *D.tristicula*, although this may merely be an environmental effect of no particular taxonomic consequence.

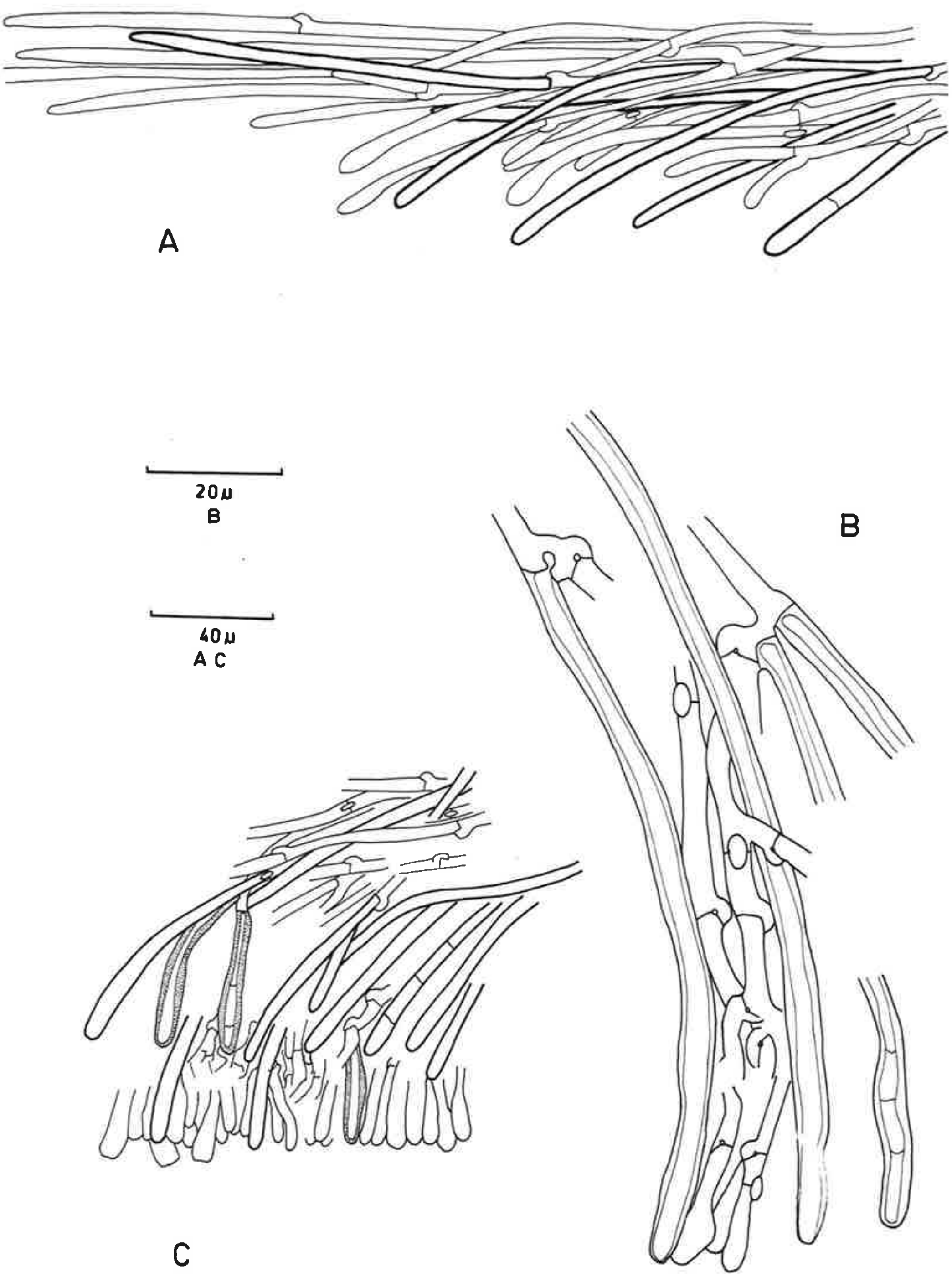
A notable developmental difference between fructifications of the two species was mentioned by Talbot (1951) and later by Cunningham (1957), and was confirmed in the present studies. In *D.tristicula* young fructifications, and margins of older fructifications, are darker than mature parts because the skeletocystidia in general project beyond the level of the generative hyphae and the basidia; the fructifications become lighter in color as the hymenium thickens and overlays the apices of the skeletocystidia. But in D.fulva the reverse is true: young fructifications are lighter in color than old ones because the generative hyphae apparently grow in pace with the skeletocystidia. The apices of the skeletal hyphae are therefore either at the same level as the generative hyphae or immersed below this level (fig.9:B). Although a small proportion of the skeletocystidia may project beyond the generative hyphae or hymenial level, it is only when the hymenium collapses in old material that the majority of skeletocystidial apices become exposed and impart a darker color to the hymenial surface of the fructification.

FIG. 9 *Duportella fulva*

A. Growing edge composed of generative and skeletal hyphae.

B. Young hymenium before basidia have been produced, showing skeletocystidia at the same level as the basidiferous hyphae.

C. Hymenium in which basidia are nearly nature. The hymenium has grown beyond the general level of the skeletocystidia.


A
20µ
B
40µ
A C
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C

Gloeocystidiellum lactescens (Berk.) Boidin (1951; cited in Christiansen, 1960)

Syn.: Corticium lactescens Berkeley (1860:274)
Gloeocystidium lactescens (Berk.) v.Höhnel & Litschauer sensu Bourdot & Galzin (1928:259)

The fructification is effused, thick membranous to fleshy, and composed of hyaline generative hyphae lacking clamp connexions. A context of downwardly-directed hyphae develops from the repent hyphae of the basal layer. The thickness of the basal layer is variable between specimens but is usually quite considerable.

Young gloeocystidia are formed from the apices of some of the basal hyphae which become swollen and tortuous, with contents staining more deeply than the surrounding context hyphae. Soon after they are initiated, they grow and elongate downwards in the same direction as the generative hyphae. Terminal and intercalary swellings were sometimes found in the repent marginal hyphae of the fructification (fig.10:A) and probably represent a very early stage in the development of gloeocystidia, as swellings were frequently seen on the horizontal basal portion of older gloeocystidia (fig.10:C).

Some gloeocystidia are bi-radicate (fig.10:E) or have a lateral heel. This is the result of one arm of a bifurcate young gloeocystidium (fig.10:B) growing vertically and developing at the expense of the other, which remains as a lateral process at the base of the gloeocystidium.

The hymenium forms over the surface of the context, and after the first basidia mature very few new gloeocystidia are observed. Thus the majority of gloeocystidia are formed before the hymenium; they lengthen in pace with thickening of the context and continue to elongate as the hymenium thickens. Consequently the gloeocystidia in this species become very long and vermiform, particularly in older parts of the fructification (fig.10:G). Attempts were made to determine whether some of the gloeocystidia were hymenial in origin, but these were inconclusive because the basidia of this species are unusually long and it was impossible to ascertain whether some of the structures in the basidial fascicles were young gloeocystidia or immature basidia. It is likely, however, that the majority of gloeocystidia have no association with the hymenium, since none were seen originating in the distal part of the context, where they might have been expected if formed in association with a thickening hymenium.

Cytoplasm was never found to occupy the entire length of older gloeocystidia. Apparently as the young gloeocystidia elongate they are filled with cytoplasm only until a certain length is attained, and subsequently the bulk of the cytoplasm remains in the apical portion leaving the basal part of the gloeocystidium apparently empty.

Secondary septa (fig.10:H) are formed at intervals as the column of cytoplasm becomes concentrated towards the distal end of the gloeocystidium. Such septa may also act as struts which prevent collapse of the empty bases of the gloeocystidia.

The spores of this species become only very faintly blue in Melzer's solution and the gloeocystidia react positively with sulfo-aldehyde solution.

FIG. 10 *Gloeocystidiellum lactescens*

A. Terminal and intercalary swellings found in the growing edge.

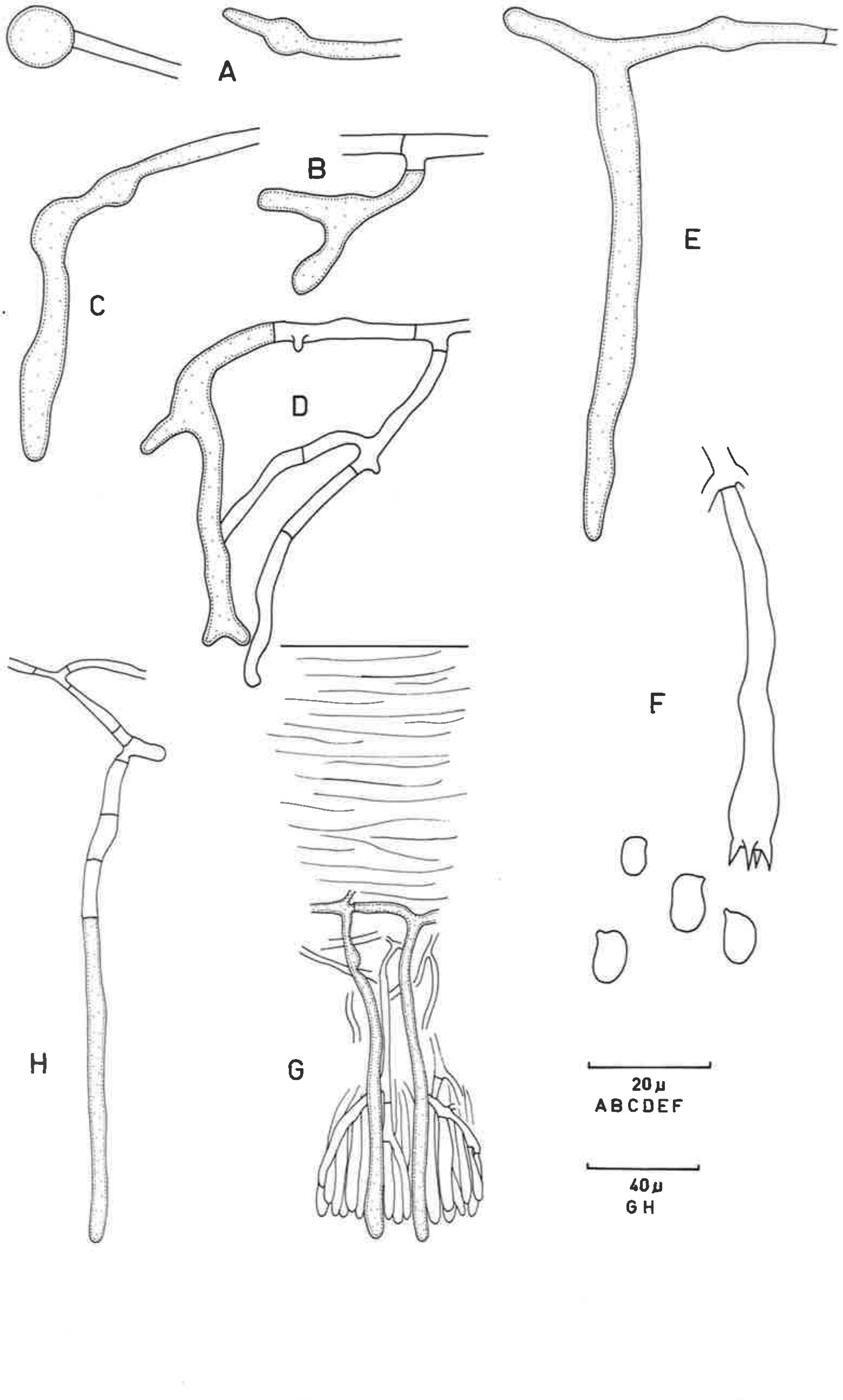
B,C,D. Young gloeocystidia.

E. Gloeocystidium with a bi-radicate base.

F. Basidium and spores.

G. Section of mature fructification showing long gloeocystidia extending from the basal layer to the current hymenium.

H. Old gloeocystidium with the cytoplasm in the distal portion and secondary septa at intervals in the proximal portion.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20 µ
A B C D E F
40 µ
G H

Gloeocystidiellum leucoxanthum (Bres.) Boidin (1957:122)

Syn. Corticium Leucoxanthum Bresadola (1898:57)

Gloeocystidium leucoxanthum (Bres.) v.Höhnel & Litschauer (1907:6)

The fructification is effused, waxy to fleshy with a monomitic hyphal system consisting of clamped generative hyphae.

The growing margin of the fructification is thin and appressed to the substratum. It contains many basal hyphae with swollen apices, the majority appearing bifurcate (fig.11:B); these represent the first-formed gloeocystidia. When vertical growth of hyphae commences in the fructification it seems to dominate over horizontal growth; thus when one of the swollen arms of a young gloeocystidium turns downwards it dominates in growth at the expense of the other which becomes impoverished, dies back and remains as a lateral heel at the base of the developing gloeocystidium. A great number of young gloeocystidia are formed from the basal hyphae, but not all survive. Nearer the centre of the young fructification, basidiferous hyphae and basidia are differentiated from the basal hyphae, and the hymenium gradually thickens. The apices of the persisting gloeocystidia elongate in pace with the thickening of the hymenium and eventually, in a mature fructification, there is a palisade of gloeocystidia traversing the fructification from the base of the context to the surface of the current hymenium (fig.11:E).

As soon as vertical hyphal growth becomes dominant, basidia and a hymenium are formed. The first-formed basidia begin their development as short branches with a basal clamp connexion; but occasionally a similar branch develops into a gloeocystidium instead (fig.11:D). Such gloeocystidia, while young, are the same shape as basidia and do not possess a heel such as is found in gloeocystidia formed from basal hyphae. Gloeocystidia formed in the hymenium also elongate in pace with the thickening of the hymenium and add to the palisade of gloeocystidia. It is evident, then, that in a mature fructification there will be gloeocystidia arising at various levels, although the majority are deep-seated in origin. It is also evident that some of the gloeocystidia are essentially hymenial in origin while others come from the basal hyphae prior to the formation of a hymenium. With the latter, a lateral heel usually persists, but otherwise the final form of both types is very similar. Each has a tendency to become moniliform towards the apex.

Simple hyphidia and sparingly-branched dendrohyphidia are also present in the hymenium and arise from the basidial fascicles. Spores of this species are strongly amyloid and the gloeocystidia react positively with sulfo-aldehyde solution.

FIG. 11 Gloeocystidiellum leucoxanthum

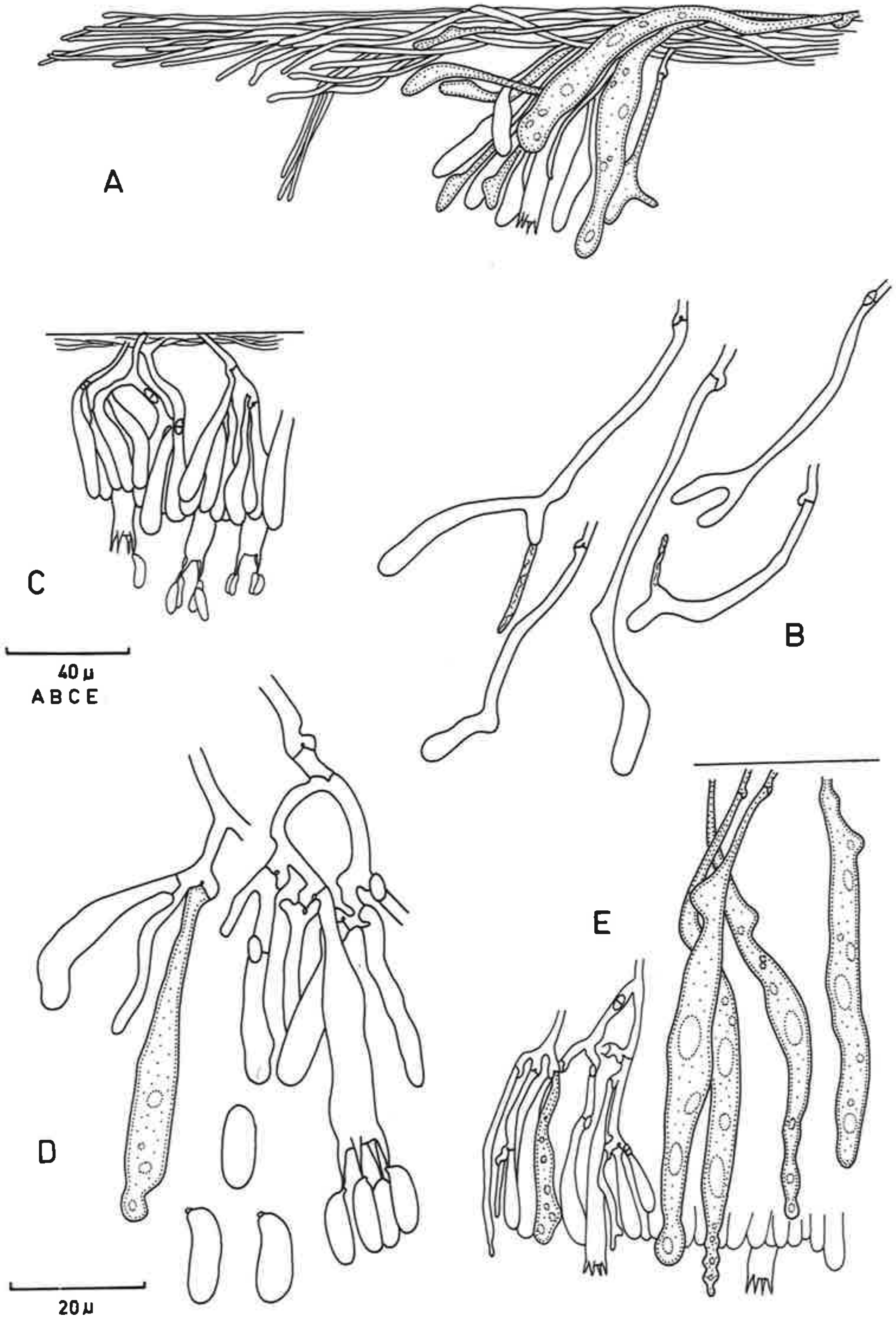
A. Growing edge of fructification showing basal hyphae, gloeocystidia and basidia.

B. Gloeocystidial basal hyphae in the growing edge.

C. Young hymenium.

D. Detail of the spores, shape of basidia and the connection of the gloeocystidia formed in the hymenium with the basidial fascicles.

E. Section of a mature part of the fructification showing the palisade gloeocystidia.


A
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40 µ
A B C E
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20 µ

Hyphoderma setigerum (Fr.) Donk (1957a:15)

Syn.: Thelephora setigera Fries (1828:208)
Peniophora setigera (Fr.) Höhnel & Litschauer (1906a:289)
Peniophora aspera (Pers.) Saccardo (1916:1182).

The fructification is effused, membranous, with a byssoid margin and composed of clamped generative hyphae. The growing edge is a thin basal layer from which downwardly-growing lateral branches develop. These may develop immediately into cystidia or basidia (fig.12:A,B), or branch loosely before forming cystidia or basidia. Later branching is more compact, the texture denser and a definite hymenial layer is formed. Cystidia and basidia develop at about the same time in the growing edge, the cystidia slightly before the basidia. Side branches from cystidial and basidial pedicels either develop immediately into basidia or branch slightly before producing basidia. Thus cystidia are often part of a basidial fascicle (fig. 12:C). Although the cystidia often develop in close association with the basidia they are unlikely to be homologous, since the basidia are utriform and thus differ from cystidia in developmental pattern.

The cystidia are large, thick-walled septate hypho-cystidia encrusted with crystals. They elongate as the hymenium thickens and become quite long; thus early-formed cystidia extend from near the base of the fructification to the hymenium, or well beyond (fig.12:F). The septate hyphocystidia branch readily but it is not certain whether this occurs after apical damage or if the apex dies back after a branch is formed. In some collections aseptate cystidia were present (fig.12:E); in other respects these cystidia were identical with the septate cystidia. Mature fructifications are often slightly hydnoid. This is probably the result of the fructification building up around a projecting cystidium.

FIG. 12 <u>Hyphoderma setigerum</u>

A. Young cystidium developing from a basal hypha.

B. A basidium developing in an equivalent position to A.

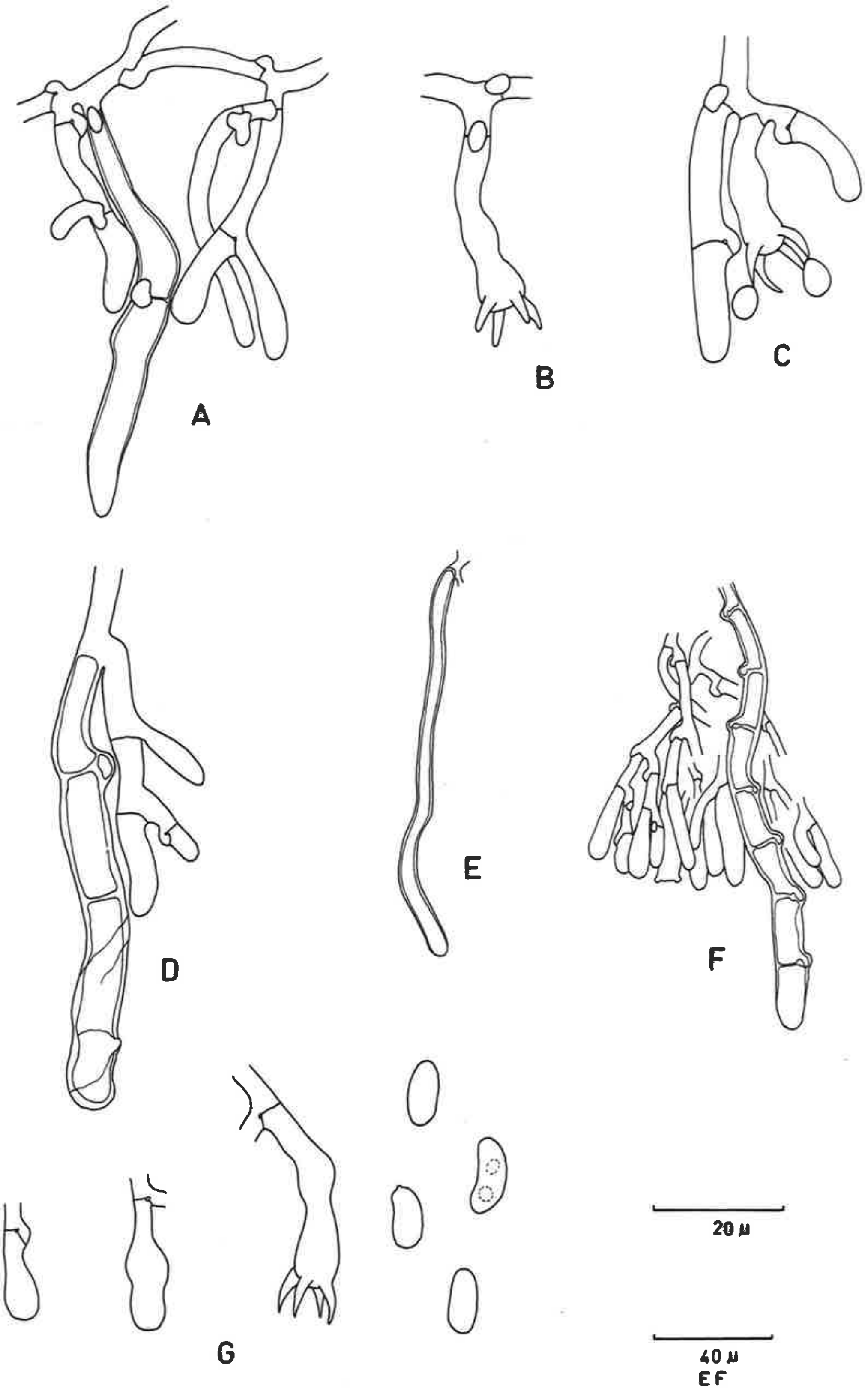
C. A basidium and cystidium developing in the same fascicle.

D. A cystidium developing as a modified apex of a context hypha.

E. Mature cystidium without transverse septa.

F. A septate hyphocystidium extending from the context to beyond the hymenial level.

G. Showing spores and stages in the development of a basidium.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EF

Hyphoderma tenue (Pat.) Donk (1957a:15)

Syn.: Corticium tenue Patouillard (1885:152)
Peniophora tenuis (Pat.) Massee (1889:149)
Gloeocystidium tenue (Pat.) Hohnel & Litschauer (1908:70)
Gloeocystidium caliciferum Litschauer (1928:126)
Corticium torquatum Cunningham (1954b:283)

For further synonyms see Rogers & Jackson (1943).

The fructification is effused, at first thin and byssoid-membranous becoming thick and waxy-membranous. The hyphal system consists of clamped generative hyphae. The growing edge is a thin layer of basal hyphae on which basidia and cystidia develop directly, the cystidia slightly before the basidia. The basidia (fig.13:B) and cystidia are produced from vertical branches of the basal hyphae; those cystidia which develop directly as side-branches from the basal hyphae have radicate bases (fig. 13:C), but these are found only in the growing edge and once a hymenium has been established cystidia develop solely from vertical hyphae. Two morphological forms of cystidia are present in this species and a study of the development of the cystidia and basidia showed that all three structures developed from the same type of primordial cell in the hymenium. In fig.13:E stages in the development of all three structures are shown. With the young stages it is impossible to tell what the final structure will be. As they develop, a pointed apex or a more or less cylindrical cell indicates that the final structure will be either of the two forms of cystidium. Whereas a constricted cell or one with a wide flat apex (as happens in young basidia prior to the formation of sterigmata) indicates that the structure is a basidium. New cystidia are continuously formed in the hymenium from cells homologous with basidia.

Cystidia in this species have been termed gloeocystidia by some authors, while others recognise gloeocystidia and cystidia. In the specimens studied one form of cystidium is cylindrical, of determinate length, projecting beyond the hymenium and with a rounded apex often topped with a crystalline cap (fig. 13:H,J). As the cystidia mature the walls become slightly thicker, the contents gradually disappear and sometimes secondary septa are formed (fig.13:K). From the mode of development and morphology this form of cystidium is a leptocystidium. The other form of cystidium is thin-walled with a slightly swollen base and subulate apex (fig.13:G), and without a crystalline cap. They remain embedded in the fructification, often lengthening and becoming long and tenuous as the fructification thickens (fig.13:L). The contents stain deeply but do not darken in sulfo-aldehyde solution. Although these cystidia develop in the same manner as the leptocystidia, by their contents and shape they are recognised as gloeocystidia. Well-defined leptocystidia and gloeocystidia are the extremes of a morphological range of cystidial structures. Therefore Rogers & Jackson (1943) were correct in regarding Peniophora tenuis s.str. and Peniophora pertenuis (Karst.) Burt as synonymous, and the end limits of a variable species.

The basidia (fig.13:F) are large, conspicuously constricted (utriform) and typical of the genus Hyphoderma (Eriksson, 1958a). As the hymenium develops directly on the basal layer in the growing edge, the depth of the fructification is built up by the thickening of the hymenium. Stephanocysts were also found in this species and these are discussed separately.

Stephanocysts

Stephanocysts are unusual structures which have been found in only a few species (Boidin, 1958b); I found them in only one collection of Hyphoderma tenue. The stephanocysts of this species are pyriform, two-celled, sharply delineated from the hyphae from which they arise, and have a girdle of digitate processes around the septum between the two cells. They are thin-walled and have densely staining contents which do not darken in sulfoaldehyde solution (Boidin, 1958a). There are clamp connections on all septa although they are sometimes difficult to detect on the central septum when hidden underneath the stephanocyst or obscured by the digitate processes. How stephanocysts were initiated and how the digitate processes developed were not ascertained. Fig. 14:A,B may represent young stephanocysts; if so they commence as a short single-celled or two-celled branch which becomes greatly swollen and develops digitate processes. In the specimen studied stephanocysts were found throughout the fructification, in the context (fig.14:F) and in the hymenium (fig.14:D,E), although Donk (1964) believed that stephanocysts did not have any connection with the hymenial region. The stephanocysts in this species are probably a peculiar form of gloeocystidium. Rogers & Jackson (1943) found that there were numerous intergrading structures connecting caliciform bodies (stephanocysts) with simple globoid gloeocystidia.

Cunningham (1954b) described a new species, Corticium torquatum, which was characterised by the presence of unique two-celled stephanocysts. The description of this species fits that of H.tenue. Although Cunningham does not specifically mention cystidia, he says that some gloeocystidia project to 20u; these are most likely to be what other authors have designated cystidia, especially as the cystidia of this species are thin-walled and relatively inconspicuous.

FIG. 13 Hyphoderma tenue

A. Branch in the growing edge which could become a cystidium, basidium or basidial fascicle.

B. Basidia in the growing edge, produced directly from basal hyphae.

C. A leptocystidium produced laterally from a basal hypha in the growing edge.

D. Spores.

E. Series showing the development of leptocystidia, gloeocystidia and basidia from the same type of primordial cell.

F. A basidium.

G. A gloeocystidium.

H. A young leptocystidium.

J. A mature leptocystidium with a cap of crystals.

K. An old leptocystidium with secondary septa.

L. A section through a mature hymenium showing basidia, cystidia, and a long embedded gloeocystidium.

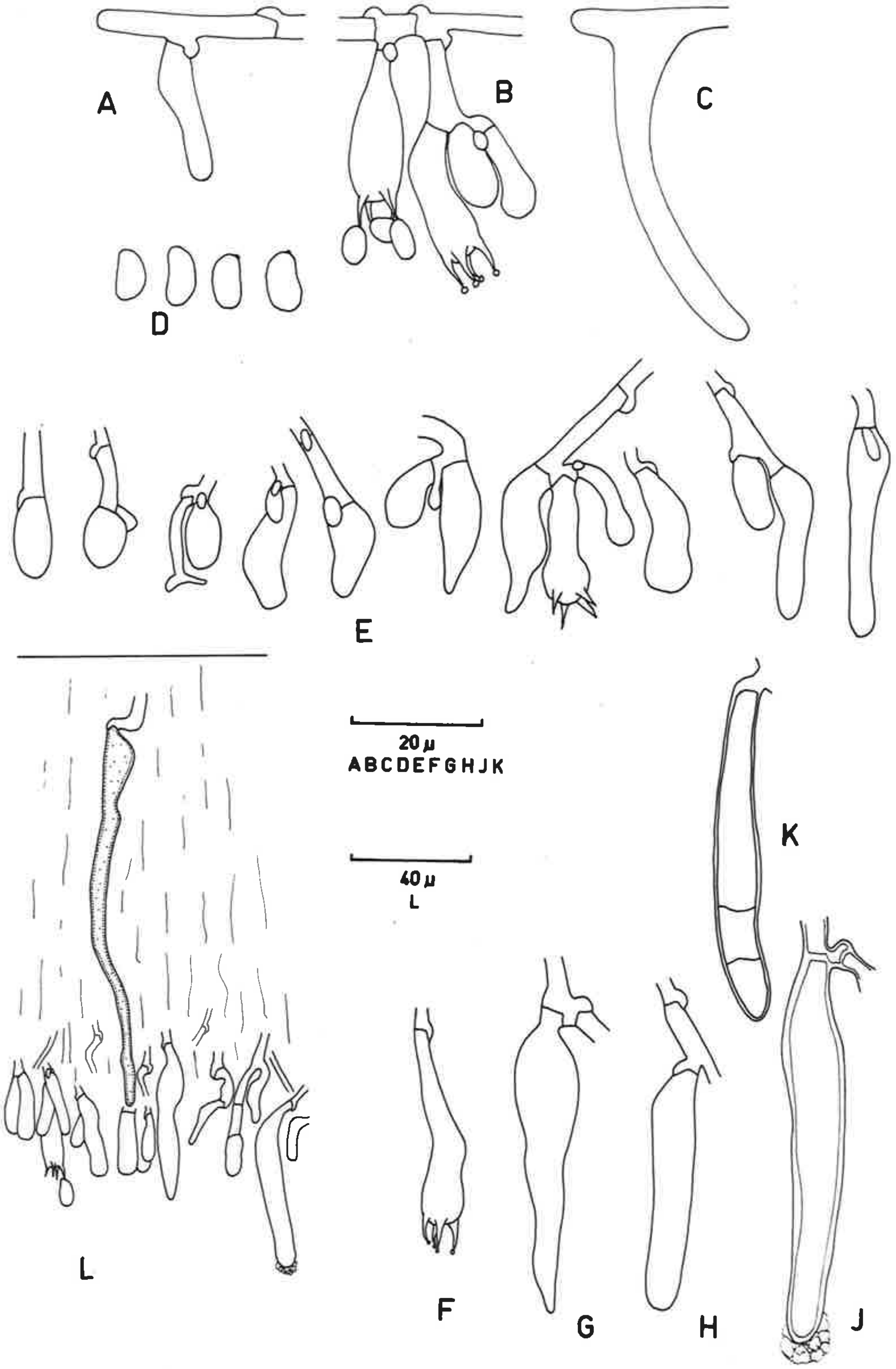
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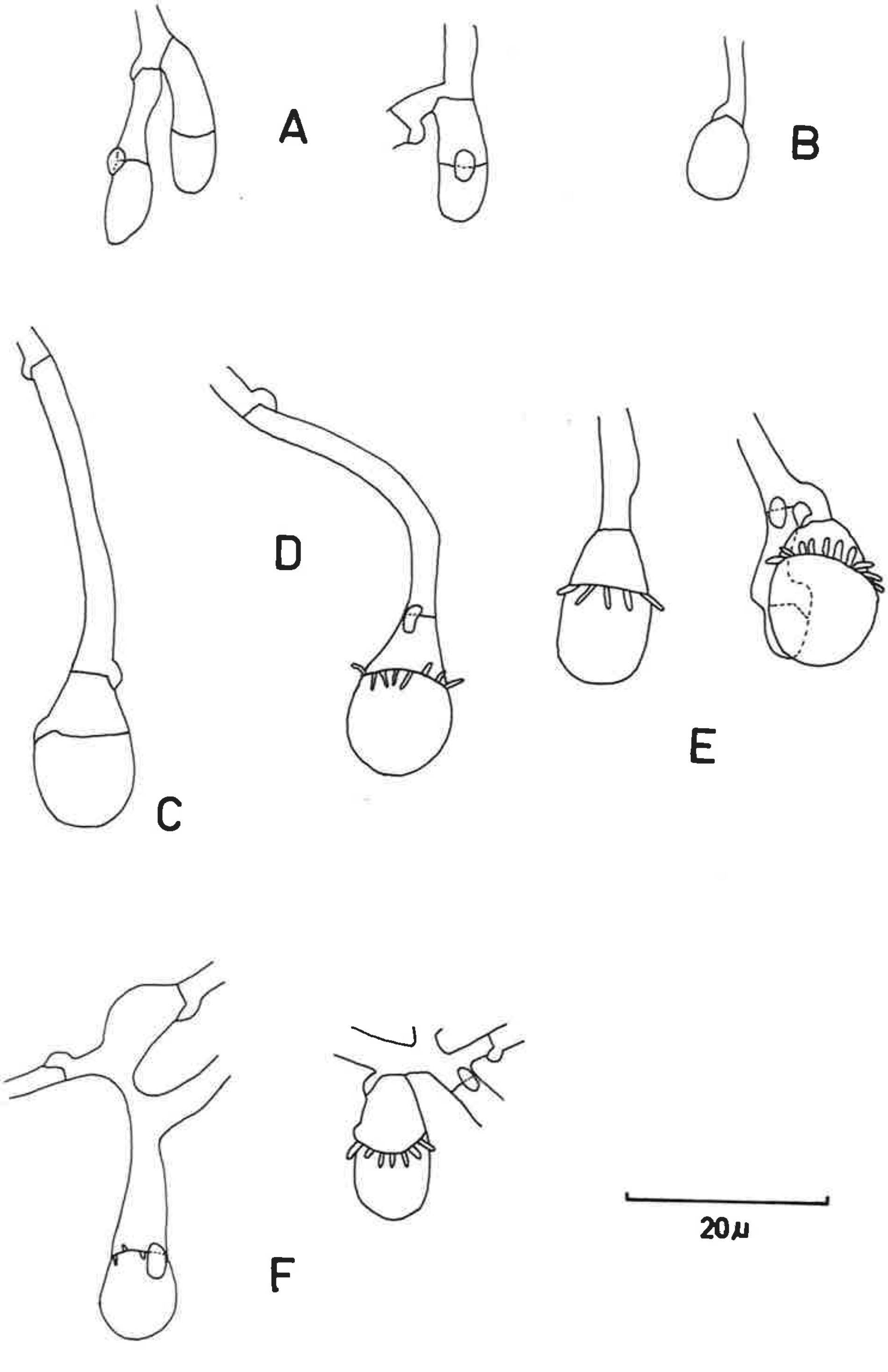
FIG. 14 *Hyphoderma tenue*

A & B. Cells possibly representing young stephanocysts.

C. Stephanocyst without digitate processes; position in the fructification is unknown.

D & E. Stephanocysts from the hymenium.

F. Stephanocysts from the context.


A
B
C
D
E
F
20µ

Hyphoderma puberum (Fr.) Wallroth (1833:576)

Syn.: *Thelephore pubera* Fries (1828:215)
Peniophora pubera (Fr.) Saccardo (1888:646)
Phlebia pubera (Fr.) Christiansen (1960:171)

For further synonyms see Rogers & Jackson (1943).

The fructification is effused, ceraceous, and composed of clamped generative hyphae. The growing edge is a thin layer of reticulated horizontal hyphae, not easily separable from the substratum. It extends over a wide area before downward growth is initiated. As soon as downward growth commences, terminal cells of vertical hyphae mature into either basidia or cystidia. Side branches from above these cells grow down and add to the thickening hymenium.

There are two types of cystidium in this species: thick-walled crystal-encrusted metuloids, and gloeocystidia. It is not possible to tell whether the young terminal cell will become a basidium or a metuloid or a gloeocystidium (fig.15:A). In the young stages all three are very similar (fig.15:B,C) and only in the later stages can gloeocystidia, metuloids and basidia be distinguished (fig.15:D,E,J). New cystidia are continuously formed in the hymenium from cells homologous with basidia. At first the metuloids project for a considerable distance beyond the hymenium (fig.15:F) but they gradually become embedded as the hymenium thickens. The gloeocystidia always remain embedded and often lengthen with the thickening of the hymenium thus becoming very long (fig.15:H). The basidia are the utriform shape characteristic of Hyphoderma (fig.15:J).

FIG. 15 Hyphoderma puberum

A. An undifferentiated terminal cell which may develop into either a basidium or a cystidium.

B. Young basidia.

C. Young cystidia: one cannot tell whether they will develop into gloeocystidia or metuloids.

D. A young gloeocystidium.

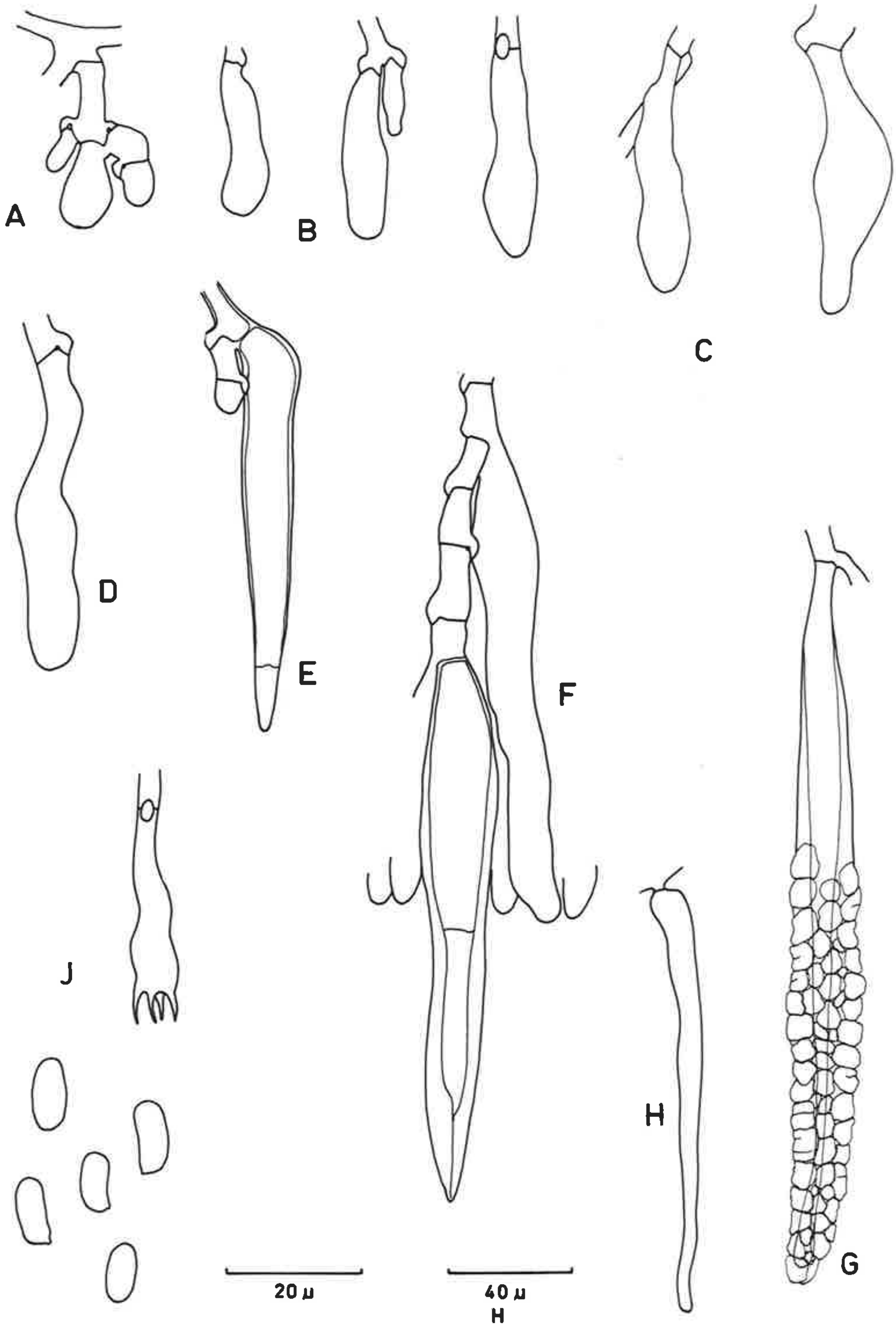
E. A young metuloid.

F. A side branch from a gloeocystidial pedicel has later developed a metuloid.

G. A mature metuloid.

H. A mature gloeocystidium.

J. A basidium and spores.


A
B
C
D
E
F
G
H
J
20 µ
40 µ
H

Hyphoderma species

The thin, effused, membranous fructification is white in colour. Under the dissecting microscope projecting cystidia with brown granules on their walls can be seen. The hyphal system consists of clamped generative hyphae. The growing edge and subsequent development of the fructification and hymenium follow the same pattern as in Hyphoderma tenue.

Two Morphological forms of cystidia were found in the specimens studied. Most noticeable were the long thin-walled cylindrical to obclavate cystidia projecting for some distance beyond the hymenium. The other form of cystidium was shorter, did not project far beyond the hymenium and had an inflated apex but a base no wider than the hypha from which it developed. Both forms are shown in fig.16:B. The cystidia lengthen somewhat as the hymenium thickens, but the older ones eventually become embedded.

Both types of cystidia and the basidia arise from the same type of cell in the hymenium. These are very variable in shape (fig.16:A). From the shape of the mature basidia (fig.16:C) it is apparent that they develop from ovoid cells; cystidia with inflated bases also develop from ovoid cells. Therefore in the young stages it cannot be foretold if an ovoid cell will become a cystidium or a basidium. Both forms of cystidia are leptocystidia as they are thin-walled and develop from the same type of hymenial cell as the basidia.

The identity of this fungus is not known. The development of the fructification and cystidia is like that in *H.tenue* and in addition the basidia are utriform and the spores fit the generic diagnosis of *Hyphoderma* for size and shape. As well as these considerations the fungus appeared to be very like the descriptions of *Hyphoderma* (*Peniophora*) *argillacea* (Bourdot & Galzin, 1928; Christiansen, 1960). Therefore this fungus is placed in *Hyphoderma* although this genus is now heterogeneous.

FIG. 16 *Hyphoderma* species

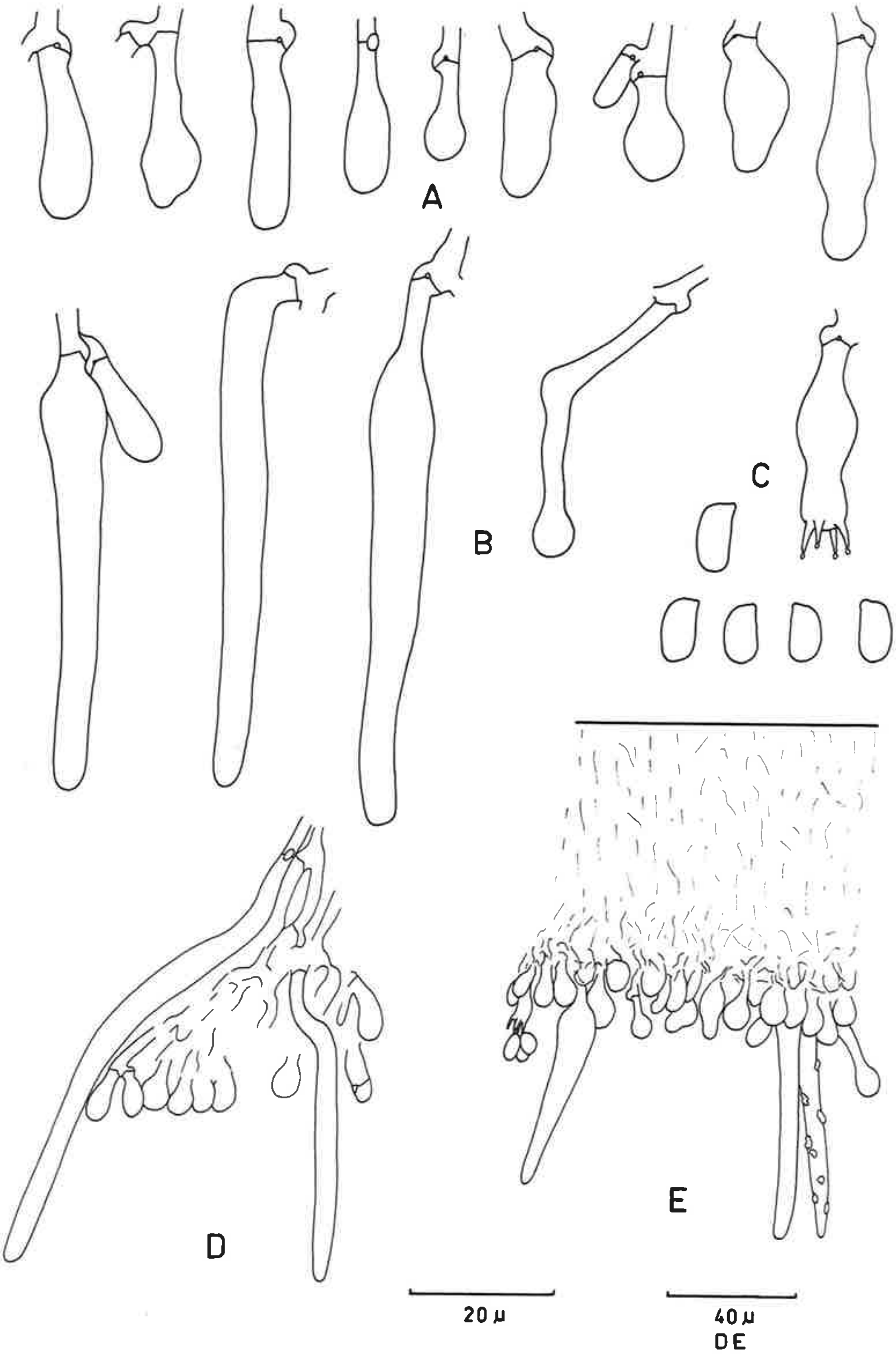
A. Variety in the shape of hymenial cells. From such cells develop the basidia and two forms of cystidia.

B. Three examples of the cylindric-obclavate cystidia and one of a small cystidium with inflated apex.

C. A basidium and spores.

D. Section through the hymenium showing projecting cystidia with their bases at different levels in the fructification. The cystidia can become quite long, as they lengthen with the thickening of the hymenium.

E. Section of a mature portion of the fructification showing the relationship between the various structures.


A
B
C
D
E
20 µ
40 µ
DE

Hyphodontia alutaria (Burt) Eriksson (1958a:104)
Syn.: *Peniophora alutaria* Burt (1925:332).

The effused, loosely membranous fructification is monomitic with clamped generative hyphae. The growing edge is a thin layer of basal hyphae. Terminal chlamydospores were the first structures produced from the basal hyphae (fig.17:A). Chlamydospores have not previously been reported for this species. Many of the first vertical hyphae to develop on the basal layer narrow to a long thick-walled apex which becomes encrusted with a regular pattern of acicular crystals (fig.17:A,B). Later these crystal-encrusted subulate cystidia are formed anywhere in the fructification, on cells homologous with the septate hyphocystidia (fig.17:C) and with the basidia (fig.17:D). Side branches often develop from the cells with this type of modified apex (fig.17:B,D). These subulate cystidia do not fit any of the recognised categories of cystidia, although those developing in the hymenium are close to the category of leptocystidia.

A hymenium is initiated very soon after vertical hyphae develop in the growing edge. Just prior to the formation of basidia the apices of some context hyphae develop into septate hyphocystidia (fig.17:C). As the cystidia mature they become multi-septate and lengthen apically in stages. At each halt in growth the apex becomes inflated. Thus in older cystidia, lengthening with the thickening of the hymenium, bulges along their length mark the positions of previous apices (fig.17:F). Crystals when present are concentrated on these bulges and at the apex. It is not unusual for the septate hyphocystidia to branch or to resume growth from the side of an apex (fig.17:F). Septate hyphocystidia continue to form after a hymenium is established. The basidia are small and clavate to utriform in shape.

FIG. 17 *Hyphodontia alutaria*

A. Development of chlamydospores from basal hyphae in the growing edge. A young crystal-encrusted subulate cystidium is also shown.

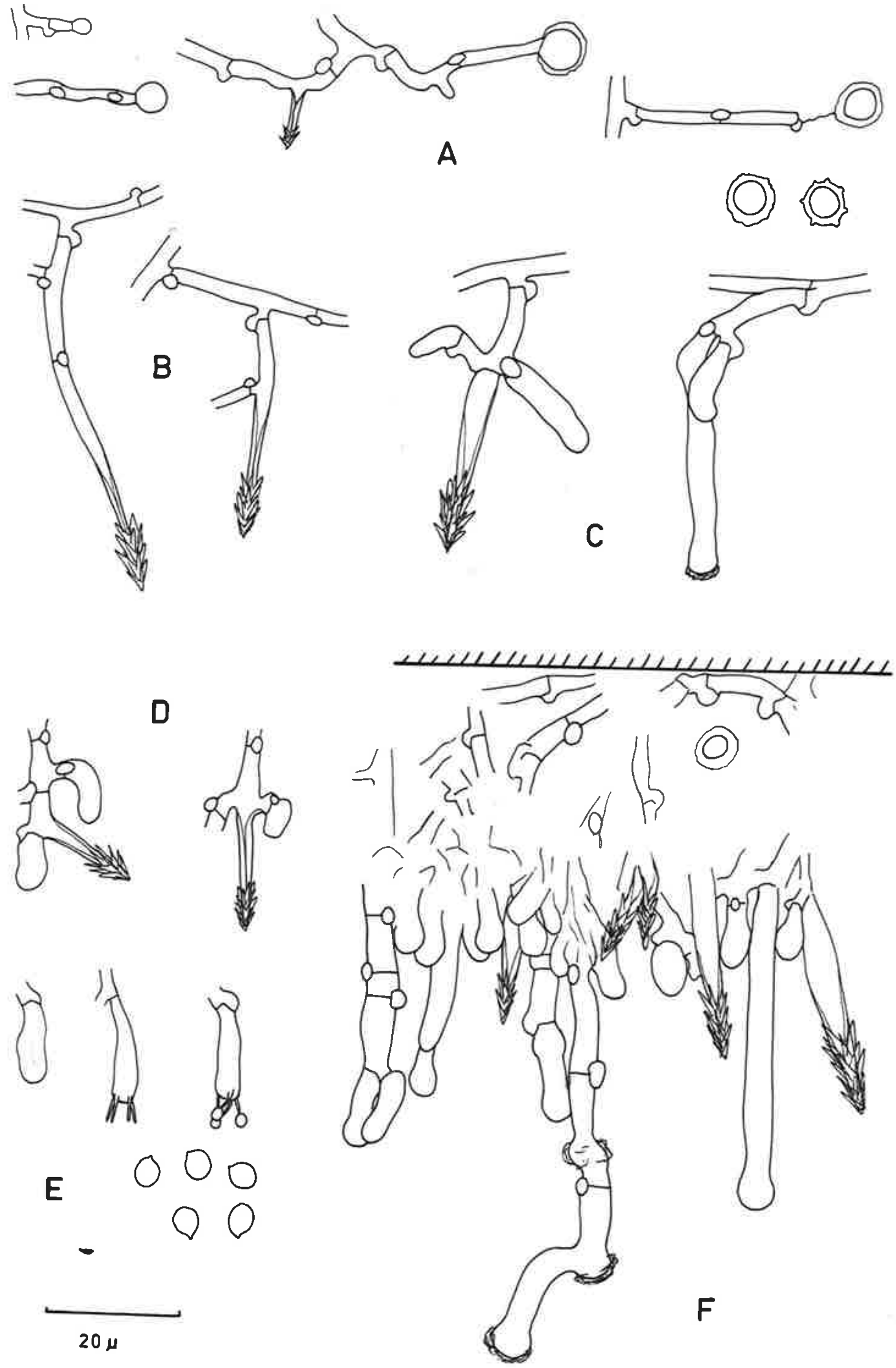
B. Apices of context hyphae modified to crystal-encrusted subulate cystidia.

C. A young hyphocystidium (right) forming just prior to the development of a hymenium. A subulate cystidium (left) formed in a homologous position to the hyphocystidium.

D. Subulate cystidia in the hymenium. Branches can develop from the cells with the subulate apices.

E. Basidia and spores.

F. Section through a mature portion of the fructification showing branching of the septate hyphocystidia and the relationship of the structures in the fructification.


A
B
C
D
E
F
20 µ

Hyphochnicium punctulatum (Cooke) Eriksson (1958a:101)
Syn.: Corticium punctulatum Cooke (1878:132)

The fruit-body is effused, thick and membranous, monomitic and composed of clamped generative hyphae. In the growing edge there is a thin layer of basal hyphae and the vertical hyphae developing from this give rise to a hymenium almost immediately. At this stage the fructification is thin and arachnoid. It was noticed that branching of the vertical hyphae was almost solely by the proliferation of clamp connexions.

In this species the hymenial cells (fig.18:A) can develop into either basidia (fig.18:B) or cystidia (fig. 18:C). The cystidia are cylindrical with rounded apices and thin walls at first. In old cystidia the walls become somewhat thickened and secondary septa are common. There are no crystals on these cystidia. From their morphology and the nature of their development the cystidia of this species are leptocystidia.

As the hymenium develops early in the growing edge the depth of the fructification is built up by the thickening of the hymenium. At first the cystidia project beyond the hymenium but once they are mature they gradually become embedded by the thickening hymenium. It is these embedded cystidia that become relatively thick-walled and secondarily septate. Their contents disappear and formation of the septa is probably associated with this. The basidia are clavate to slightly utriform and the spores are thick-walled and densely warted.

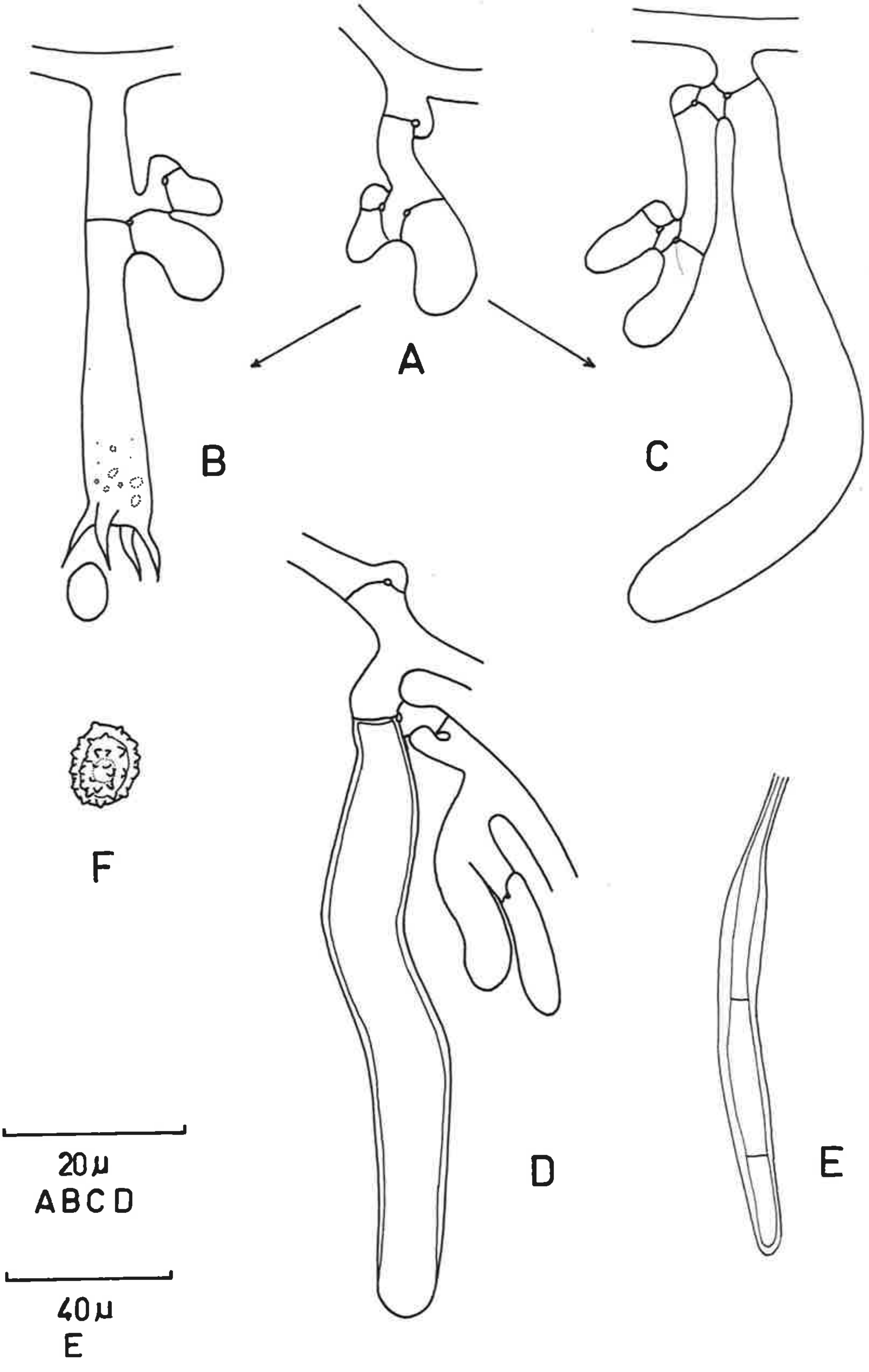
FIG. 18 *Hypochnicium punctulatum*

A. A vertical branch formed from the basal layer in the growing edge. The terminal cell can develop into either a basidium B, or a cystidium C.

D. A mature leptocystidium.

E. An old cystidium with thickened walls and secondary septa.

F. Mature spores are thick-walled with prominent warts.


A
B
C
D
E
F
20µ
ABCD
40µ
E

Laxitextum bicolor (Pers. ex Fr.) Lentz (1955:19)

Syn.: Thelephora bicolor Persoon ex Fries (1821:438)

Stereum bicolor (Pers. ex Fr.) Fries (1838:549)

For further synonyms see Lentz (1955).

In the young fructification, a broad interwoven context is formed before hymenial elements are differentiated; thus the margin is thick, spongy in texture and composed of the ends of context hyphae and cortex hyphae in the pileate portions. The context and cortical hyphae become brownish, somewhat thick-walled, with conspicuous clamp connexions (fig.20:H), and form a monomitic hyphal system. The context, and cortex when present, forms a thick brown loose-textured layer which is sharply differentiated from the hyaline, vertical and somewhat indistinct hyphae of the thickened hymenium; hence the specific epithet of this fungus. The spores are very distinctive; small, amyloid and finely verrucose.

Gloeocystidia are formed either terminally or laterally from lower-surface hyphae near the growing margin which are curving down to the vertical and at first are distinguishable only by their widened apices (fig.19:B). The terminal gloeocystidia have a basal clamp connexion which, together with the next one or two proximal clamps down the hypha, usually proliferates to form a lateral branch. Such lateral branches again branch to produce a basidiferous layer and eventually basidia (figs.19:C,D;

20:A,B,C). A hyphal apex which does not become a terminal gloeocystidium, branches to become part of the basidiferous layer; in such instances a lateral gloeocystidium often develops as a proliferation from one of the clamps near the hyphal apex (fig.19:D). This indicates that the hyphal apices and lateral branches each have the potential of developing either into a gloeocystidium or into a branch of the basidiferous layer.

At a young stage in the development of the fructification most of the gloeocystidia contain one large globule of an unidentified yellowish substance (fig.19:F) and, since the gloeocystidia are formed at about the same level, a section shows a conspicuous horizontal yellow line corresponding with the position of the globules (fig.19:A). As has been shown, the gloeocystidia arise at the level of the lowest branches of the basidiferous layer and are essentially hymenial elements. They persist, and lengthen in pace with the thickening of the hymenium so that their apices are always at about the same level as the layer of active basidia; but in old fructifications their bases are well below the current hymenial level. Thus they eventually form a palisade between the context and the layer of active basidia. At this stage the gloeocystidia of most specimens appear as discontinuous lines represented by their solidified contents (fig.20:F). If such a gloeocystidium is teased from the rest of the fructification it can be seen that it has not completely disintegrated but that the contents are held by the collapsed walls of the gloeocystidium (fig.20:E). In some specimens the gloeocystidia had not collapsed but remained as turgid, vacuolate structures with moniliform apices (fig.19:E). New gloeocystidia are produced from basidiferous branches (fig.20:C) as the hymenium thickens and they also lengthen in pace with the thickening hymenium, adding to the palisade of gloeocystidia.

Fine, branched, aseptate hyphae were observed throughout the tissue formed by the thickening hymenium (fig.20:D). They ended in the hymenium as simple hyphidia or sparingly-branched dendrohyphidia (fig.19:E). In one specimen these fine hyphae were seen to originate from sub-hymenial branches (fig.19:C).

Many of the hyphae in the context and especially in the growing edge had refractile contents which disintegrated in the same way as old gloeocystidia. However, it could not be ascertained whether these hyphae constituted a gloeo-system.

FIG. 19 Laxitextum bicolor

(drawings from a fructification cultured on soil)

A. Sketch of the structure of the fructification showing the relationship of the stages a,b,c,&d.

B. A young terminal gloeocystidium.

C. A terminal gloeocystidium at a later stage; a hymenial branch has developed at the base of the gloeocystidium and the right-hand branch of this is the start of a thin, ramifying hypha.

D. A gloeocystidium formed in a lateral position from the parent hypha.

E. Section of a mature part of the fructification showing basidia, finely verrucose spores, long gloeocystidia and hyphidia.

F. Young gloeocystidia: the right-hand one with a large globule of an unidentified substance and the left-hand one with a "heel".

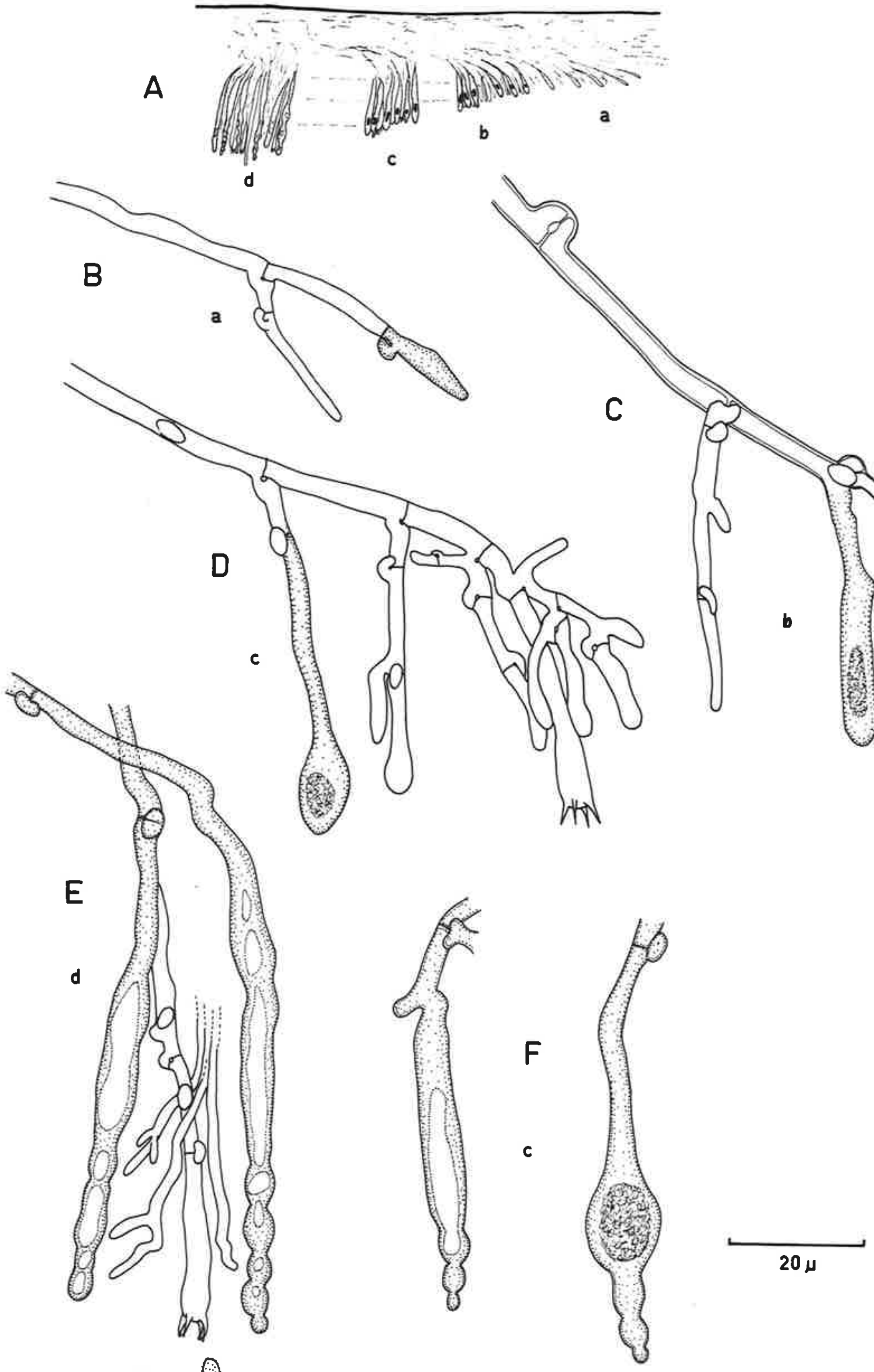

A
a
b
c
d
B
a
C
b
D
c
E
d
F
c
20 µ

FIG. 20 *Laxitextum bicolor*

(drawings from a natural fructification)

A. A young terminal gloeocystidium.

B. An older stage: the side branch is developing basidiferous tissue.

C. Contents of gloeocystidium becoming refractile. A young gloeocystidium developing in the side branch.

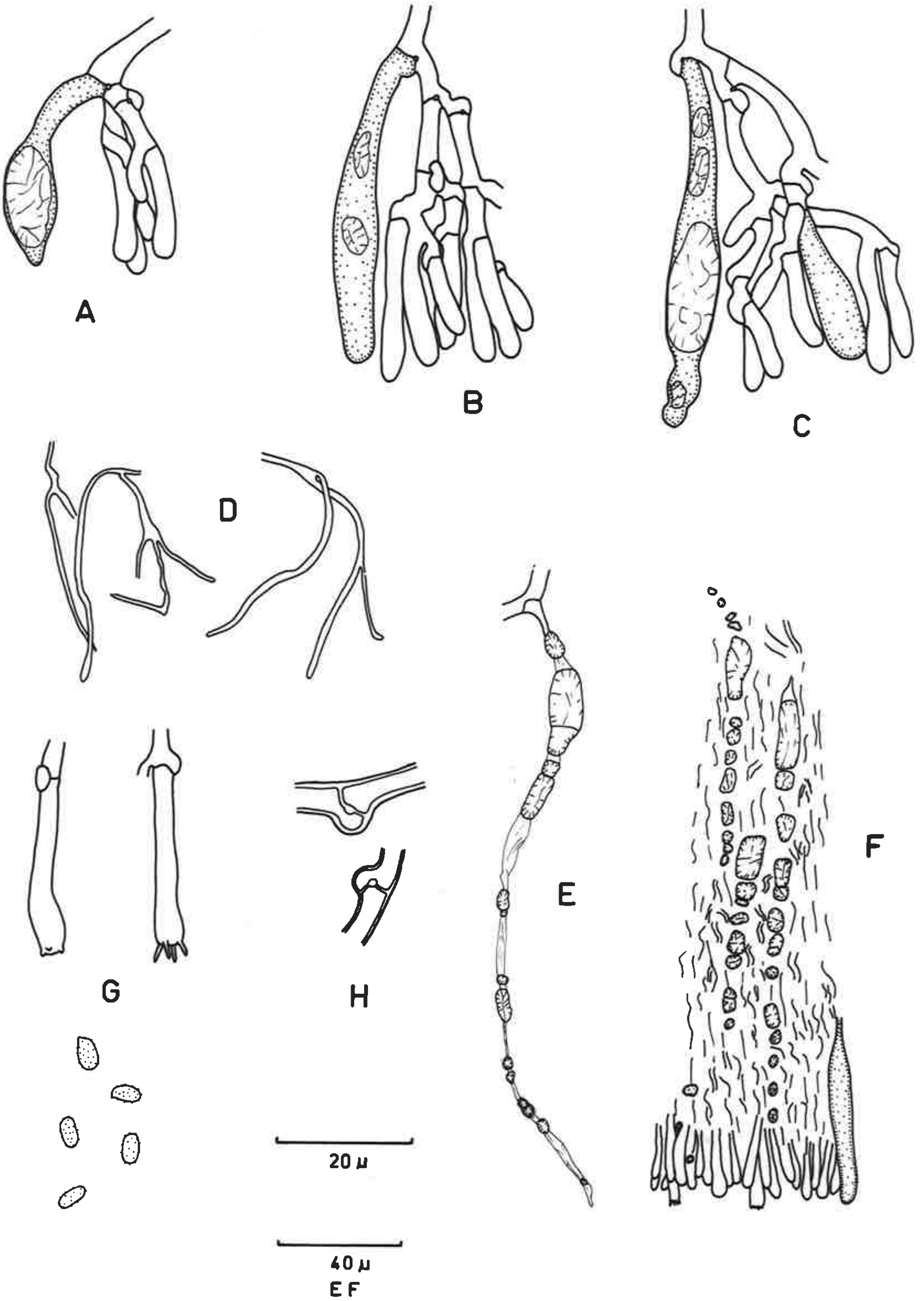
D. Fine, branched, aseptate hyphae which ramify throughout the thickened hymenium and end at the current hymenial level.

E. An old gloeocystidium: the scattered refractile contents are held by the collapsed walls.

F. Section of a mature hymenium showing disintegrated gloeocystidia.

G. Basidia and spores.

H. Conspicuous clamp connexions in context hyphae.


A
B
C
D
E
F
G
H
20 µ
40 µ
EF

Litschauerella abietis (Bourd. & Galz.) Oberwinkler
(1965:44)

Syn.: Peniophora abietis Bourdot & Galzin (1928:286)
Tubulicrinis gladiola (Cunn.) Cunningham (1963:134).

The fructification is effused, membranous, and the hymenial surface is minutely hispid through the presence of large projecting subulate multi-radicate cystidia (fig.21:B). The hyphal system consists of clamped generative hyphae only. The growing edge is a layer of basal hyphae from which develop the multi-radicate cystidia. Well-developed cystidia were found at the extreme margin of the growing edge (fig,21:A), but it could not be determined how they were initiated. As the cystidia mature the roots become more branched and the walls thicken considerably so that only a narrow lumen is left in the apical portion of the cystidium.

Cystidia of this species do not dissolve in KOH solution and are pseudoamyloid in Melzer's solution with approximately the basal third of the cystidium, including the many roots, becoming brick-red. The portions of the roots giving this reaction also stain deeply in aniline blue solution; consequently either in Melzer's or aniline blue solutions the roots of the cystidia are sharply demarcated from the ordinary vegetative hyphae. The cystidia do not have a covering of fine dendritic hyphae as do similar cystidia in Tubulicium vermiferum, although a few hyphae of the same width as the basal hyphae grow down around the cystidia. Instead the cystidia appear to be encrusted with fine acicular crystals. However, when cystidia are mounted in Melzer's solution the wall is found to consist of two layers, a thick inner layer and a much thinner outer layer which is then seen to be extensively fissured and presents a "crystalline" appearance (fig.21:C).

The basidia of L.abietis are pleurobasidia (fig.21:D) and develop from the basal hyphae after the initiation of cystidia. A layer of basidia and cystidia is formed, then the fructification thickens by vertical growth between the basidia of generative hyphae which diverge laterally to form another layer of horizontal hyphae over the old hymenium. Another layer of pleurobasidia and cystidia is produced from the new "basal" layer and when the basidia have matured the thickening process is repeated. Cavities are left in each palisade of vertical hyphae through the collapse of old basidia. The bases of old cystidia are left in the fructification, which eventually has a layered appearance due to the particular method of thickening (fig.21:E).

FIG. 21 *Litschauerella abietis*

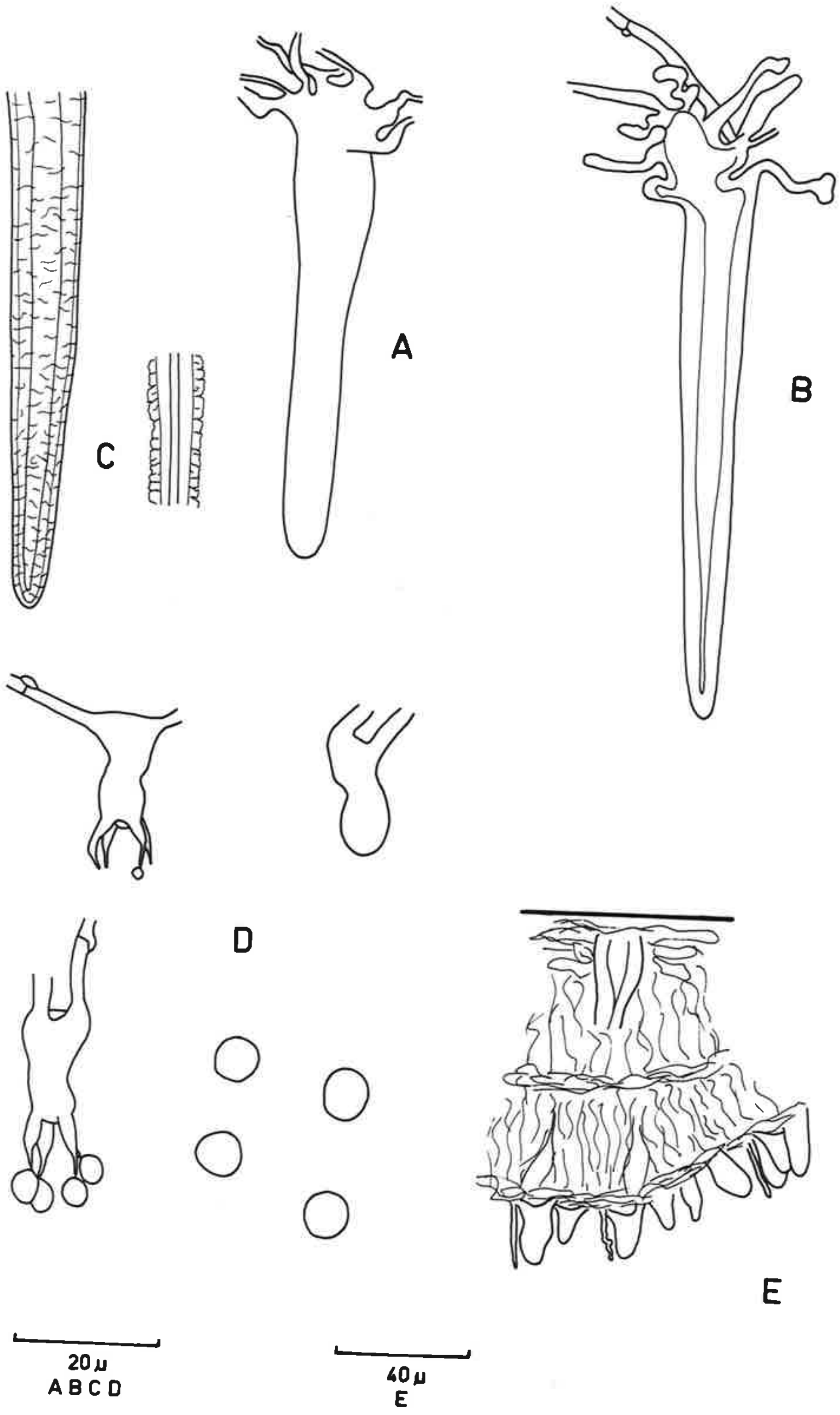
A. Young cystidium from the growing edge.

B. A mature multi-radicate cystidium.

C. Apparently crystal-covered cystidium (left) and detail of the outer wall (right).

D. Basidia and spores.

E. Section through a mature fructification showing an embedded base of a cystidium, the current hymenium and the layering caused by the particular method of fructification thickening.


C
A
B
D
E
20 µ
A B C D
40 µ
E

Lopharia cinerascens (Schw.) Cunningham (1956a:622)

Syn.: *Thelephora cinerascens* Schweinitz (1832:167)
Hymenochaete cinerascens (Schw.) Léveille (1846:152)
Radulum mirabile Berkeley & Broome (1873:61)
Peniophora cinerascens (Schw.) Saccardo (1888:646)
Stereum cinerascens (Schw.) Massee (1890:179)

For further synonyms see Cunningham (1963)

The hyphal system is dimitic with skeletal hyphae and clamped generative hyphae. Deep-seated hyphae may be yellow, otherwise they are hyaline.

The growing margin of the fructification is composed of radiating skeletal hyphae originating from proximal, deep-seated generative hyphae. The skeletal hyphae are unbranched, with a thin-walled apex, but thick-walled in the proximal part; usually they are aseptate but secondary septa may occur. Generative hyphae are apparent in the young growth a short distance behind the margin and are thin-walled, much branched, with clamped septa. Some of the generative hyphae project beyond the mature hymenium to form shortly-branched dendrohyphidia (fig.22:C). Large thick-walled, crystal-encrusted cystidia are a notable feature of this species and it is not unusual for narrow generative hyphae to climb down the cystidia, as shown in fig. 23:C.

The mature fructification has a typical "stereoid" distribution of tissues: there is a trichoderm composed of skeletal hyphae closely appressed to the substratum, a yellowish cortex of horizontally arranged hyphae, and a context of downward-sweeping hyphae leading towards the hymenial surface. Young cystidia are found in the growing margin where the context hyphae begin to curve downwards. Here some of the downturned skeletal hyphae may become wider, but still have a narrow lumen and a thick-walled acute apex (fig.23:A). In fig.23:B a more mature part is shown in which the marked downward surve of the cystidium is seen. Such early-formed cystidia are modified ends of skeletal hyphae, usually with pedicels too long to be traced back to the parent generative hyphae. Fig.22:G shows a normal, though very short, skeletal hypha, while fig.22:H shows a long skeletal hypha with a thickened cystidioid apex. Fig.22:F represents a very short skeletal hypha which has become sufficiently widened along its whole length to be termed a cystidium; this structure was formed nearer to the developing hymenium than the longer one shown in fig.22:H.

While the cystidia are developing from skeletal hyphae near the growing margin, the more proximal generative hyphae grow downward (together with other skeletal hyphae) and eventually start producing a basidiferous layer. At about this stage a much wider form of cystidium (fig.22:A) is formed by modification of context skeletal hyphae. These are often initially quite thin-walled but eventually become thick-walled, fusoid, and encrusted with crystals, i.e. typically metuloid in form. It is clear, however, from the presence of numerous intermediate types (fig.22:B) that the metuloid type is a further modification of the skeletal-like cystidium in this species. The pedicels of these later-formed cystidia were very variable in length but usually not too long to be traced quite easily to a clamp connexion at the point of origin from a generative hypha. As the smooth thin-walled cystidia thicken and become encrusted, their pedicels lengthen and become thickened; thus many of these cystidia continue to project below the thickening hymenium and do not become embedded until their development has ceased. Cystidia are then found embedded throughout the depth of the thickened hymenium (fig.23:D) and the context. Lacunae may develop around the deeper-embedded cystidia and are probably formed by the disappearance of crystals originally encrusting the cystidia; it is possible, however, that they are artefacts caused by sectioning technique.

It is clear that in this species the cystidia precede the formation of a mature hymenium and are not hymenial in origin; their manner of development indicates that they are modified skeletal hyphae. This is obvious at the growing margin where the pedicels are very long and identical with normal skeletal hyphae; but the distal part is wider than a skeletal hypha, the apex acute, and a slight encrustation of crystals may sometimes be present.

The intermediate form of cystidium usually has a shorter pedicel, but its overall appearance is that of a wider and shorter form of the skeletocystidium. The thin-walled structure which finally becomes a metuloid shows little resemblance to a skeletal hypha except in its pedicellate part. This type is formed closer to the developing hymenium than the other forms of cystidium and it would appear that it is formed by modification of almost the whole skeletal hypha instead of merely its distal part.

The basidia are long and clavate (fig.22:D); the spores are non-amyloid.

FIG. 22 *Lopharia cinerascens*

A, B. Modified skeletocystidia.

C. A dendrohyphidium.

D. Basidium.

E. Spores.

F,H. Skeletocystidia, only slightly modified.

G. Skeletal hypha.

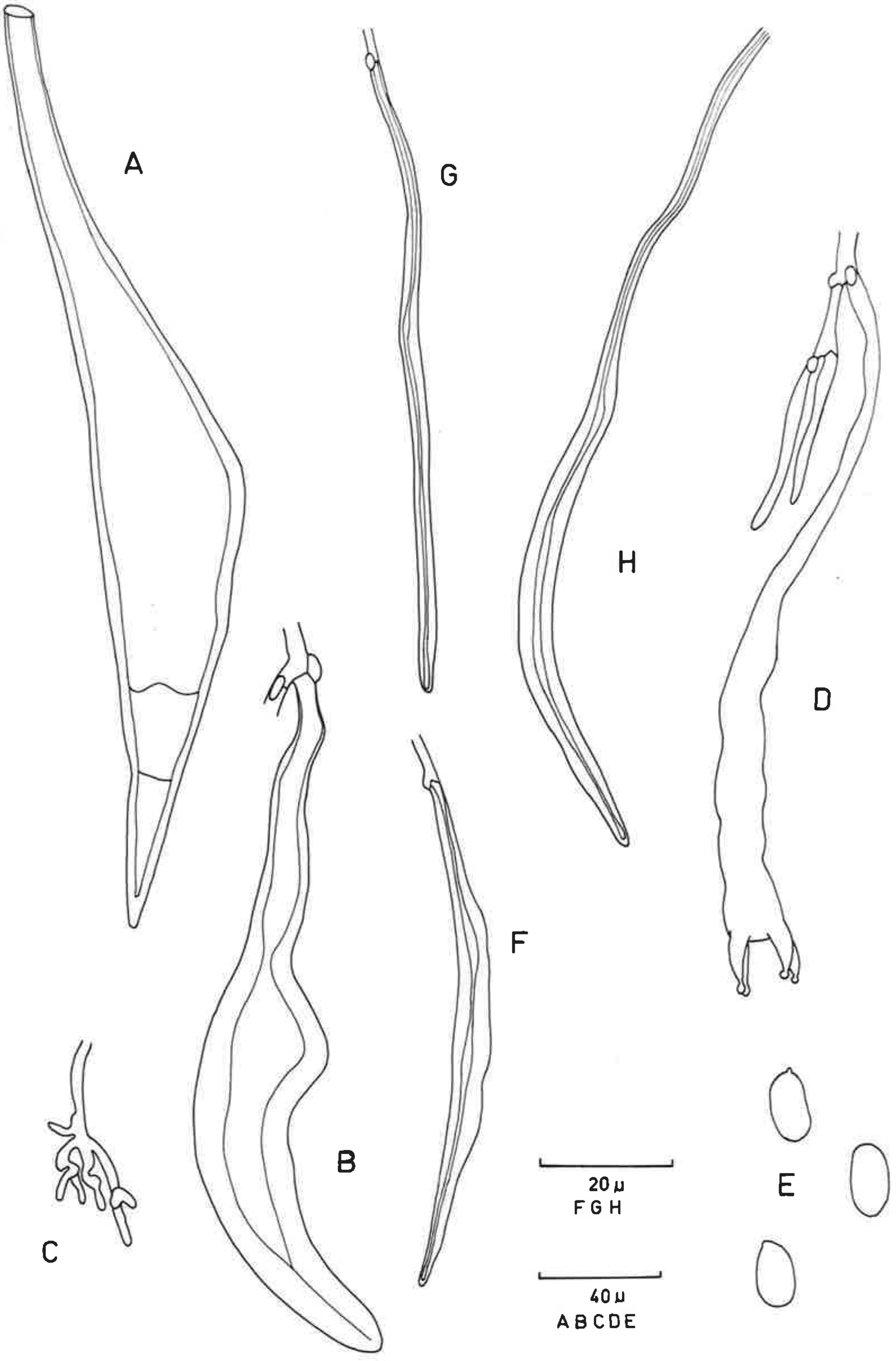

A
G
H
D
B
F
C
E
20 µ
F G H
40 µ
A B C D E

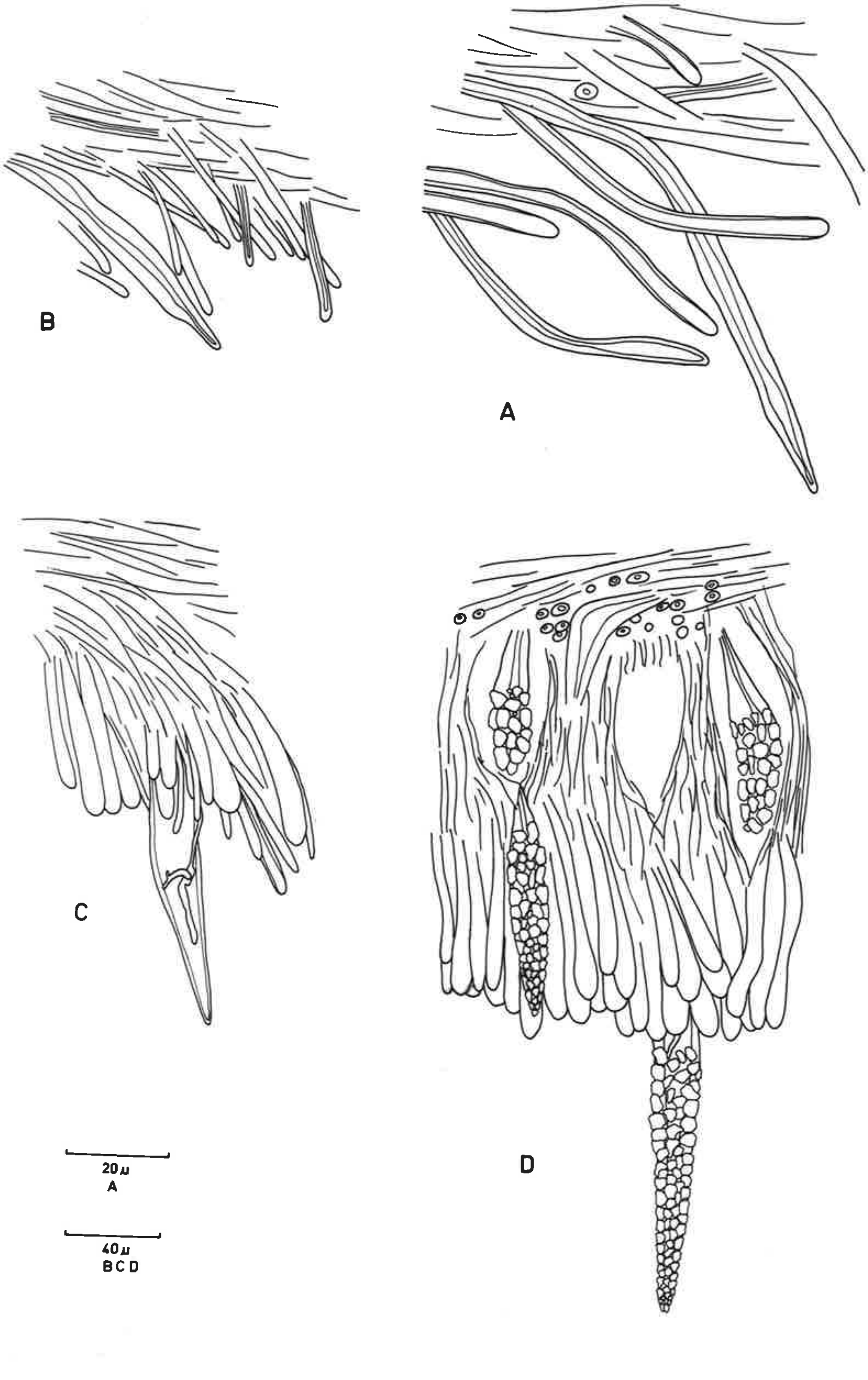
FIG. 23 *Lopharia cinerascens*

A. Growing edge with down-curved skeletal hyphae, the longest of which is a young skeletocystidium.

B. A more mature part of the growing edge with a skeletocystidium.

C. Young hymenium with a young modified skeletocystidium.

D. Mature part of the fructification with embedded and emergent crystal-encrusted cystidia.


B
A
C
D
20µ
A
40µ
B C D

Lopharia crassa (Lév.) Boidin (1958c:479)

Syn.: *Thelephora crassa* Léveille (1844:209)
Stereum umbrinum Berkeley & Curtis (Berkeley, 1873:164)
Hymenochaete crassa (Lév.) Berkeley ex Cooke (1880:148)
Peniophora intermedia Massee (1889:143)
Laxitextum crassum (Lév.) Lentz (1955:20)

For further synonyms see Cunningham (1963).

The fructification is effused to effuso-reflexed, loosely membranous, and generally considered to be monomitic with non-clamped generative hyphae. The hyphae in the growing edge are generative hyphae and long, slightly thick-walled non-septate hyphae which arise from the generative hyphae (fig.24:A). The apices of the thicker-walled hyphae are often more acute than those of the generative hyphae and usually small crystals are scattered over their walls. These thicker-walled hyphae are young cystidial pedicels and as they age the walls become thicker and dark in color; the apices become acute and crystal-encrusted and the whole structure is termed a cystidium. Mature cystidial pedicels are often branched and sometimes septate (fig.24:C); the septa vary in thickness but are probably all secondary septa. Each branch grows on to develop into another complete cystidium. I interpret the cystidia, especially the cystidial pedicels, of *L.crassa* as skeletal hyphae and representing a reduced skeletal system in this species.

The cystidial pedicels in the growing edge project well beyond the generative hyphae and turndownwards. Generative hyphae then grow down between them and eventually a hymenium is formed. Unfortunately in the specimens studied a distinct mature hymenium had not yet developed. Cystidia usually lengthen with the thickening of the fructification and most develop long pedicels. Those initiated near the margin have very long pedicels, curved near their base where the hyphae turned downwards to become vertical. As the fructification thickens, additional cystidia are formed and these are shorter and more vertical than those originating near the base.

In the specimens studied there was wide variation in the form of cystidium. Cystidial pedicels with thick, dark walls and practically no crystal encrustation were found in some collections. In other collections the cystidial pedicels were wider, not as thick-walled and often hyaline when young. This form was usually crystal-encrusted, especially near the apex, and sometimes the more heavily encrusted apices resembled metuloids; that is, the wide lumen suddenly narrowed to capillary width then at the tip it widened again, forming a small bulb (fig.24:D). In one specimen the cystidial pedicels had dark-brown thick walls with crystals on them, but the apices were hyaline and metuloid in appearance. The sudden change from colored pedicel to hyaline metuloid apex may have been associated with a change in environment. The cystidia of another collection were similar to the setoid skeletal hyphae of Duportella tristicula and D. fulva. This specimen also showed the phenomenon of slight layering mentioned by Cunningham (1963). Most of the context was brown and the apices of the cystidia were at approximately the same level, forming a palisade. Below this was a new hyaline growth in which another layer of cystidia had developed. Pedicels of the new cystidia were comparatively thin-walled, wide, hyaline to lightly colored and crystal encrusted, especially near the apex. The basidia are clavate (fig.24:E); the spores are non-amyloid.

FIG. 24 *Lopharia crassa*

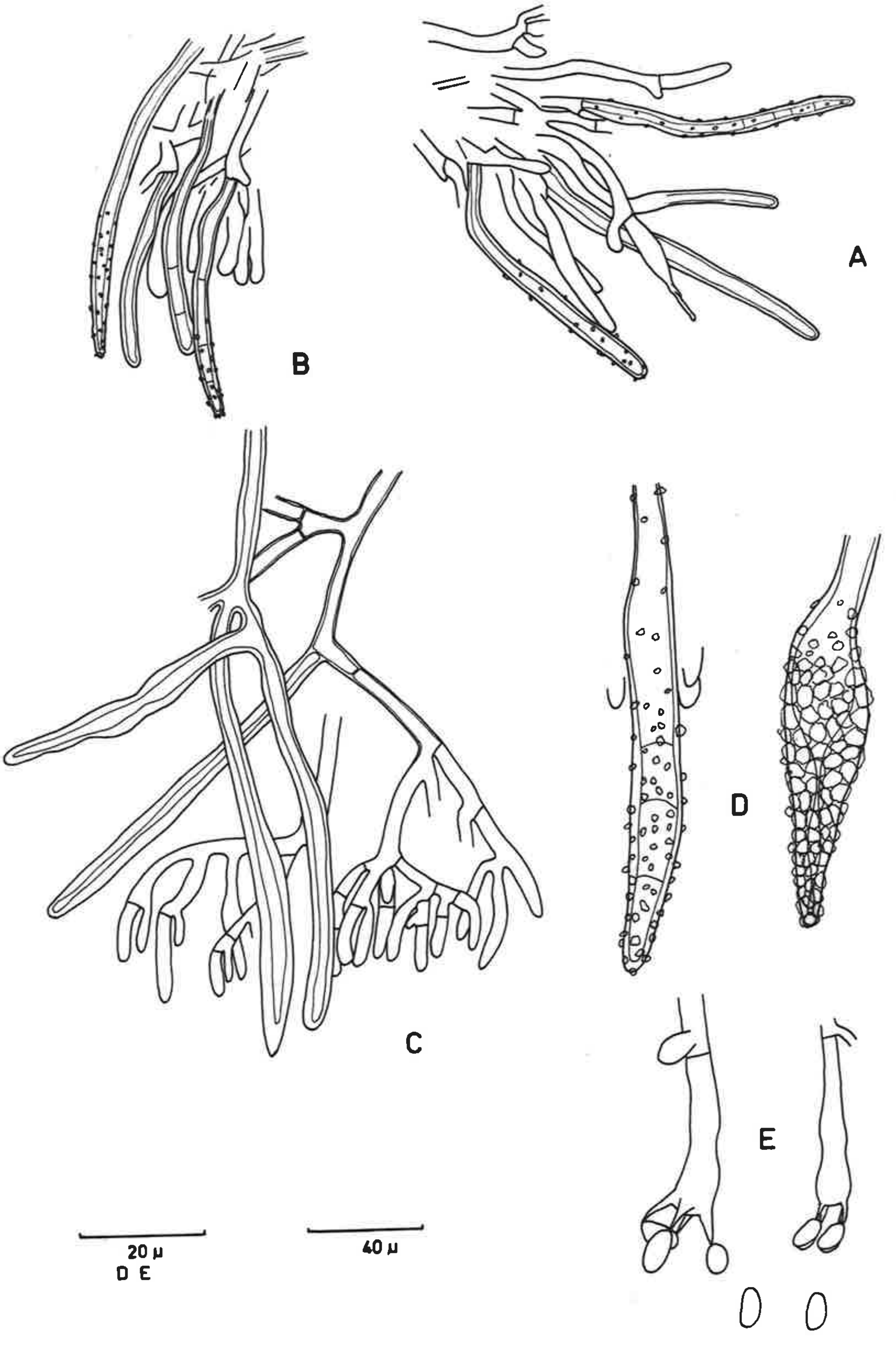
A. Growing margin with generative hyphae and the thicker-walled cystidial pedicels.

B. Older part of growing edge with vertical hyphae and cystidia.

C. Young hymenium showing branched cystidial pedicels and the relationship of the cystidia to the basidiferous tissue.

D. Showing the two extremes in cystidial apices: on the left, the moderately thin-walled and lightly crystal-encrusted form; on the right, the metuloid type with heavy crystal-encrustation.

E. Basidia and spores.


A
B
C
D
E
20 µ
D E
40 µ

Oliveonia pauxilla (Jacks.) Donk (1958:20)

Syn.: Corticium pauxillum Jackson (1950c:724)

Heteromyces pauxillum (Jacks.) Olive (1957:433).

In this species, the full extent of the mycelium and the exact relationship of the basal and hymenial layers could not be determined as the material was examined from soil. It would appear, however, that the fructification is very thin, consisting of a discontinuous basidial layer arising from a thin web of repent hyphae effused over the substratum. Generative hyphae without clamps are the only type of hypha present. Growth in thickness of the fructification commences with the production from the repent hyphae of lateral outgrowths which are mostly about the same width as the repent hyphae and elongate for a short distance before expanding to form a broad, often somewhat rectilinear probasidium with a septum at the base of the expanded part (fig.25:C). The lateral outgrowth may sometimes elongate and form a few cells before expanding into a probasidium. New basidia may proliferate from below an older basidium either directly or as the termination of a short branch (for the latter see Warcup & Talbot, 1962, p.499). Fascicles of basidia are rare and instead most basidia are solitary. The spores of this species germinate by repetition producing secondary basidiospores.

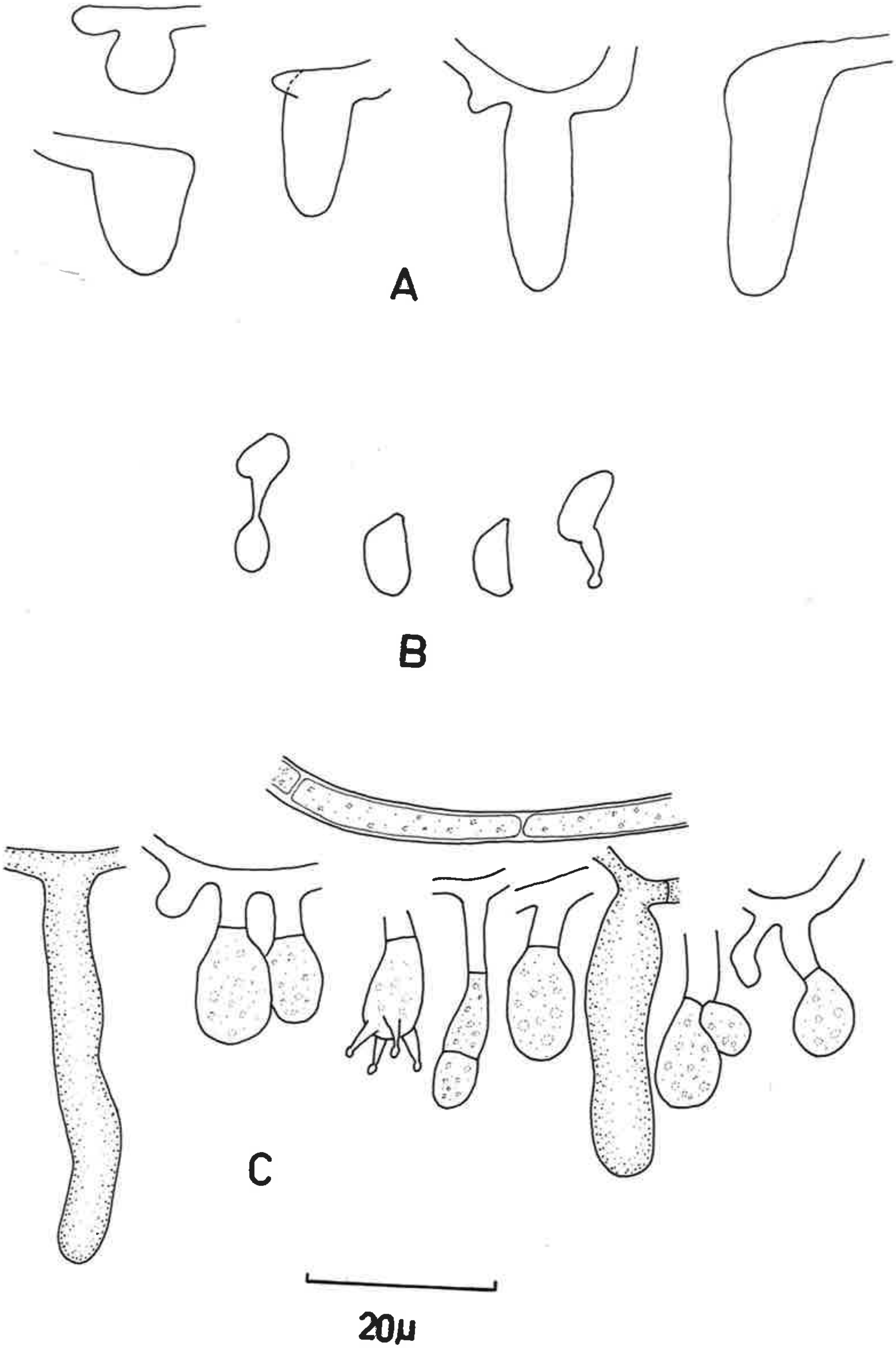
A few lateral outgrowths, much wider than the repent hyphae from which they arise (fig.25:A), continue their downward growth and eventually project for a considerable proportion of their length beyond the level of the basidia (fig.25:C). They are usually formed near the growing apices of basal hyphae which then continue growing, but some appear to terminate the basal hyphae. These structures are cylindrical with a rounded apex, thin-walled, not encrusted, with homogeneous contents; the base is sessile, broad and bi-radicate. The contents do not darken with sulfo-aldehyde solution, and stain with the same intensity as the rest of the tissues in KOH-phloxine. These structures have been called gloeocystidia by Jackson (1950), and "gloeocystidium-like (? cystidia)" by Olive (1957). Since they give a negative aldehyde test, do not possess oily or granular contents, are not flexuous in shape, and project for the most part beyond the basidial level, they are not typical gloeocystidia. The bi-radicate cystidia of this species remain thin-walled and are therefore not typical of the radicate cystidia found in other species. However, this is the most suitable category in which to place these cystidia.

FIG. 25 *Oliveonia pauxilla*

A. Series showing the development of cystidia from repent basal generative hyphae.

B. Spores, two germinating by repetition and producing secondary spores.

C. Reconstruction of the hymenium showing basidia and cystidia.


A
B
C
20μ

Peniophora cinerea (Fr.) Cooke (1879:20)
Syn.: Thelephora cinerea Fries (1821:453)
For further synonyms see Eriksson (1950).

The fructification is effused, firmly compacted, ceraceous, and composed of clamped generative hyphae. The basal portion of the fructification is deep brown in color, while the part formed by the thickening hymenium is hyaline but may be light brown in the older parts near the base. In sections of the fructification there is generally a sharp distinction between the hyaline and brown portions.

The growing margin is composed of brown repent hyphae. A short distance behind the growing edge the apices of some of the basal hyphae turn downwards and become modified into cystidioid structures. A frequent form of cystidium, found only in the growing edge, develops as the round, swollen apex of basal hyphae (fig.26:A,D). These apices become crystal-encrusted (fig.26:E,F) and the resulting large ovoid metuloids are obvious in the basal portions of sections of fructification (fig.27:A). These ovoid metuloids are visible under the dissecting microscope; in comparison the metuloids projecting from the hymenium are small and inconspicuous (fig.27:A). Fusoid metuloids are generally formed in the basal layer only with the commencement of vertical growth of the fruit-body.

A second type of cystidium which develops from the basal hyphae is thick-walled, cylindrical, with the apices rounded to subulate and not encrusted (fig.26:B,C,G). Many of these cystidia with a subulate apex lengthen as the fructification thickens, and extend from the basal layer to the hymenial level sometimes projecting slightly beyond the hymenium (fig.27:A). Consequently the wall color in these cystidia ranges from brown in the basal portion to hyaline in the apical portion. Not all of the thick-walled cylindrical cystidia arise from the base of the fructification; a number are formed at various levels as the fructification thickens. The contents of these cystidia, especially those with a rounded apex, often stain more deeply than the surrounding tissues.

As the growing margin matures some of the downward projecting hyphae do not form cystidia but remain undifferentiated or develop into the first basidia. Thus the hymenium is formed directly on the basal layer and the depth of the fructification is built up by the thickening of the hymenium. The structures formed in the hymenium are basidia, cystidia and simple dendrohyphidia (fig.27:A). The cystidia are persistent and become embedded as the hymenium thickens. Two types of cystidia are formed in the hymenium: fusoid metuloids, and non-encrusted thick-walled cylindrical cystidia as described above (fig.27:B). The cystidia formed in the hymenium have straight pedicels with a clamp at the base, although the clamp is often difficult to see because of the densely packed hyphae of the fructification. Young cystidia form in the hymenium but could not be distinguished with certainty until the apices had become acute or the walls had become slightly thickened. In this study it could not be ascertained whether the cystidia were aborted basidia or if there was no homology between cystidia and basidia, although both originated from similar hymenial hyphae. Also it is not certain if the two different types of cystidioid structures have an entirely separate development or if a young cystidial cell can develop into either of the two types. The structure second from the left in fig. 27:B could possibly develop into either type of cystidium. Perhaps the difference between them is mainly the presence or absence of crystals. Possibly if a young cystidium becomes crystal-encrusted its growth is curtailed, but if no crystals form then it continues to grow, becoming long and thick-walled.

Sometimes cystidia formed in the basal layer are bi-rooted (fig.26:E,G) and these have developed as early side-branches from basal hyphae.

The cylindrical, thick-walled, non-encrusted cystidia are not mentioned in descriptions of this species, although Cunningham (1963) shows similar structures in his drawing of P.cinerea but regards them as young cystidia. These structures cannot be young cystidia as many develop in the basal layer, persist as the hymenium thickens, and never become crystal-encrusted; also their walls are generally much thicker than those of the metuloids.

FIG. 26 *Peniophora cinerea*

A. Growing edge showing the down-turned apices of generative hyphae developing into cystidia.

B. A young cylindrical cystidium in the growing edge.

C. A cylindrical cystidium with an acute apex.

D. Cystidia formed from swollen apices of down-turned basal hyphae.

E. Cystidia may also develop laterally from the basal hyphae so that they are radicate.

F. The cystidia from the basal hyphae become heavily crystal-encrusted and the walls thicken considerably.

G. A series showing the development of cylindrical cystidia from basal hyphae.

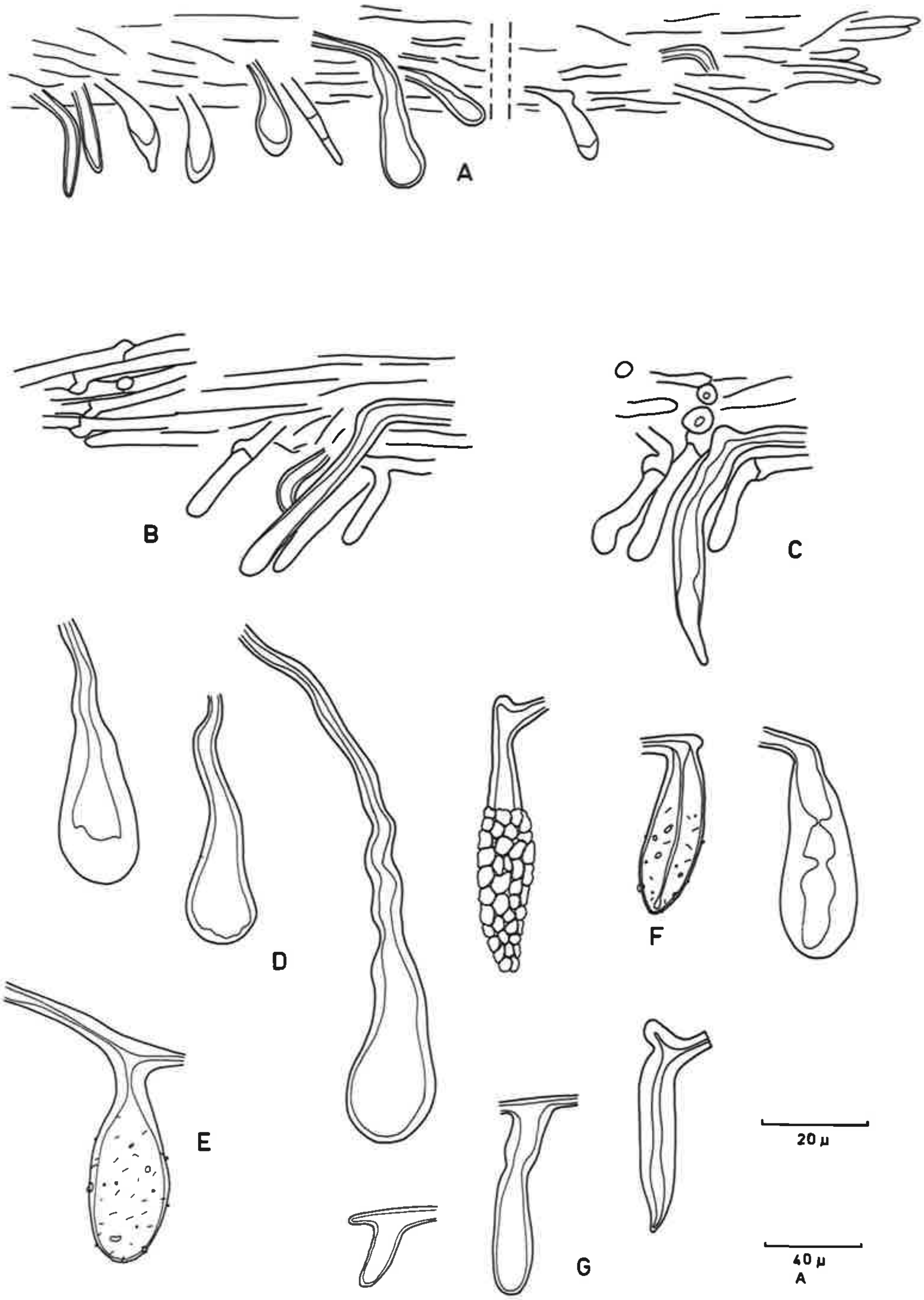
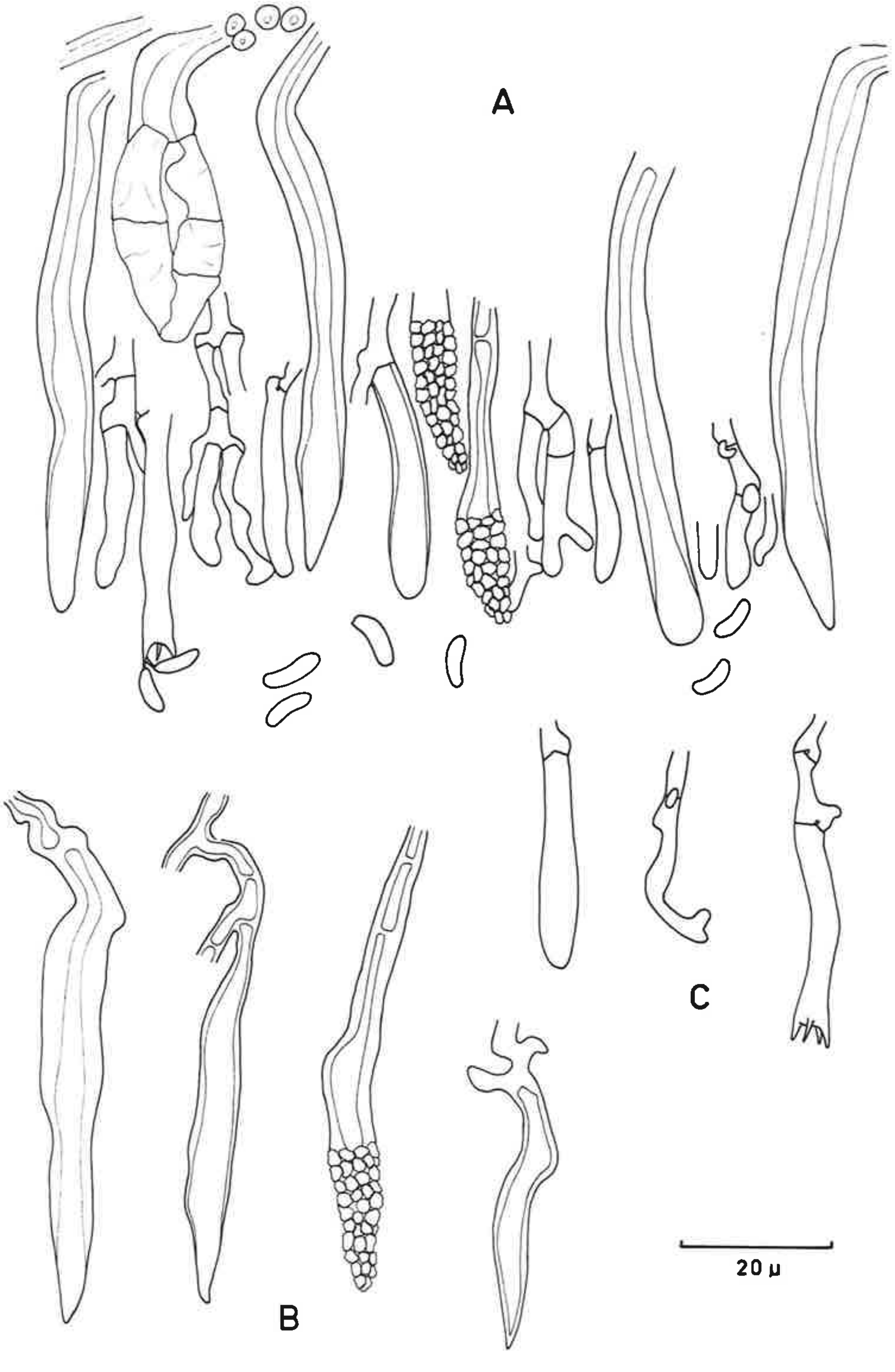

A
B
C
D
E
F
G
20 µ
40 µ
A

FIG. 27 <u>Peniophora cinerea</u>

A. Mature hymenium showing cylindrical cystidia, metuloid cystidia, simple dendrohyphidia, basidia and spores.

B. Cylindrical and metuloid cystidia formed from vertical hyphae after a hymenium has been established.

C. Left - a young basidium.
Centre - a simple dendrohyphidium.
Right - a mature basidium.


A
B
C
20 µ

Peniophora cremea (Bres.) Saccardo & Sydow (1902:195)
Syn.: Corticium cremeum Bresadola (1898:63)
For further synonyms see Rogers & Jackson (1943).

The fructification is effused, membranous, and composed of generative hyphae without clamps. The growing edge is a scant basal layer on which develops a wide layer of loosely interwoven hyphae. The floccose nature of this layer is the result of the characteristic wide-angled branching of the hyphae. Back from the growing edge some of the apices of hyphae at the surface of the floccose layer become slightly inflated (fig.28:A); these are young cystidia. At the time that cystidia start to form, the angle of branching of the vertical hyphae becomes more acute and a denser tissue is produced which becomes the basidiferous layer. Lateral branches from the pedicels of early-formed cystidia grow down and add to this layer (fig.28,B,C). Mature cystidia become embedded as the hymenium thickens. Young cystidia in the hymenium are formed as modified apices of hymenial hyphae, and branches from the cystidial pedicels grow down and add to the hymenium.

The cystidia of this species have only moderately thick walls and a wide lumen. They are cylindrical with rounded apices, or fusiform with acuminate apices. On the outside of the walls, especially near the apex, there are scattered irregular crystals, which are also found on context hyphae in the younger portions of the fructification (fig.28:C). The cystidia of this species are not typical metuloids even though they are crystal-encrusted, and they do not fit into any other category of cystidium. Until more cystidia of this type are described it would be unwise to propose a new category in which to classify them.

FIG. 28 *Peniophora cremea*

A. Young cystidia in the growing edge.

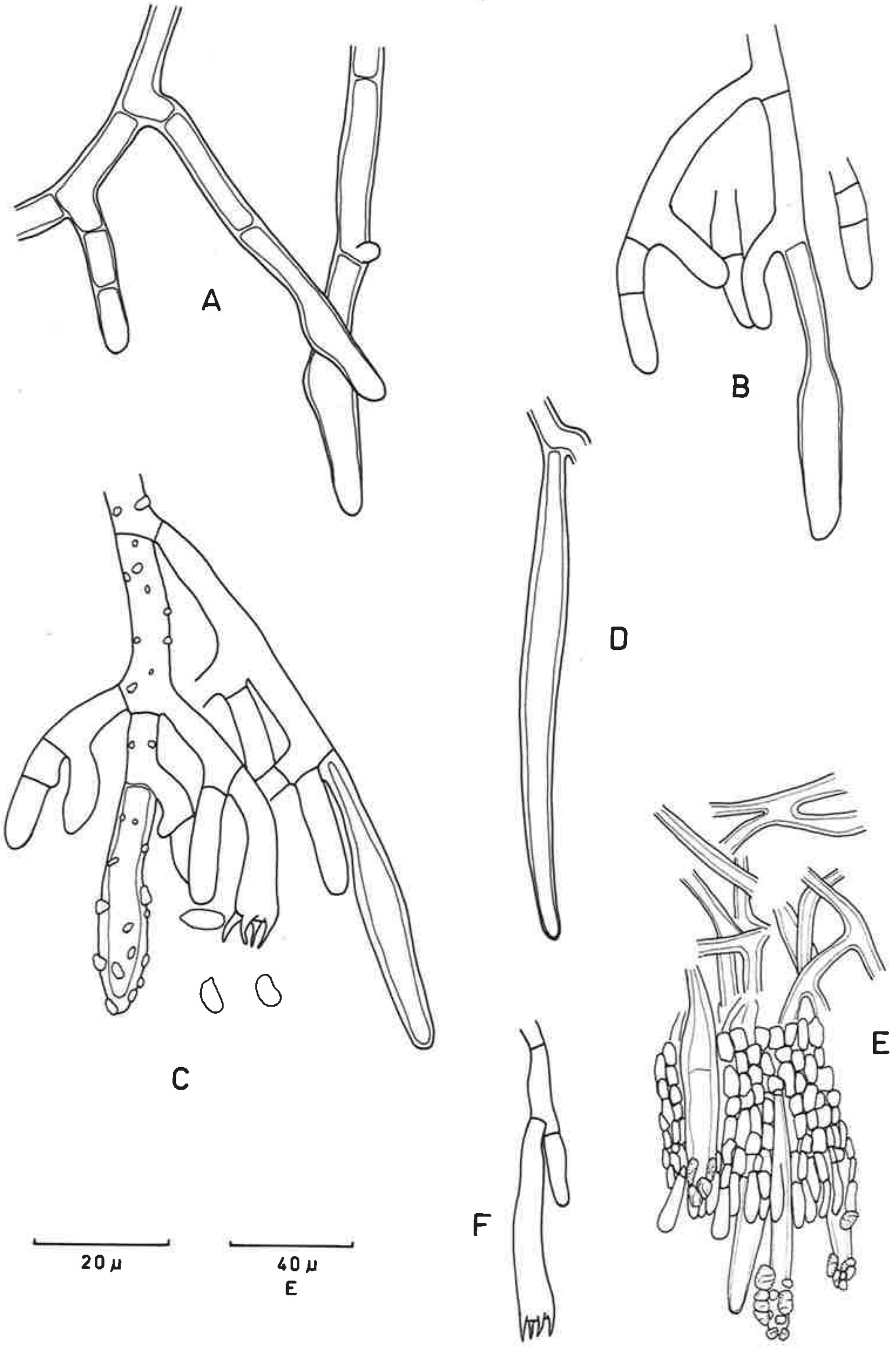
B. Slightly older cystidium with a branch from the cystidial pedical.

C. Cystidia, basidia and spores. Also showing the relationship between the cystidia and basidia.

D. The size and shape of old, mature cystidia. The walls remain relatively thin.

E. Section through a mature portion of the fructification showing the loosely interwoven context, thickened hymenium with crystal-encrusted cystidia of various ages.

F. A mature basidium.


A
B
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D
E
F
20 µ
40 µ
E

Peniophora incarnata (Pers. ex Fr.) Karsten (1889b:27)

Syn.: Thelephora incarnata Persoon ex Fries (1821:444)

Corticium incarnatum (Pers. ex Fr.) Fries (1838:564)

For further synonyms see Eriksson (1950).

The effused, ceraceous fructification is composed of clamped, thin-walled generative hyphae. The growing edge has a slight byssoid appearance and is lighter in color than the hymenium; it consists of a thin layer of hyaline basal hyphae from which arise many downwardly-directed lateral swellings, and later vertical hyphae which form a hymenium.

There are two types of cystidia in this species: gloeocystidia and metuloids. Both types are formed in the growing edge before a hymenium is established, and in this position they have radicate bases. The development of gloeocystidia can be traced from the lateral swellings found in the growing edge (fig.29:A,C). The swelling simply enlarges and its apex grows downwards (fig.29:D). Young stages of radicate metuloids were not found but it is presumed that as the development of the species is like that of Peniophora nuda then some of the lateral swellings will develop into metuloids instead of gloeocystidia. In both the gloeocystidia and metuloids found in the growing edge it is not uncommon for one side of the radicate base to be reduced to a "heel".

After downward growth of hyphae is established basidia are produced and subsequent cystidia develop as the modified apices of vertical hyphae. Unlike in P.nuda there is not a marked tendency for the hymenial cystidia of P.incarnata to have "heels" projecting at an angle.

The majority of gloeocystidia are produced in the basal layer. These lengthen with the thickening of the hymenium and extend from the base to the hymenial level (fig.29:B). After a certain length is achieved most gloeocystidia stop lengthening although a few continue to grow and extend the full thickness of the fructification. Some new gloeocystidia are formed as the hymenium thickens and the development of these from apical cells of vertical hyphae can be traced from relatively young stages. These gloeocystidia also lengthen with the thickening of the hymenium but are sparsely distributed in comparison with the dense palisade near the base. Gloeocystidia in this species darken in sulfo-aldehyde solution.

The development of hymenial metuloids could not be traced from very young stages and they could be identified with certainty only after they had reached a fairly advanced stage (fig.29:L,N). Many of the young cystidia found in the hymenium of the specimen studied appeared deformed (fig.29:L), but as only one collection was available for study it is not known if they are typical or aberrant.

The gloeocystidia and metuloids in this species generally have a long pedicel which expands into the modified apex. In gloeocystidia the change is usually abrupt whereas in the metuloids it is more gradual. Cystidia and basidia found in the hymenium develop from the undifferentiated ends of hymenial hyphae, but it could not be established if the cystidia were homologues of sterile basidia or not.

Basidia with a septum two-thirds of the way down their length were sometimes seen but not nearly as frequently as in P.nuda. Sparingly-branched dendrohyphidia were very common in the hymenium (fig.29:J). In the specimen studied the thin-walled acutely-pointed structures projecting beyond the hymenium were found to be the apices of gloeocystidia (fig.29:H), and were not young cystidia as thought by Eriksson (1950).

FIG. 29 *Peniophora incarnata*

A. Growing edge with young gloeocystidia.

B. An older stage, after the hymenium is established, with well developed gloeocystidia and a metuloid cystidium.

C. A swelling in a basal hypha which will develop into a gloeocystidium.

D. A gloeocystidium in the growing edge which has developed laterally from a basal hypha.

E. A metuloid cystidium from the growing edge. This has also developed laterally from a basal hypha.

F. A gloeocystidium from stage B.

G. A mature portion of the fructification showing gloeocystidia, metuloids and the hymenium.

H. Left - a young gloeocystidium which has developed from a vertical hypha.
Right - a gloeocystidium with an acute, projecting apex.

J. A simple dendrohyphidium.

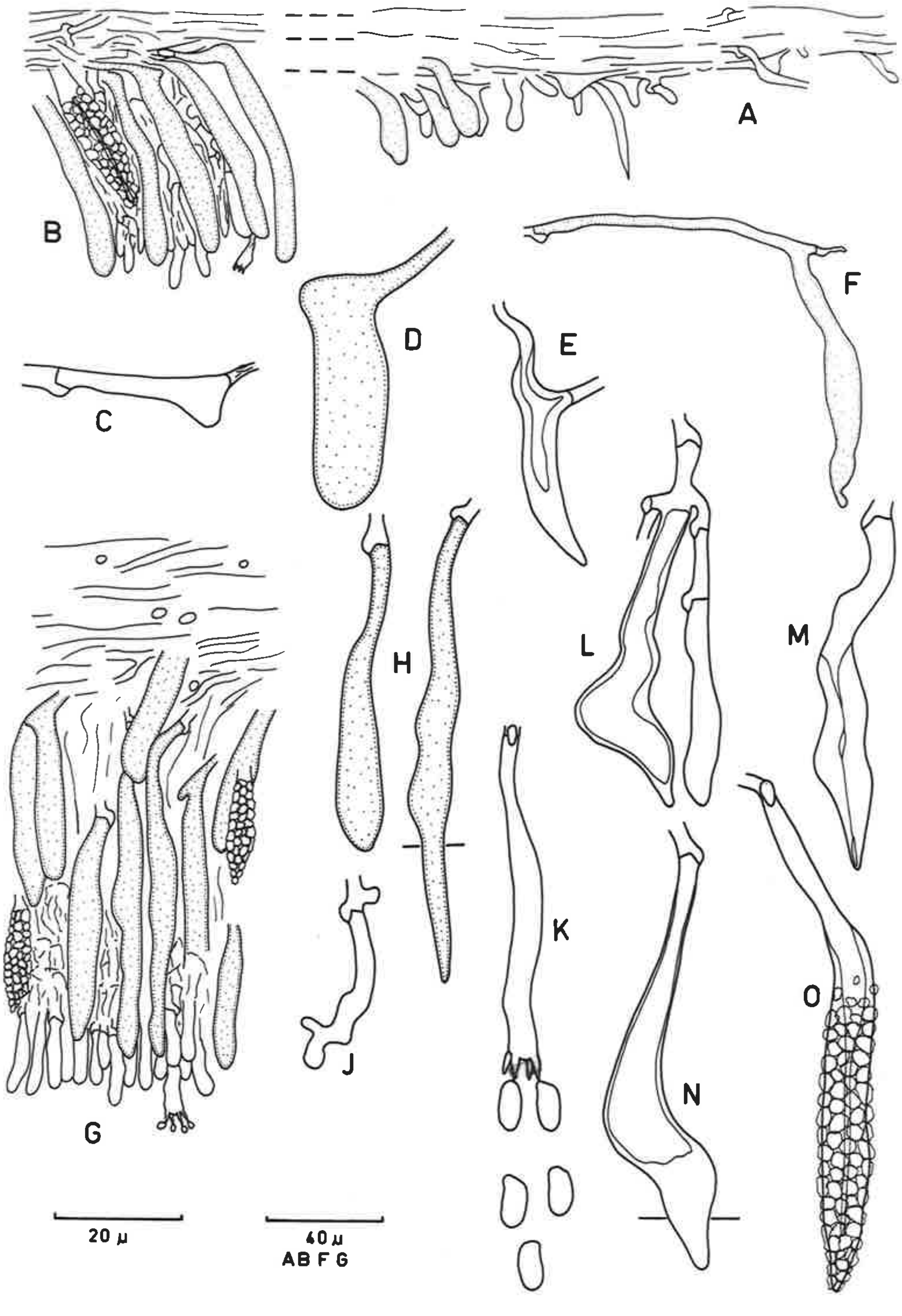
K. A basidium and spores.

L. A young metuloid cystidium with a hymenial branch growing from the cystidial pedicel.

M. A mature metuloid.

N. A developing metuloid at an older stage than L. The apex has thickened and projects beyond the hymenial level.

O. A typical crystal-encrusted metuloid.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N
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20 µ
40 µ
AB F G

Peniophora longispora (Pat.) Höhnel (1905:325)

Syn.: Hypochnus longispora Patouillard (1894:221)

For further synonyms see Rogers & Jackson (1943).

This distinctive fungus has an effused, white floccose fructification composed of clamped generative hyphae. The cystidia are delicate, long, tapering, thin-walled structures encrusted with small, regularly arranged, tuberculate crystals. The crystal-encrustation ceases with a distinctively shaped crystal (fig.30:A) a short distance before the apex. The thin-walled apex is unsupported and consequently easily collapses or bends over (Cunningham, 1963) (fig.30:B).

In the growing edge there is a scanty basal layer on which develop loosely interwoven vertical hyphae. These are often lightly encrusted with tuberculate crystals and many of the hyphae, often after very little vertical growth, are terminated by a cystidium (fig.30:B). Branches from the cystidial pedicels grow down and in turn can become terminated by cystidia. Those hyphae that do not end as cystidia branch more profusely, eventually forming a basidiferous layer over the context of loosely interwoven hyphae and cystidia.

Cystidia formed in the growing edge and while the context is developing usually have only one root although often a "heel" develops near the base (fig.30:E). Once a hymenium has become established single-rooted cystidia are found only infrequently and most of the cystidia formed are bi-rooted or occasionally tri-rooted (fig.30:J,K). Another feature of cystidia in this species is that they often have swollen, slightly thick-walled bases (fig.30:D).

It is not certain how cystidia, in particular those with more than one root, are formed in the hymenium. Single-rooted cystidia (fig.30:C) probably develop from narrow hymenial hyphae (fig.30:G). Anastomosis is a possible means by which multi-rooted cystidia could develop in the hymenium. Anastomoses between various structures in the context and the hymenium were frequently seen in this species (fig.30:F). Narrow sterile hyphae (fig.30:G) are found in basidial fasicles and presumably the structure shown in fig.30:H is formed by anastomosis of the apices of two such hyphae which then grow on downwards as one structure that develops into a cystidium (fig.30:J). It seems unlikely that the bi-rooted structure in fig.30:J could have been formed as a lateral branch from a hymenial hypha that had grown back towards the substratum against the growth forces of the fructification. A multi-rooted cystidium could also be formed if the heel at the base of the young cell (fig.30:L) grew out as a hypha.

The cystidia of this species are unusual in their morphology and development and do not fit into any of the categories of cystidia. Although many of the cystidia are bi- or tri-rooted they do not fit the category of a radicate cystidium as it is currently defined.

FIG. 30 Peniophora longispora

A. The distinctive crystal encrustation at the apex of the cystidium. Left and centre are different aspects of the crystal. In cystidia where the thin-walled apex has collapsed the crystal shape on the right is often found.

B. Vertical hyphae in the growing edge modified as cystidia. The unprotected thin-walled apices of the cystidia often bend over.

C. A cystidium formed in the hymenium; a basidial branch has developed from the cystidial pedicel.

D. A swollen, slightly thick-walled base of a cystidium.

E. A cystidium with a "heel" at the base.

F. Two examples of anastomosis in this species, on the left between a cystidium and a hymenial cell and on the right between two hyphae.

G. A narrow hymenial hypha.

H. Two narrow hymenial hyphae have anastomosed at the apex and then grown on as a single hypha.

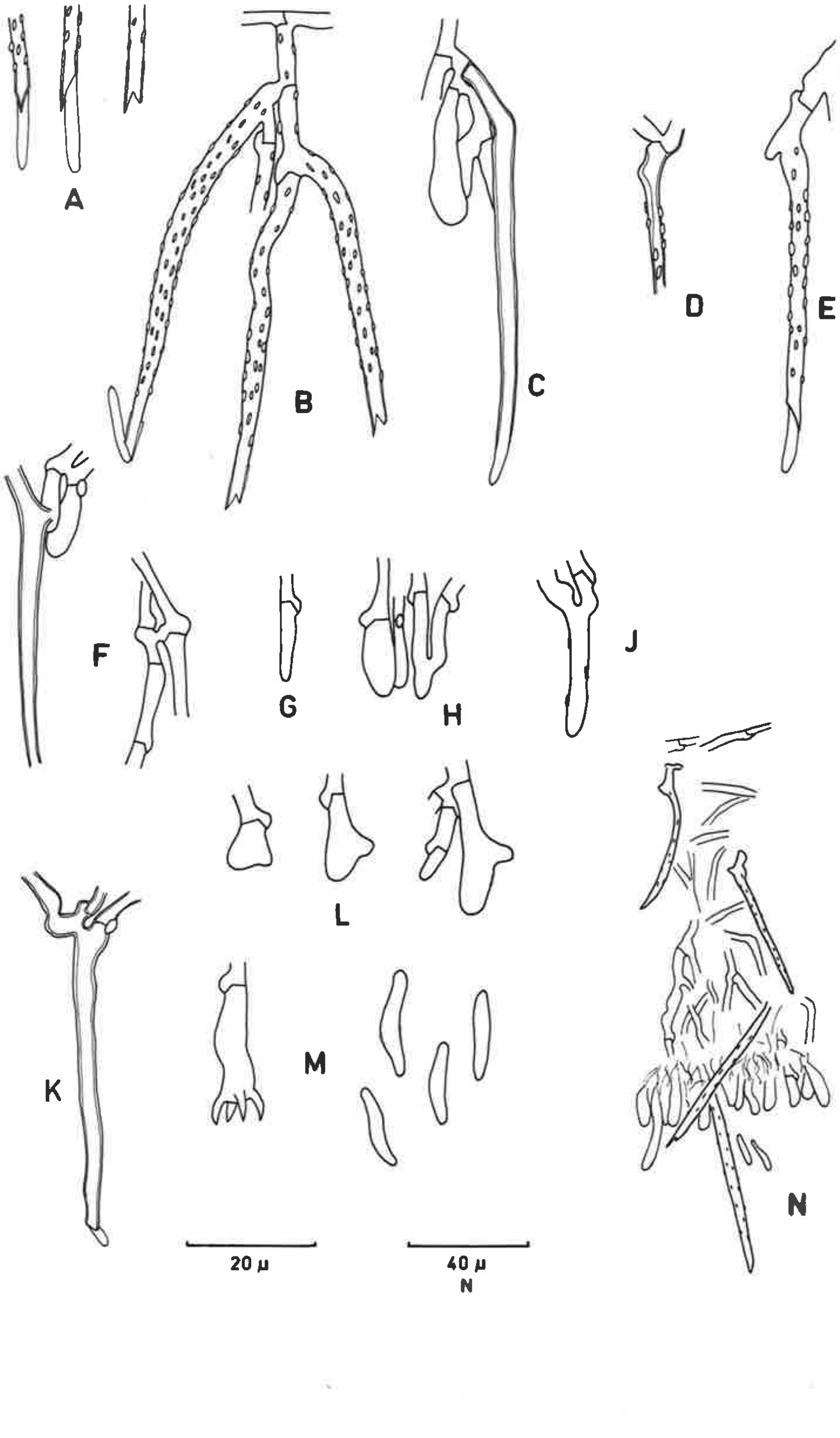
J. A young bi-radicate cystidium in the hymenium. It has probably developed from a structure such as that shown in H.

K. A tri-rooted cystidium.

L. Successive stages of the development of a "heel" on cells in the hymenium.

M. A basidium and spores.

N. Section of a mature fructification showing the loose context, embedded and emergent cystidia and the hymenium.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Peniophora nuda (Fr.) Bresadola (1897:114)

Syn.: Thelephora nuda Fries (1821:447)

Corticium nudum (Fr.) Fries (1838:564)

For further synonyms see Eriksson (1950).

The effused fructification has a ceraceous texture and is composed of clamped generative hyphae. The growing edge is a single layer of hyaline repent hyphae. Lateral swellings with downwardly directed apices develop in these marginal hyphae (fig.31:A). The scantiness of the marginal basal layer, hyaline color of the hyphae and the numerous lateral swellings serve to make the margin lighter in color than the hymenium and faintly byssoid in appearance. Apices of the swellings in the marginal hyphae are either rounded or acute. Swellings with a rounded apex become ovoid, the contents stain deeply and give a positive sulfo-aldehyde test, and the structures are gloeocystidia (fig. 31:B,C). The walls of the swellings with acute apices (fig.31:F) become thickened and externally encrusted with crystals and are metuloids (fig.31:E,H). Occasionally structures intermediate between these two types were found. These were rounded with slightly thickened walls and an external covering of crystals (fig.31:G).

All cystidiform structures found in the growing edge are radicate although in many instances one of the basal hyphae may remain only a "heel". If a swelling forms in the ultimate cell of a repent hypha then often the growing apex beyond the swelling dies back to the swelling. Usually it does not die back completely but leaves a short length of hypha giving the appearance of a heel at the base of the cystidiform structure (fig.31:B,F,H).

Basidia form as soon as downwardly-growing hyphae develop and a thickening hymenium is established. After this new cystidiform structures form as modified apices of vertical hyphae. There is a clamp at their base and in the young stages they are thin-walled with a rounded or acute apex. Usually the cells with an acute apex project beyond the hymenial level. As in the growing edge the young cystidiform structures with rounded apices develop into gloeocystidia (fig.31:J,K), although the gloeocystidia formed in the hymenium are more elongated than those formed in the growing edge. Those structures with an acute apex are regarded as young metuloids (fig.31:L,M).

Often the metuloids and especially the gloeocystidia formed in the early stages of the thickening hymenium have a "heel" projecting at an angle from near the base (fig. 31:J,L). It seems that in the early stages of vertical growth although the cystidiform structures are formed as the modified apices of vertical hyphae, and are therefore pedicellate, there is still a tendency for them to be radicate. This results in a lump developing at an angle to the direction of growth of the apex. This may remain as a lump or grow out as a short hypha. The hypha then usually dies back to the cystidiform structure as in the growing edge, leaving a "heel". Such "heels" were observed only rarely on cystidiform structures formed in a well-established, thickened hymenium.

In the specimens studied most gloeocystidia were in the base of the fructification (fig.31:O). Numerous gloeocystidia are formed in the growing edge but relatively few are formed as the hymenium thickens. Also those in the base of the fructification were usually much larger than any formed in the hymenium, but this may simply have been a matter of relative age.

Old basidia in the specimens studied often had a secondary septum about two-thirds of the way down their length (fig.31:N). After the spores have been discharged the apical third appears empty and collapses to the septum while the basal portion with some cytoplasm still left takes longer to collapse.

The basal portion of well-developed fructifications is brown in color, although not such a dark brown as in Peniophora cinerea. This is probably because the marginal hyphae in P.nuda are hyaline and the basal layer gradually becomes brown with age, whereas in P.cinerea the marginal hyphae are brown and simply deepen in color with age.

FIG. 31 Peniophora nuda

Development of structures in the growing edge.

A. Young gloeocystidia developing from lateral swellings of basal hyphae.

B,C. Gloeocystidia at a more mature stage than A.

D. A section through the growing edge showing gloeocystidia, a metuloid and the developing hymenium.

E. A basal hypha showing early vertical hyphae and a young lateral metuloid.

F. Young metuloids developing from the basal hyphae.

G. This structure is intermediate between a gloeocystidium and a metuloid.

H. Mature metuloids. They are radicate because they have developed laterally from basal hyphae.

Development of structures in the mature fructification.

J. The gloeocystidia are terminal but with a lateral "heel".

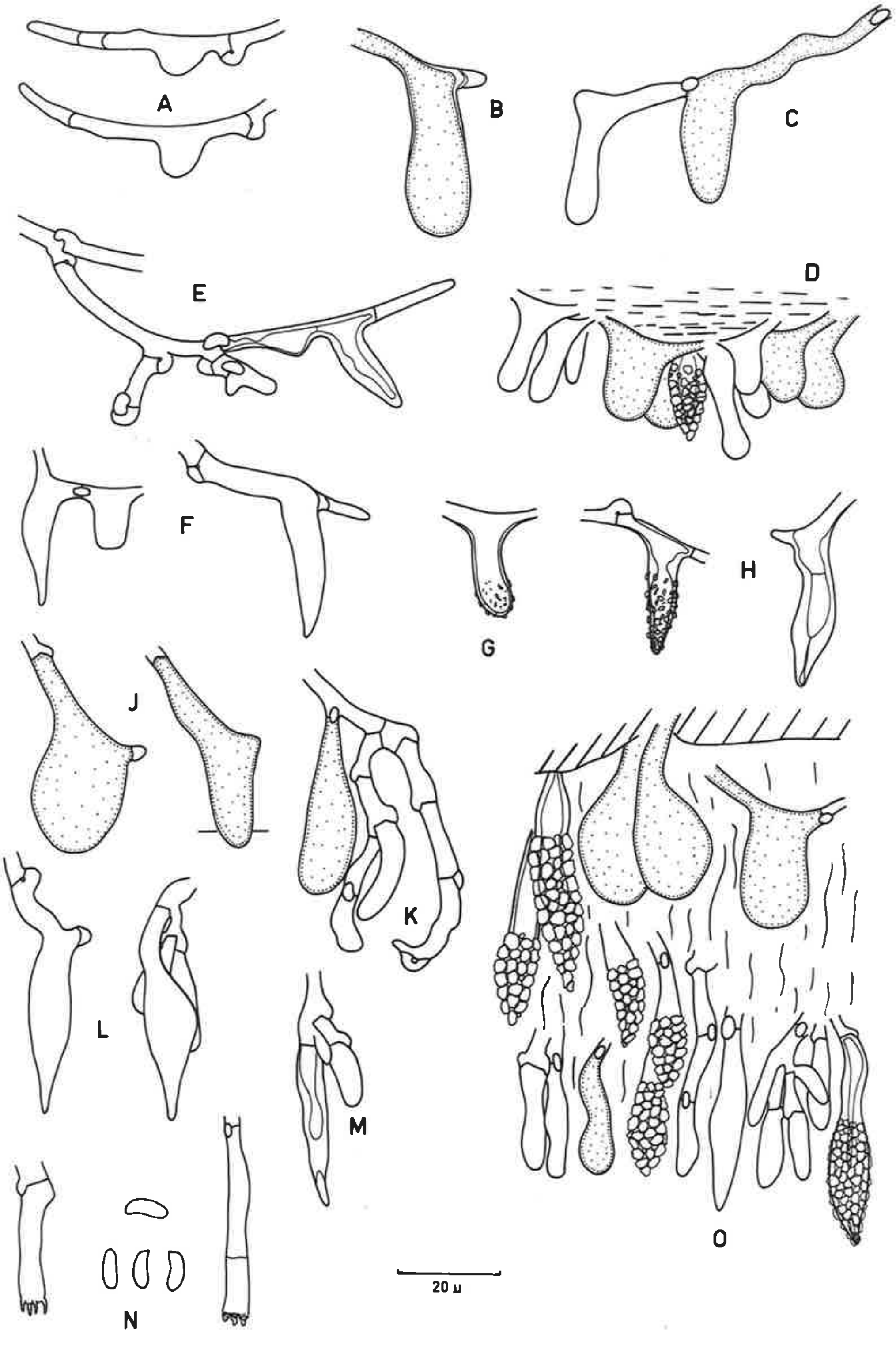
K. Branches from the gloeocystidial pedicel contribute to the hymenium.

L. Young metuloids; they arise terminally but sometimes have a lateral "heel".

M. A mature metuloid with a hymenial branch developing from the cystidial pedicel.

N. Basidia and spores. The basidium on the right has a secondary septum.

O. Section through a mature portion of the fructification showing young and old gloeocystidia and metuloids, and the hymenium.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Phlebia gigantea (Fr. ex Fr.) Donk (1957a:12)

Syn.: *Thelephora gigantea* Fries ex Fries (1821:448)

Peniophora gigantea (Fr. ex Fr.) Massee (1889:142)

For further synonyms see Rogers and Jackson (1943).

The effused fructification is composed of thick-walled generative hyphae compacted into a gelatinous tissue which becomes horny on drying. Clamp connexions were not observed in the specimens studied but infrequent clamps have been reported in this species (Bourdot & Galzin, 1928; Christiansen, 1960: Cunningham, 1963).

The growing edge is a thick layer of compacted horizontal hyphae. Some distance behind the advancing edge the apices of hyphae near the surface turn downwards. A few of the apices are swollen (fig.32:A) and the contents stain more deeply than those of the surrounding hyphae. These structures develop into cystidia (fig.32:B); the apex grows downwards, becoming acute and covered with crystals and the walls thicken considerably (fig.32:C). Cystidia are initiated well before the development of a mature hymenium. While the young cystidium is growing downwards more horizontal hyphae grow over the surface before vertical growth of hyphae is established. Consequently the proximal portions of cystidia are quite deeply embedded in the basal layer by the time the cystidia are mature and a hymenial layer has formed (fig.32:C).

The hymenium is a thickening hymenium and produces a considerable depth of vertical tissue in the fructification (fig.32:G). As the hymenium thickens new cystidia form as modified apices of hymenial hyphae. Early stages in their development were not found and the youngest recognised stage is shown in fig.32:E. As the cystidia mature the apices become acute and crystal-encrusted, projecting well beyond the hymenium (fig.32:F). Mature cystidia become embedded as the hymenium thickens (fig.32:G).

The basidia are small and clavate with sterigmata that develop in two phases (Oberwinkler, 1965) so that the broad base suddenly narrows to a thin pointed apex (fig.32:D). The spores of this species are also very small.

FIG. 32 Phlebia gigantea

A. Swollen apices of basal hyphae in the growing edge.

B. A young cystidium in the growing edge.

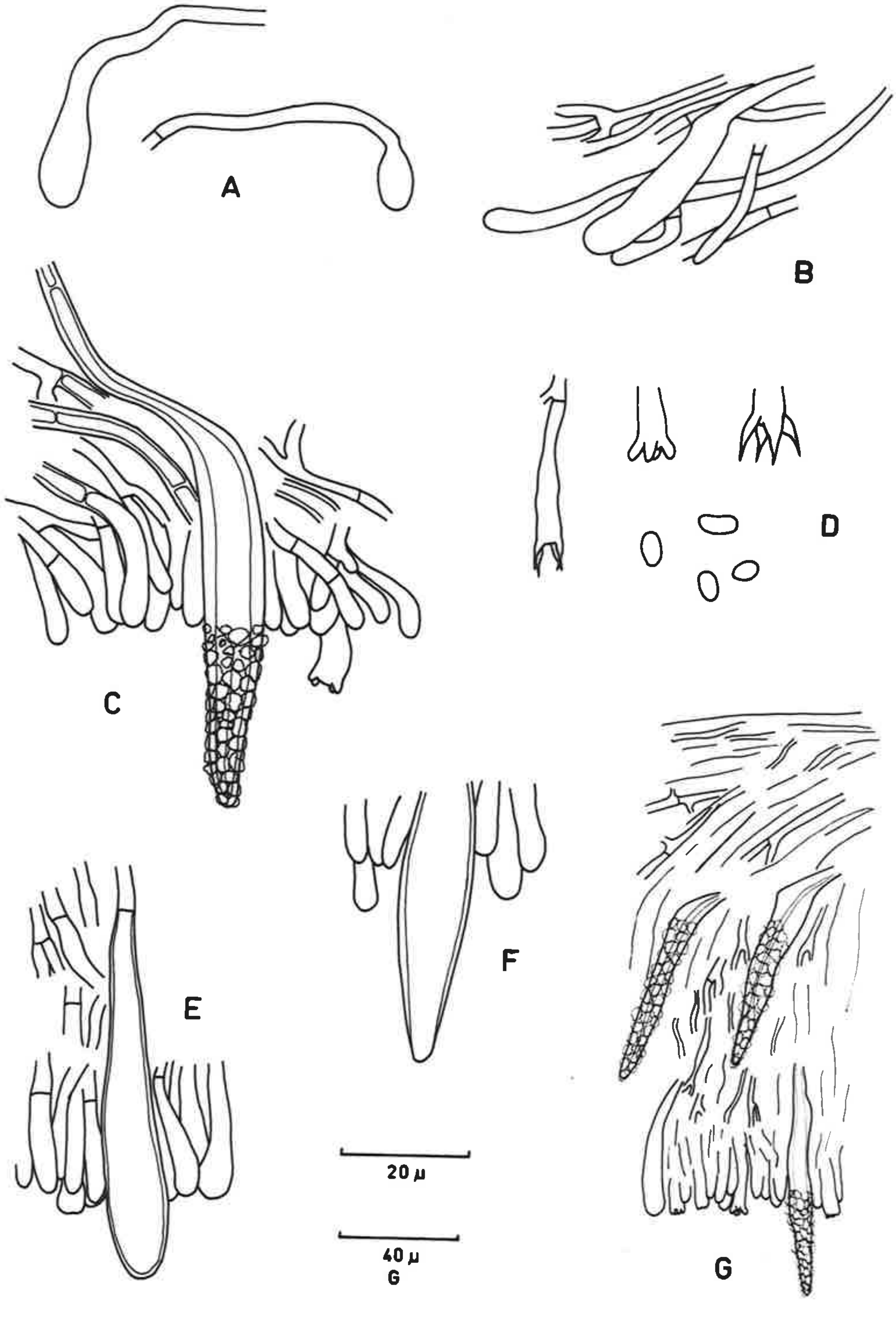
C. The young hymenium and a mature metuloid cystidium.

D. Basidia and spores.

E. A young cystidium developing in the hymenium.

F. A later stage than E; the apex has become pointed and projects well beyond the hymenial level.

G. Section through the mature fructification showing embedded cystidia and the current hymenium.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20 µ
40 µ
G
G

Phlebia hydnoides (Cke. & Mass.) Christiansen (1960:175)

Syn.: Peniophora hydnoides Cooke & Massee (Cooke, 1888:77)

Odontia hydnoides (Cke. & Mass.) Höhnel (1909:817).

The fructification is effused, thin and waxy; the mature hymenium projects down into spines but the hymenial surface is usually not distinctly hydnoid. Generative hyphae, only, are present in the fructification and they are non-clamped, but Boidin (1958a) reports clamps in the margin.

The growing margin of the fructification consists of a thin mat of horizontal hyphae appressed to the substratum. A short distance behind the margin, the apices of some of the repent hyphae become swollen (fig.33:A), bend downwards and grow distally (fig.33:B), often leaving a distinct "heel" at the base of the swelling opposite its place of attachment to the parent hypha. In other instances the swelling may be lateral on a repent hypha and it then appears bi-radicate. As the swollen part expands and elongates, it becomes subulate and its walls thicken and become encrusted with crystals (fig.33:C,D,G). These cystidia are metuloids and the thickening of the walls follows a definite pattern: in the proximal two-thirds of the cystidium the lumen is comparatively wide, then it narrows abruptly into a capillary channel in the remainder of the cystidium, except at the apex where it expands into a small thin-walled bulb.

The basal hyphae are laid down in successive layers, each of which produces metuloid cystidia; thus some of the latter are embedded in a mature fructification while the last formed project below the hymenial level. In a mature fructification, the parallel basal hyphae, mostly thick-walled, are densely compacted and appear to be cemented into a pseudoparenchymatous tissue (fig.33:L). The hymenium arises directly from this tissue and the basidia, either singly or in small fascicles, from erect hyphae only one or two short cells in length. When the basidia collapse these cells add to the pseudoparenchymatous tissue. There is actually no close developmental association between metuloids and basidia although with the compactly constructed fructification they appear to be closely connected.

Inflated apices of undifferentiated hyphae occasionally form in the hymenium and may develop there either into metuloids or into septate hyphocystidia, the other type of cystidium found in this species. When a swelling develops into a septate hyphocystidium it grows and elongates apically, septa being laid down at fairly regular intervals during elongation (fig.33:E,F,H). The walls and septa become thickened, and crystals form outside the walls. Septate hyphocystidia develop once the hymenium is well established, whereas very few metuloid cystidia develop after its establishment, an exception being those formed on the crowded or scattered odontioid spines which are a feature of this species.

In the materials studied, spines were formed only where there was some erect structure in the hymenium which could act as a support for climbing hyphae. Sometimes foreign material (e.g. a synnema of one of the Stilbellaceae, as in fig.34:D) acted as a support, but usually a septate hyphocystidium formed the main type of structural support. The development of a spine is traced in fig.34: A,B,C). Around a suitable support, climbing hyphae grow downward; this provides a new growing margin which matures in the same way as the growing margin of the whole fructification lying on a flat substratum. The apices of some of the climbing hyphae become inflated, turn outward from the spine and develop into metuloids; others form the hymenium among the bases of the metuloids. Later, as the spines increase in size, more septate hyphocystidia may develop.

The basidia and spores of this species are quite small.

FIG. 33 Phlebia hydnoides

A. Terminal swelling of a basal hypha in the growing edge.

B. A more advanced stage of A.

C,D,G. Stages in the development of the metuloid type of cystidium.

E,F,H. Stages in the development of the septate hyphocystidium.

J. A septate hyphocystidium which has produced a hypha from the apex.

K. A cystidium intermediate between a metuloid and a septate hyphocystidium.

L. Section through a mature part of the fructification showing metuloids and the hymenium. Drawings of basidia and spores are also included.

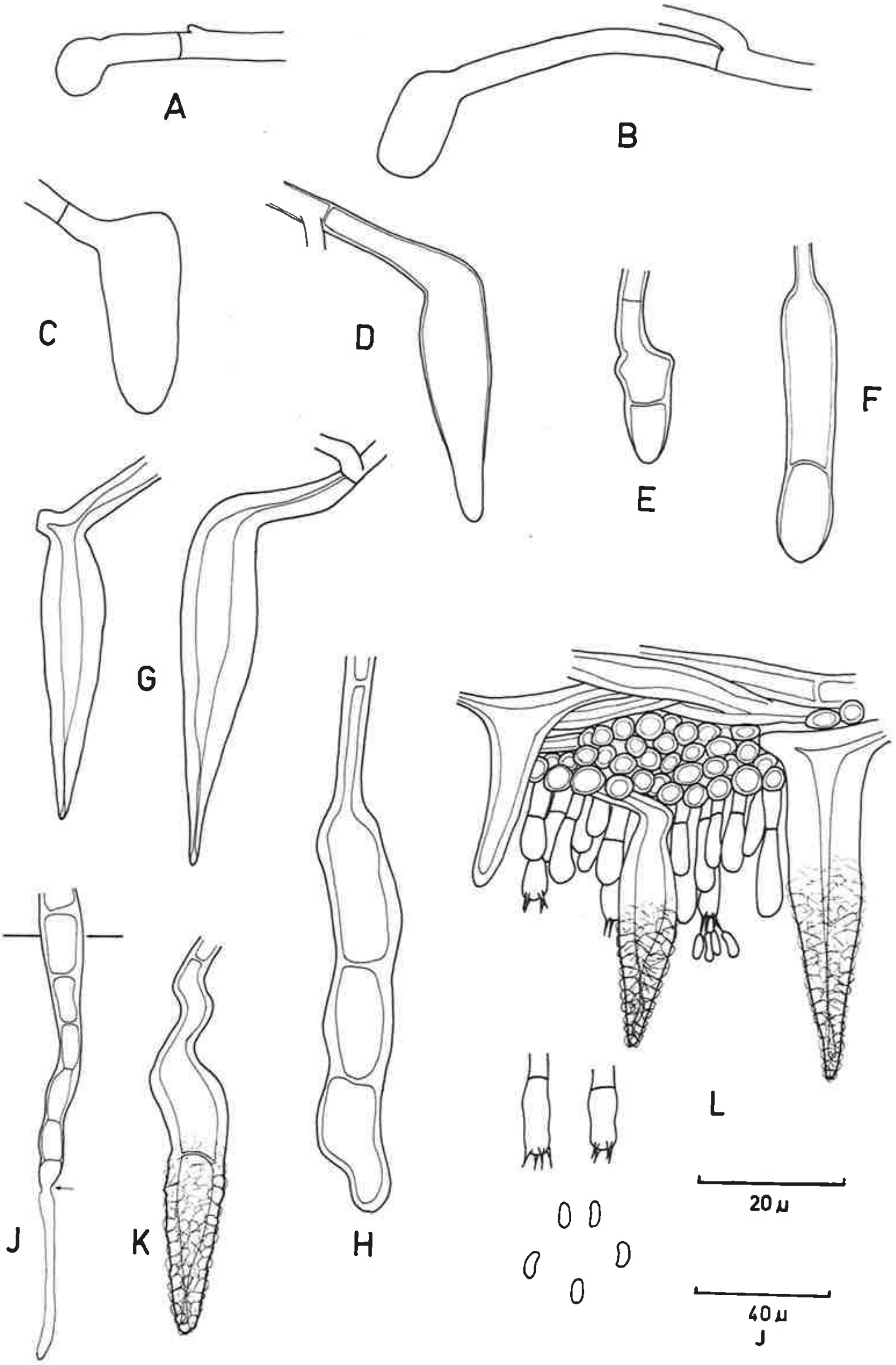

A
B
C
D
E
F
G
H
J
K
L
20 µ
40 µ
J

FIG. 34 Phlebia hydnoides.

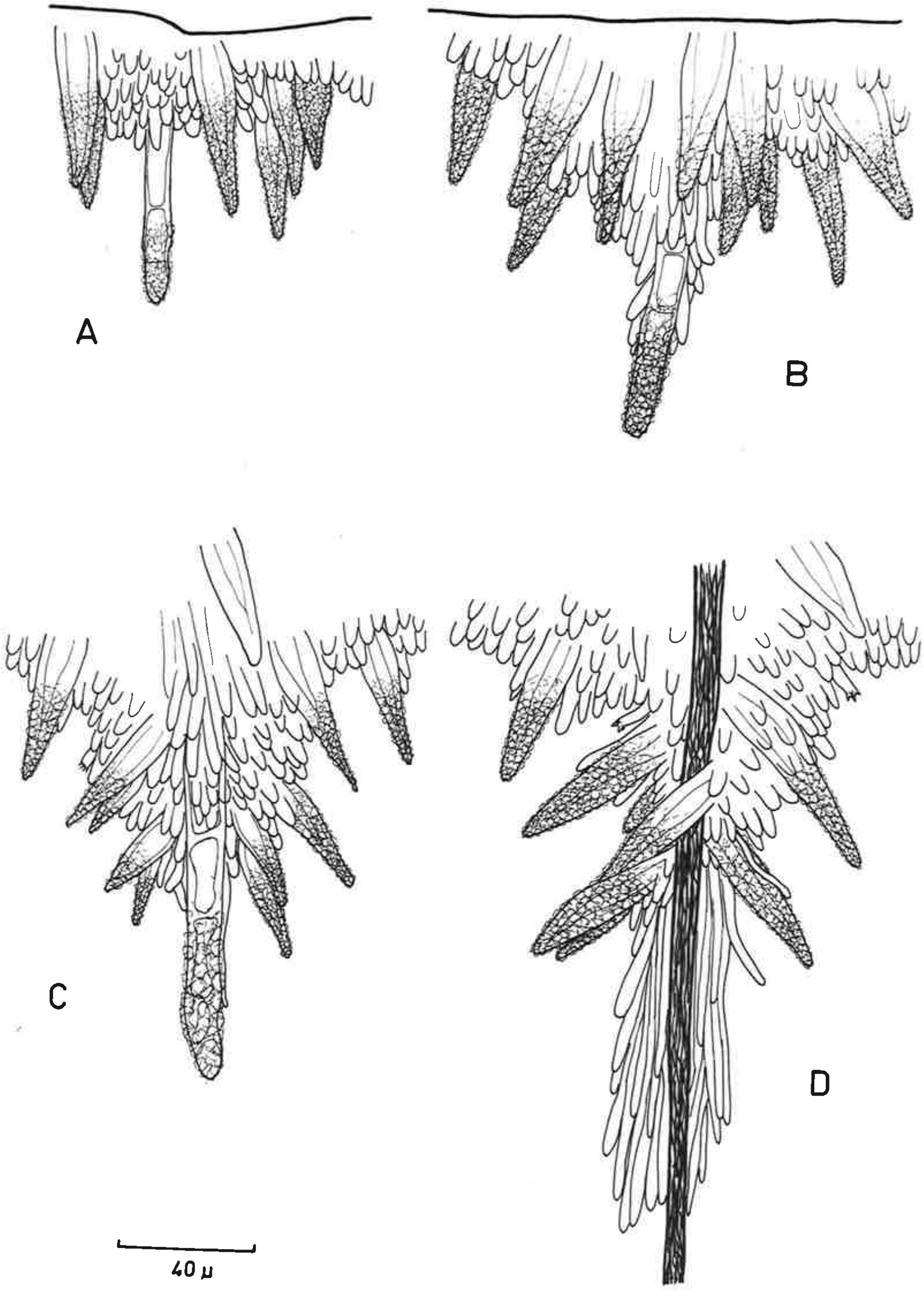
Illustrations showing the development of spines.

A. "Smooth" hymenial surface with metuloids and a septate hyphocystidium.

B. Hymenial hyphae are starting to grow down around a septate hyphocystidium.

C. A new growing edge has been formed along the sides of a septate hyphocystidium and this has produced basidia and cystidia and thus a spine has been formed.

D. A spine that has been formed around an old synnema of a Hyphomycete.


A
B
C
D
40 µ

Punctularia species

In this species the basidiocarp is broadly effused with reflexed margins. The pileus surface is tomentose, concentrically zoned and chestnut in color, while the hymenial surface is smooth and grey to black in color. Tissues in the fructification are arranged in a typical stereoid manner. The hyphal system is monomitic with clamped generative hyphae. Hyphae are thin-walled near the hymenium and in the growing edge, grading to very thick-walled in the cortex and tomentum (fig.35:F).

A characteristic feature of the hymenium is a dense development of dendrohyphidia. It seems that hyphae near the hymenium have a tendency to branch profusely along their length (fig.35:E), and especially at the apices (fig.35:A). The young hymenium consists of a mass of finely branched apices of context hyphae which have curved downwards. Developing basidia are pushed through this layer and project beyond the surface to produce spores (a catahymenium). At this stage some of the dendrohyphidia appear to be modified basidia (fig.35:B). After the basidia collapse the hymenium is left as a thick mat of fine, much branched hyphae whose walls become brown as they age.

No mature basidia were seen but young basidia indicate the potentially large size of the basidia. Spores are large and non-amyloid.

This is probably an undescribed species of *Punctularia*. *Punctularia strigoso-zonata* (Talbot, 1958:143) is very similar macroscopically and microscopically and also develops in a similar manner, but it has much smaller spores.

FIG. 35 *Punctularia* species

A. Various forms of dendritically-branched hyphal apices at the surface of the context and contributing to the formation of a catahymenium.

B. Dendrohyphidia which appear to be modified basidia.

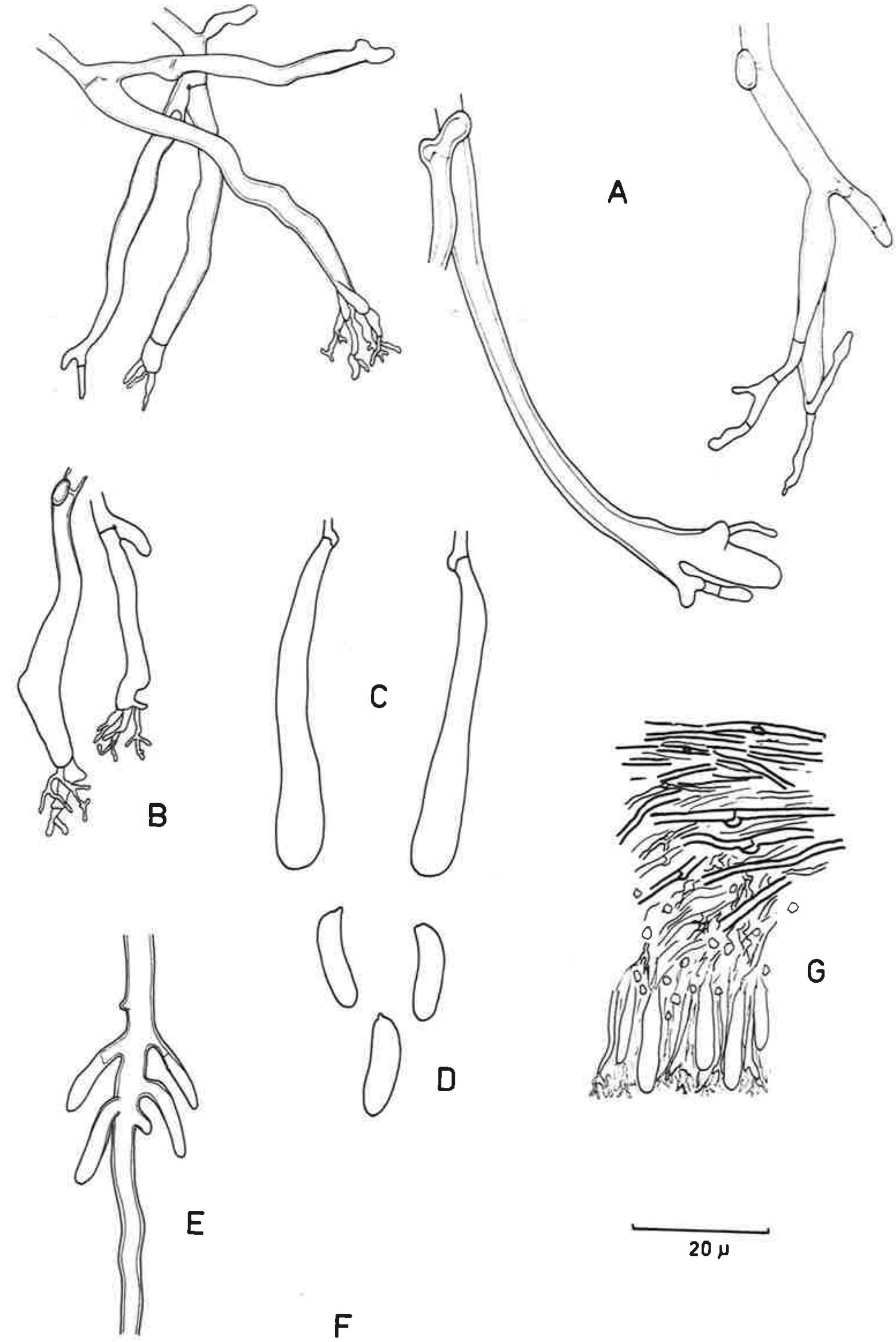
C. Young basidia.

D. Spores.

E, A context hypha with numerous side branches.

F. Thick-walled generative hypha with clamp connexions.

G. Section through a mature part of the fructification showing the catahymenium with young basidia, a context of thick and thin-walled generative hyphae and a cortex of thick-walled generative hyphae.


A
B
C
D
E
F
G
20 μ
40 μ
G

Repetobasidium mirificum Eriksson (1958a:70).

The fructification is extremely thin and delicate. The basal layer is a loose network of horizontal generative hyphae with clamps. Downwardly-growing lateral hyphae (fig.36:A) give rise to a single layer of cystidia and basidia.

The proliferating basidia of this species are distinctive and uncommon in corticioid fungi (Eriksson, 1958a). After the spores have been shed from a basidium it collapses; then the original sub-basidial cell grows a few microns in length and develops a new basidium from its apex within the shell of the collapsed old basidium. The old shell remains as a collar around the base of the new basidium and through repetition of this process a basidium is eventually produced at the apex of a long septate stem which is covered with the shells of old basidia (fig.36:A).

Cystidia originate in the same manner as the subbasidial cells. A few cystidia remain aseptate, but the majority have at least one septum and a large number have two septa (fig.36:B). Because of the variation in the number of septa it was thought that the cystidia might possibly be proliferative but no evidence was found to support this idea. The basidia are usually downwardly-growing fertile branches from the basal hyphae whereas the cystidia are sterile branches from the basal hyphae, but occasionally a basidium was found developing as a side branch from a cystidium (fig.36:B). The cystidia do not fit any of the current cystidial types. They are nearest to septate hyphocystidia, but have modified apices and therefore determinate growth, although they probably lengthen basipetally as they become more septate.

The mature cystidia have a swollen apex and if sections are mounted in Melzer's solution, a thin-walled membrane ballooning from the apex is apparent (fig.36:C). When this membrane breaks, a frill is left around the apex of the cystidium (fig.36:C). In aniline blue/lactic acid the cystidia retain a crystal encrustation on the apex (fig.36:C).

In sections of an older portion of the fungus there were two hymenial levels (fig.36:D). Apparently after a certain number of basidia had been produced on the basidial stems, the next apical cells produced sterile hyphae which formed a horizontal layer over the old basidial stems and a second hymenium then developed from this new basal layer.

FIG. 36 *Repetobasidium mirificum*

A. A series showing the development of the proliferating basidia. The spores are also figured.

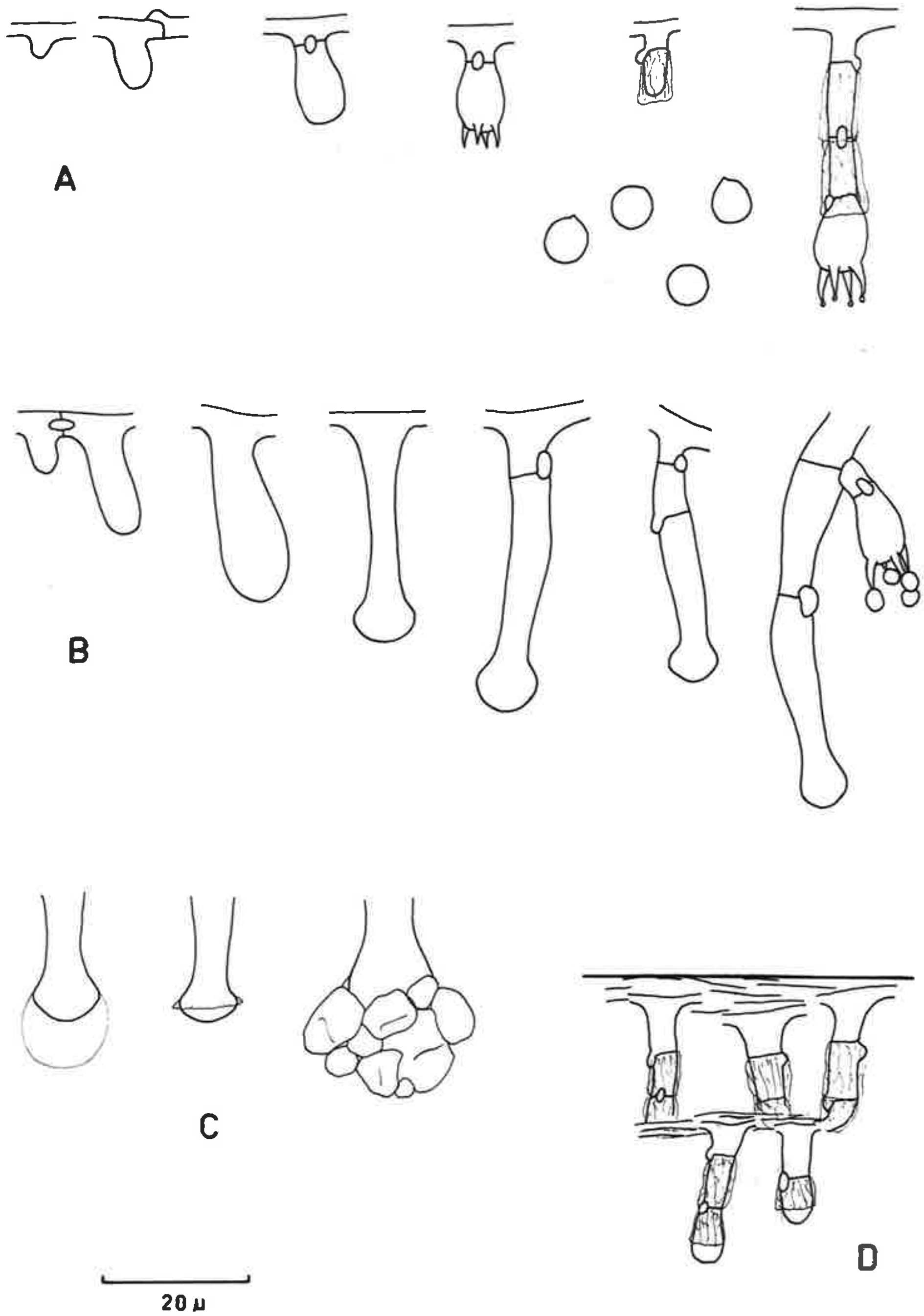
B. A series showing the development of the cystidia.

C. Left - showing the intact thin membrane at the apex of the cystidium.

Centre - the fringe left after the membrane has broken.

Right - a crystal-encrusted apex of a cystidium.

D. A second hymenium has been built over the original hymenium.


A
B
C
D
20 µ

Stereum hirsutum (Willd. ex Fr.) S.F. Gray (1821-653).
Syn.: *Thelephora hirsuta* Willdenow ex Fries (1821:439).

The growing edge of the fructification consists of aseptate skeletal hyphae with moderately thick and slightly brown walls. As the fructification thickens, spaces between the skeletal hyphae are filled with more skeletal hyphae, and with generative hyphae which are thin-walled and lack clamps. However, clamps occur in culture (Boidin, 1958a). As the basidiocarp grows the layer of hyphae near the substratum becomes compacted into a cortex. The remaining hyphae form the context. Skeletal hyphae in the cortex and context are more or less parallel to the substratum. The hyphae of the context curve gradually from the horizontal to become more or less vertical by the time a hymenium starts to form. The hymenium is formed by branching of the generative hyphae above the free ends of the skeletal hyphae and the ultimate cells form basidia at the same level as the apices of the skeletal hyphae. Apices of skeletal hyphae ending in the hymenium are undifferentiated or slightly inflated and the thick walls gradually taper so that the apices are thin-walled. After the hymenium matures, growth of the subhymenial hyphae slows down and the fructification does not continue to thicken appreciably.

After a period of resupinate growth the margin of the fructification becomes reflexed from the substratum and a tomentum of short skeletal hyphae develops from the upper surface of the cortex (fig.37:A).

The apices of skeletal hyphae ending in the hymenium are regarded as cystidiform structures (fig.37:B) and have been termed cystidioid hyphae (Cunningham, 1963) and pseudocystidia (Lentz, 1954) but the term skeletocystidium (Donk, 1964) is preferable. Some of the hymenial cells remain sterile and sometimes become aculeate-tipped (acanthohyphidia).

Stereum vellereum Berkeley (1855:183).

S.vellereum is closely related to S.hirsutum and the construction and development of the fructification is very similar. The apices of the skeletocystidia ending in the hymenium are often not as inflated as those in S.hirsutum. Also the sterile hymenial cells become slightly larger than basidia and have a pointed apex.

Stereum fasciatum (schw.) Fries (1838:546)

Syn.: Thelephora fasciata Schweinitz (1822:106)

This species also has a construction and development similar to S.hirsutum, except that the skeletal hyphae are more conspicuous and the skeletocystidia are larger and their apices more inflated than those of S.hirsutum (fig.37:C).

<u>Stereum</u> <u>sanguinolentum</u> (Alb. & Schw.) Fries (1838:549).

Syn.: <u>Thelephora</u> <u>sanguinolenta</u> Albertini & Schweinitz
ex Fries (1821:440).

The construction of this species is the same as <u>S.hirsutum</u>. The skeletal hyphae have colored contents which darken on contact with air. These hyphae are usually termed sanguinolentous hyphae (Lentz, 1954), but they differ from the skeletal hyphae of <u>S.hirsutum</u> only in degree of thickness of the walls and contents.

FIG. 37 A. B. *Stereum hirsutum*

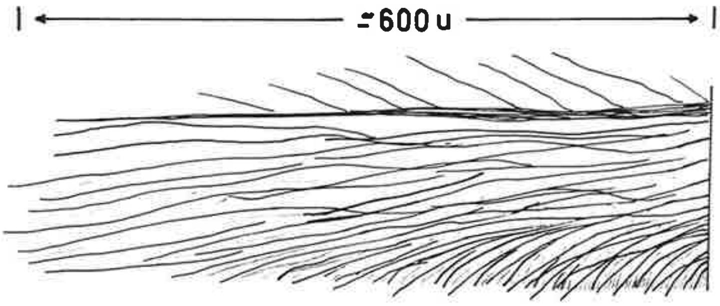
A. A sketch showing the stereoid construction of the fructification.

B. A portion of the young hymenium showing skeletocystidia and the thin-walled generative hyphae.

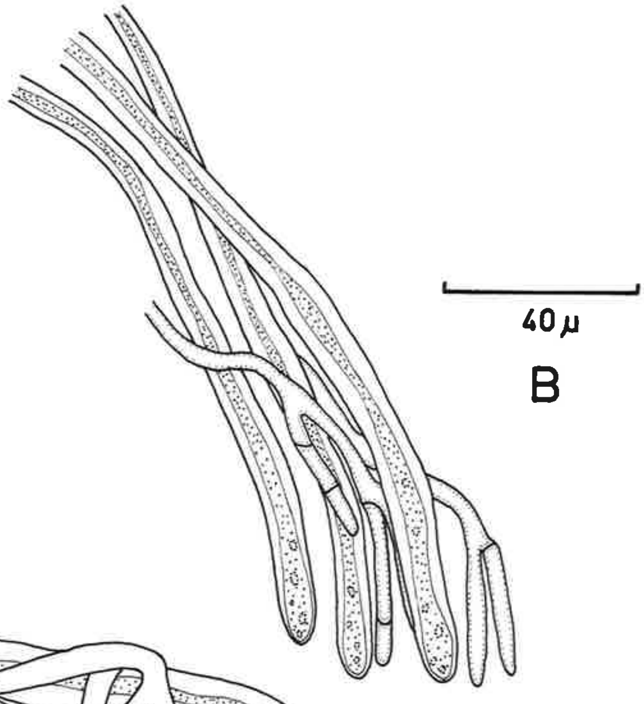
FIG. 37 C. *Stereum fasciatum*

C. A portion of the young hymenium showing the skeletocystidia ending in the hymenium and the thin-walled generative hyphae.

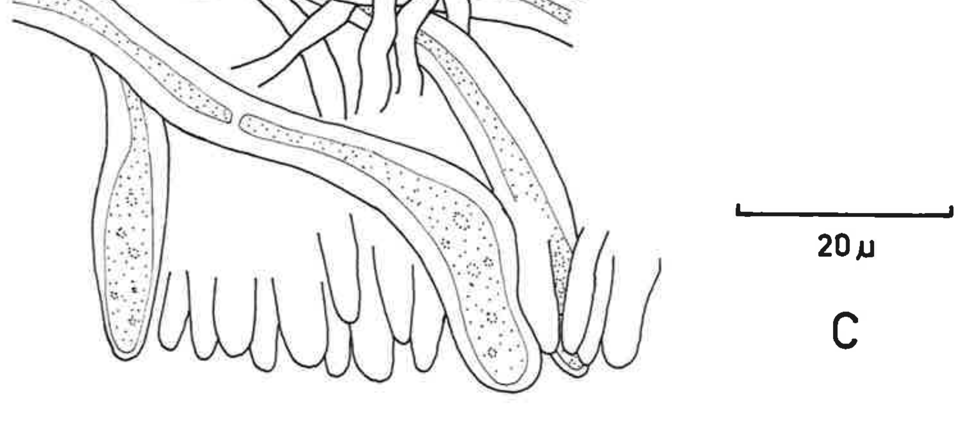
A



B



C



Tubulicium vermiferum (Bourd.) Oberwinkler (1965:54)

Syn.: *Peniophora vermifera* Bourdot (1910:11)
Tubulicrinis vermiferus (Bourd.) Christiansen (1960:136)
Xenasma vermiferum (Bourd.) Liberta (1960:900)

The fructification is effused, monomitic with clamped generative hyphae, and has a hispid appearance due to large subulate cystidia which project above the hymenium. The cystidia are multi-radicate, smooth-walled but usually sheathed with a layer of fine dendritic hyphae (fig.38:B). The growing edge is a layer of basal hyphae from which arise the multi-rooted cystidia and the podobasidia (Oberwinkler, 1965). The cystidia are formed before the basidia which arise singly or in sparse fascicles.

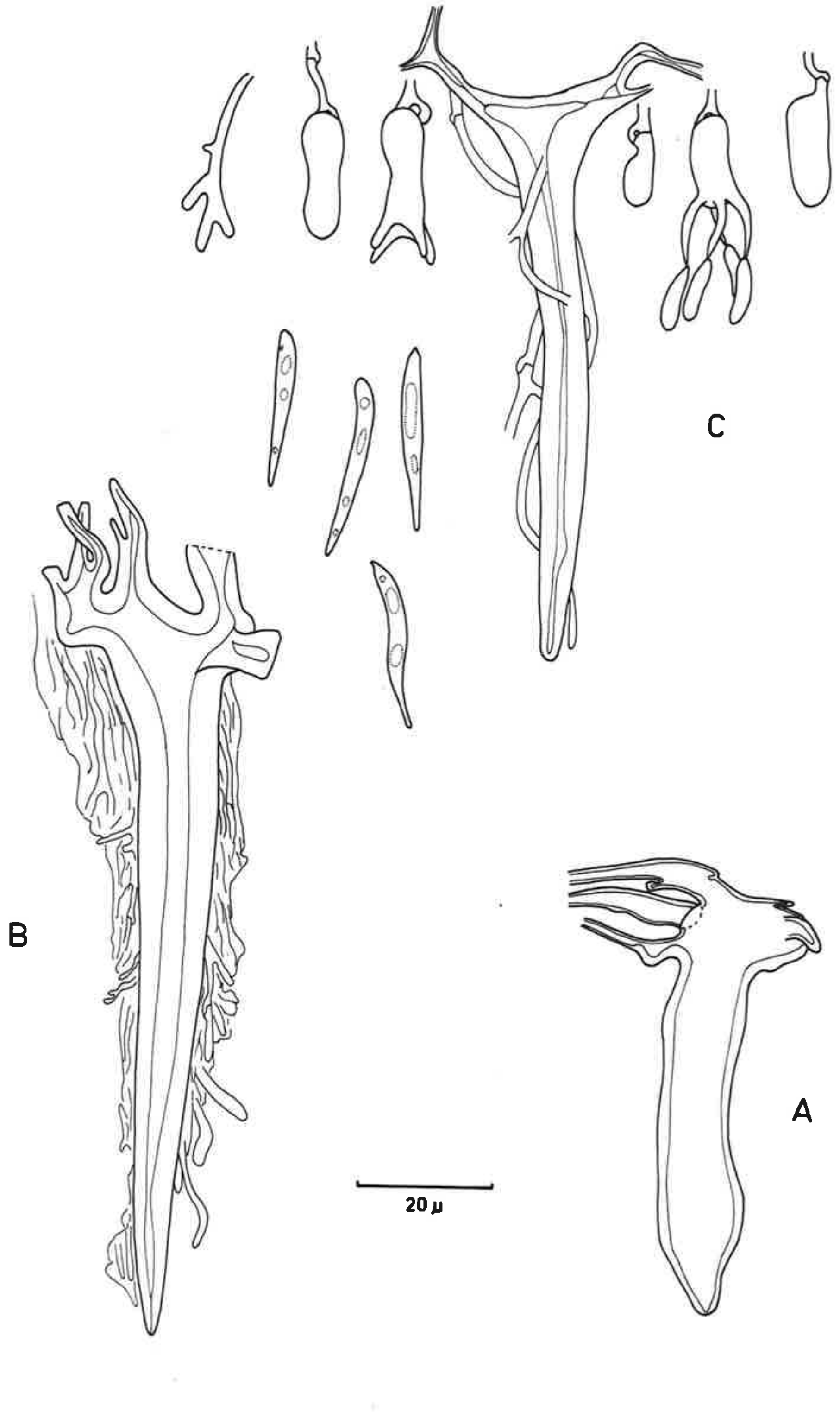
Early stages in the development of the cystidia were not found; cystidia were already well-developed even at the extreme margin of the growing edge in the available material. The youngest cystidium found was a multi-rooted, thin-walled structure shown in fig.38:A. As the cystidia mature the apex becomes subulate, the roots become more branched and the walls, including those of the roots, become greatly thickened, leaving only a relatively narrow lumen. The cystidia in this species rapidly disintegrate in KOH solution (lyocystidia). This process can be observed in slow motion if the sections are mounted in phloxine solution and the KOH solution is flooded under the coverslip. The entire cystidium first swells then bends and snaps across about halfway along its length. When this happens the broken ends of the cystidium have a frayed appearance, indicating that the thick wall is laminated. In Melzer's solution the thickened wall of the cystidium turns a pale grey-blue. Weresub (1953) regarded this color change as a light but positive amyloid reaction.

FIG. 38 *Tubulicium vermiferum*

A. A young multi-radicate cystidium from the growing edge.

B. A mature multi-radicate cystidium with a mat of fine hyphae covering it.

C. A reconstruction of the hymenium with a cystidium, basidia, spores and a simple dendrohyphidium.


C
B
A
20 µ

Tubulicrinis calothrix (Pat.) Donk (1956b:14)

Syn.: *Corticium calothrix* Patouillard (1897:59)
Peniophora calothrix (Pat.) Rogers & Jackson (1943:316).

The fructification is thin, loosely membranous and composed of clamped generative hyphae. The growing edge is a thin layer of basal hyphae on which the hymenium develops directly. Cystidia form before the basidia and develop from downwardly-projecting lateral outgrowths of the basal hyphae; consequently the cystidia are radicate. At first the walls of the young cystidia are thin (fig. 39:A), then as they lengthen the walls thicken from the basal end (fig.39:B,C). Mature cystidia are sub-cylindrical with smooth, thick walls which are amyloid in Melzer's solution, and also dissolve in KOH solution (lyocystidia). The lumen of a cystidium is capillary in the basal portion then typically it expands abruptly about one-sixth to one-third of the distance from the apex, forming a thin-walled apex except at one side where usually the thickened wall extends around the apex like a hood (fig.39:G). Sometimes hooding is absent and instead the lumen expands gradually into an obtuse thin-walled apex which is about one-third the length of the cystidium (fig.39:F). The apices of the cystidia are usually encrusted with a discrete group of acicular crystals (fig.39:F).

Basidia develop from apical cells of downwardly-growing hyphae. No pleurobasidia were found but sometimes basidia which may have developed from downturned apices of basal hyphae were found (fig.39:D). Usually the walls of the basidial pedicels and the bases of the basidia were slightly thickened, becoming swollen or dissolving in KOH solution (fig.39:D). After basidia have collapsed, their thickened bases persist and become embedded by the thickening hymenium (fig.39:G).

New cystidia are formed in the hymenium as it thickens and these are also radicate. It could not be ascertained exactly how radicate cystidia developed in the hymenium, but cells that had formed laterally from the hymenial hyphae and cells with a lateral heel were found in the hymenium (fig.39:E). It seems likely that cystidia develop from cells like these, especially as both the cystidia and cells are not horizontally bi-rooted; instead one of the roots is nearly vertical while the other diverges from it.

FIG. 39 *Tubulicrinis calothrix*

A. A young cystidium developing laterally from a repent hypha in the growing edge.

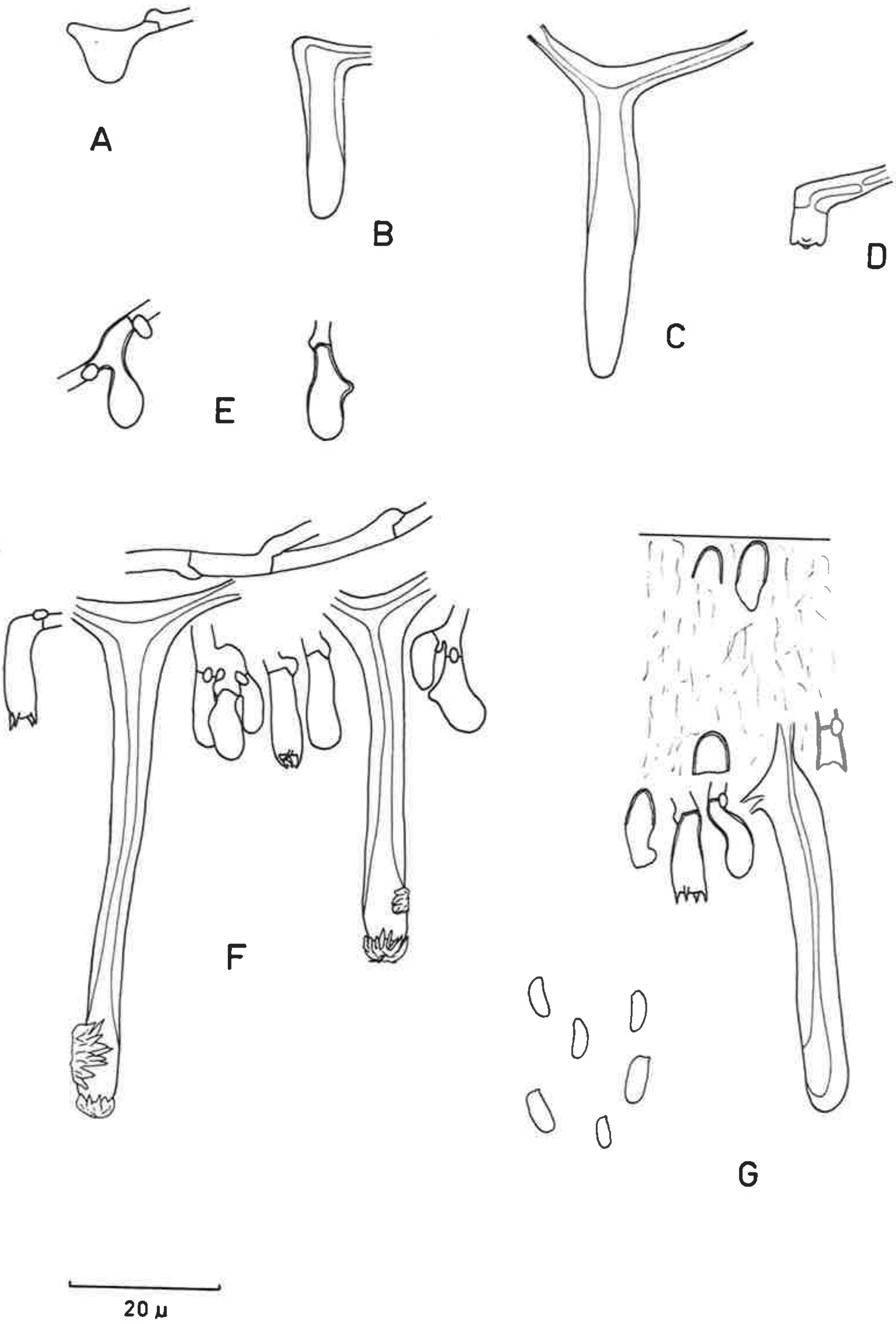
B, C. Successively older stages of A showing thickening of walls from the basal end.

D. A young basidium showing swollen walls in KOH solution.

E. Young cells in the hymenium. One has arisen laterally and the other has a lateral heel.

F. Reconstruction of the young hymenium with basidia and cystidia.

G. A portion of a mature thickened hymenium showing the basidia with basally-thickened walls and the hooded cystidia that are typical of this species.


A
B
C
D
E
F
G
20 μ

Tubulicrinis umbracula (Cunn.) Cunningham (1963:142)
Syn.: *Peniophora umbracula* Cunningham (1955:291)

The fructification is relatively thin, loosely constructed and pruinose in texture, with a monomitic hyphal system of clamped generative hyphae. The growing margin consists of a thin layer of radiating basal hyphae. Near the growing edge vertical lateral outgrowths of the basal hyphae are initiated (fig.40:A). These lateral branches may develop directly into bi-radicate cystidia (fig.40:C) or may grow into short vertical branches, the ultimate cells of which usually develop into terminal cystidia (fig.40:B). Such terminal cystidia may sometimes appear bi-radicate by the outgrowth of a lateral heel from near the base (fig.40:D); but only those cystidia formed directly on the repent basal hyphae are genuinely bi-radicate.

If a cystidium does not terminate a vertical branch, then a basidium or a basidial fascicle is formed instead. Where a cystidium terminates the branch then side branches from the cystidial pedicel develop into basidia or basidial fascicles. After a hymenium has developed over the basal layer, terminal cystidia only are produced; thus radicate cystidia are only produced in the growing edge. The cystidia project behond the hymenium for the greater part of their length, but hyphae may grow down the sides of some of the large bi-radicate cystidia.

Both types of cystidium are basically similar in appearance although the terminal ones are often smaller. The cystidia in this species are very distinctive: they are relatively large structures whose wall is much thicker on one side than on the other; they taper from the base to the apex and terminate in a ridged crystalline cap, whose ridges end in acute, recurved spines. The caps resemble miniature umbrellas, hence the specific epithet of this species. The walls of the cystidia disintegrate in KOH solution (lyocystidia).

FIG. 40 *Tubulicrinis umbracula*

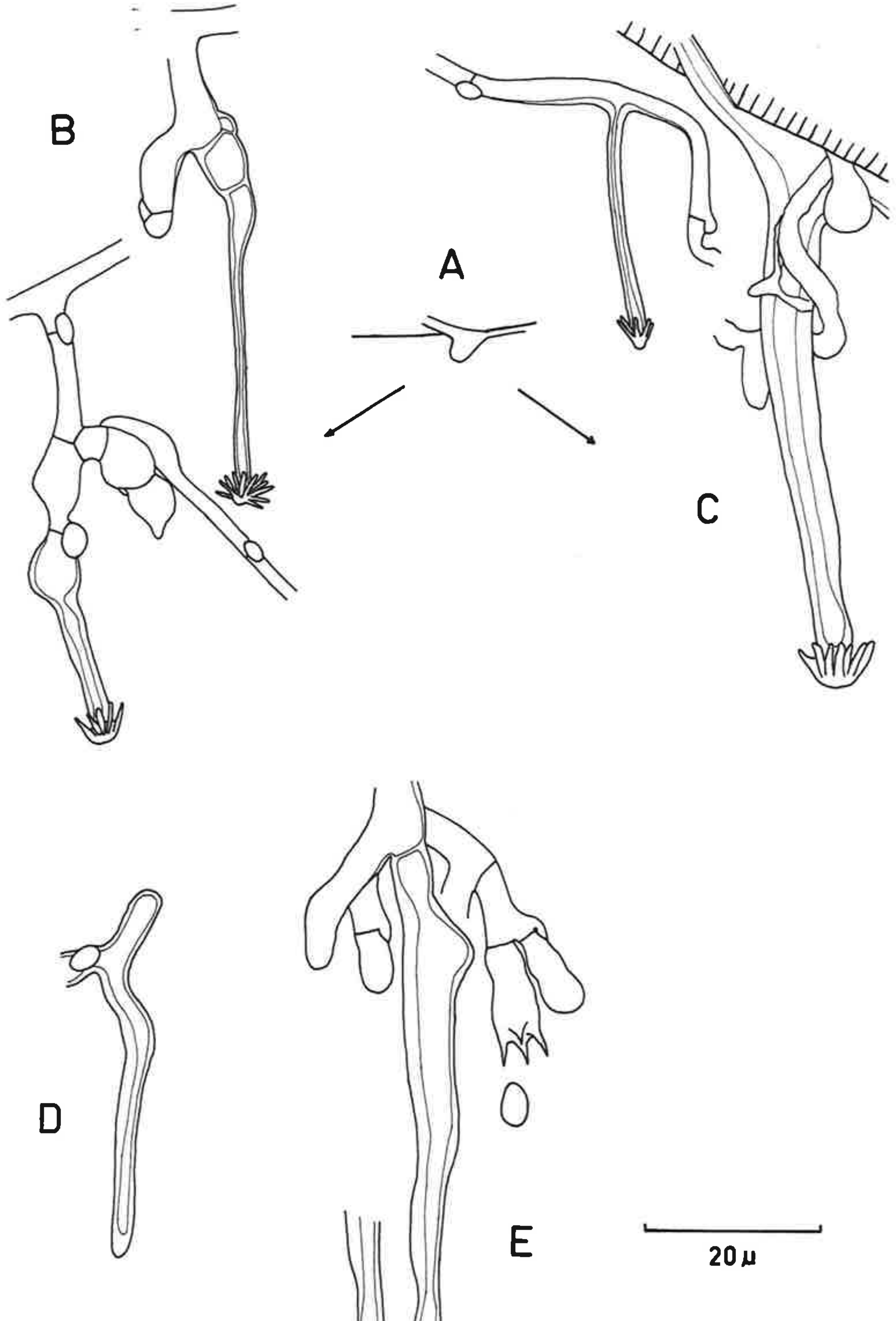
A. A young lateral branch from a basal hypha.

B. Terminal cystidia and basidiferous hyphae produced from short vertical hyphae in the growing edge.

C. Bi-radicate cystidia formed from the basal hyphae.

D. A cystidium with a distinct lateral heel.

E. Basidial fascicle with a closely associated terminal cystidium. A mature basidium and spore is shown as well as the mature cystidium, and the apex of the same cystidium without the crystalline cap.


B
A
C
D
E
20 µ

Xenasma rimicolum (Karst.) Donk (1957a:26)

Xyn.: Corticium rimicolum Karsten (1896:45)

Peniophora rimicola (Karst.) Höhnel & Litschauer (1906b:1555)

Tubulicrinis rimicola (Karst.) Cunningham (1963:138)

The fructification is effused and gelatinous to waxy in texture; it is monomitic with non-clamped generative hyphae. In the earliest stage of development the fructification consists simply of a thin layer of repent hyphae. Towards the margin, small radicate cystidia arise laterally from these hyphae (fig.41:A), while on older proximal parts much larger radicate cystidia are also formed as lateral outgrowths of the repent hyphae. The difference between the cystidia is not merely one of age. The small cystidia are narrow, with a capitate apex and with scarcely thickened walls, while the large ones are not capitate, have inflated bases, and are relatively thick-walled in the proximal half. The remnants of the two types of cystidium are also easily distinguishable in old fructifications where the cystidia are old and overgrown.

Scattered pleurobasidia are also formed on the repent hyphae at the same time as the large cystidia, thus the latter may be considered to be hymenial elements. This is also substantiated by their development, as, at the stage when basidia are to be formed, wide lateral branches arise from the repent hyphae and appear to be capable of developing either into pleurobasidia or into large cystidia. In this young stage the hymenium arises from the thin layer of basal hyphae and the basidia are discontinuous or solitary; a context is absent. The fructification then thickens by further horizontal hyphae being superimposed upon the first, embedding the hymenial elements and the small cystidia and eventually forming a thick layer of densely compacted, horizontal, gelatinized hyphae which produce a new hymenial layer. This process is repeated many times so that an old fructification is a thick layer of more or less parallel gelatinized hyphae, embedding the bases of old cystidia, and over the surface of this is the current layer of basidia and cystidia (fig.41:B). The basidiospores are finely asperulate; the markings are evident in Melzer's solution but not in KOH solution.

A common feature of this species is the formation of rhizomorphic strands of compacted parallel gelatinized hyphae which radiate in all directions from a fresh fructification. In the specimens studied, the young strands were of variable length but usually slender, and they bore small cystidia. The strands gradually became stouter by further hyphae being superimposed over the first and eventually large cystidia and basidia were produced over the surface of the strand.

Although it was not possible to trace the development of individual repent hyphae, it seems probable that first-formed lateral outgrowths develop into small cystidia, while basidia and large cystidia are developments of later lateral outgrowths.

The pleurobasidia and cystidia are characteristically bi-radicate, and a septum is usually seen a short distance from their bases in the distal parts of the repent hyphae from which they arise.

Xenasma pulverulentum (Litsch.) Donk (1957a:25)
Syn.: *Corticium pulverulentum* Litschauer (1939:112)
Peniophora pulverulenta (Litsch.) Jackson (1950b:532).

The fructification of this species is very similar in appearance and texture to *X.rimicolum* and is monomitic but with clamped generative hyphae; radiating rhizomorphic strands are also found in this species.

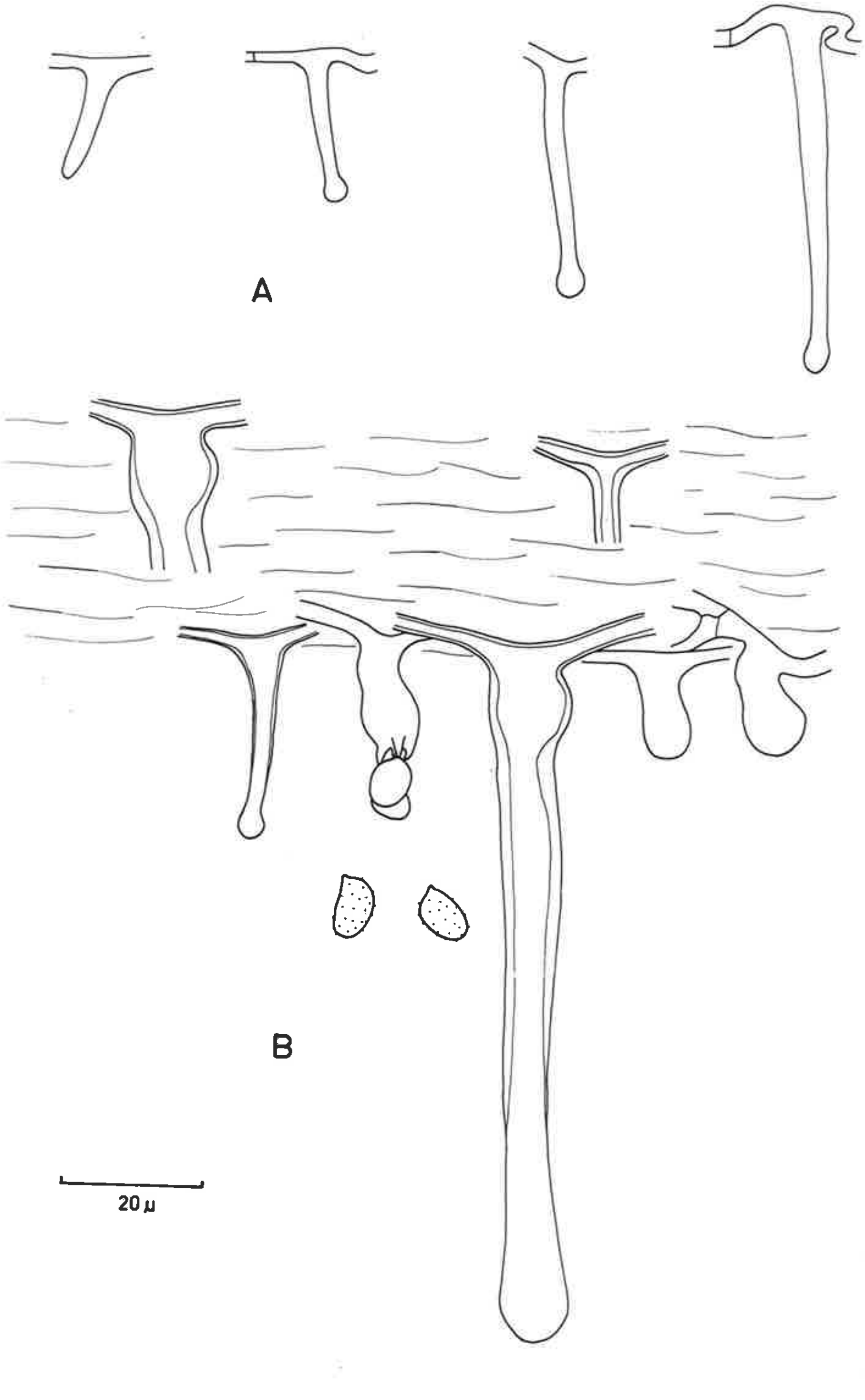
X.pulverulentum has small capitate cystidia identical in size, shape and development to the small cystidia of *X.rimicolum*. They arise close to the growing edge, which is composed of more or less parallel gelatinous hyphae. The cylindrical pleurobasidia form soon after the initiation of cystidia. When mature, the basidia project for a considerable distance beyond the surface of the fructification.

The thickened fructification of *X.pulverulentum*, instead of being a thick layer of more or less parallel hyphae as in *X.rimicolum*, is a thick basal layer of parallel hyphae on which is built up a pseudoparenchymatous thickened hymenium. Probably the fructification is still thickened in the same way as in *X.rimicolum* but in *X.pulverulentum* the pleurobasidia develop from short lengths of swollen hyphae and it is these swollen basidial bases left after the basidia collapse which give the pseudoparenchymatous appearance. The spores of *X.pulverulentum* have longitudinal striations which are evident in Melzer's solution but not in KOH solution.

FIG. 41 *Xenasma rimicolum*

A. A series showing the development of small radicate cystidia.

B. Section of a mature part of the fructification showing embedded bases of old cystidia and the current hymenial level with small and large cystidia, basidia and spores.


A
B
20 μ

Xylobolus frustulatus (Pers. ex Fr.) Boidin (1958b:341)

Syn.: Thelephora frustulata Persoon ex Fries (1821:445)

Stereum frustulatum (Pers. ex Fr.) Fuckel (1861:102)

Stereum frustulosum Fries (1838:552)

Xylobolus frustulosus (Fr.) Karsten (1881:40)

For further synonyms see Lentz (1955).

The fructification is at first a discrete pulvinate body attached centrally to the substratum. Growth of the body is more apical than lateral which results in an obconical frustule (fig.42:A). Since the fruit-bodies are gregarious, adjacent frustules eventually make contact at the margins and under mutual pressure form an apparently resupinate plaque, deeply cracked into polygonal areoles; the cracks represent lines of contact of the individual frustules. This growth habit of X.frustulatus is similar to that of Aleurodiscus amorphus (Pers.) Rabh. A section through even a very small frustule (fig.42:B) shows a large number of strata, but these indicate phases of growth intensity rather than annual growth.

Acanthohyphidia are the dominant hymenial elements of X.frustulatus. They develop before the basidia from apical cells in the hymenium (fig.42:D). At first the acanthohyphidia are thin-walled with a few aculeate processes, and similar to the aculeate-tipped basidioles of Xylobolus illudens. The young acanthohyphidia lengthen apically, the walls become thicker and brown in color, and aculeate processes become more numerous (fig.42:E). Changes in intensity of growth were seen in most of the acanthohyphidia. The rounded aculeate apex may renew its growth by putting out a thin-walled extension (fig.42:F) which soon thickens, becomes pigmented and develops into a short length of smooth-walled hypha topped by a new rounded aculeate apex. This process can be repeated a number of times before the acanthohyphidium finally stops growing; which was at about a length of 50u for most of the acanthohyphidia (fig.42:G). Apical re-growth from an acanthohyphidium is also capable of developing into a thin-walled undifferentiated hypha (fig.42:H), instead of another acanthoid apex. The thickened fruit-body is composed almost entirely of embedded acanthohyphidia.

Occasionally very long thick-walled hyphae, often with secondary septa, were seen (fig.42:J), their apices usually being at hymenial level. The walls of these hyphae may be smooth or aculeate. In the latter case the processes may be few and concentrated in one area, or many and extending over the whole length of the hypha. Those with aculeate processes are like acanthohyphidia whereas those with smooth walls could be likened to skeletocystidia. Boidin (1958b) thought of these hyphae as pseudocystidia, that is skeletocystidia in the terminology used in this work. However, as they originate in the same position as acanthohyphidia and often have the aculeate processes of acanthohyphidia, then it is doubtful if they can be regarded as skeletocystidia, especially as no aculeate processes were seen on the skeletocystidia of *X.illudens* nor in the species of *Stereum* studied. Also Welden (1967) did not see aculeate pseudocystidia in *X.illudens*. Therefore it is preferable to consider the structures as acanthohyphidia, although probably of a different type to the shorter ones so abundant in the hymenium.

X.frustulatus is generally regarded as dimitic, but although the acanthohyphidia have thick brown walls they do not constitute a skeletal system. The long thick-walled, naked hyphae could be skeletal hyphae, but because they grade into acanthoid structures they are probably not homologous with the skeletal system of *Stereum* s.str. It might also be argued that the long thick-walled hyphae are the skeletal system, although a reduced one, especially as the fructification is composed of short-celled hyphae, which are most evident in the growing edge (fig. 42:C). From these observations it is believed that the hyphal system of *X.frustulatus* cannot be clearly defined but is best described as monomitic to weakly dimitic.

FIG. 42 *Xylobolus frustulatus*

A. Habit sketch showing individual fructifications.

B. Cross section through a young fructification showing stratification.
(A & B are copies of drawings by P.H.B.Talbot)

C. Growing edge consisting of short-celled hyphae.

D. Acanthohyphidia originating from hymenial cells.

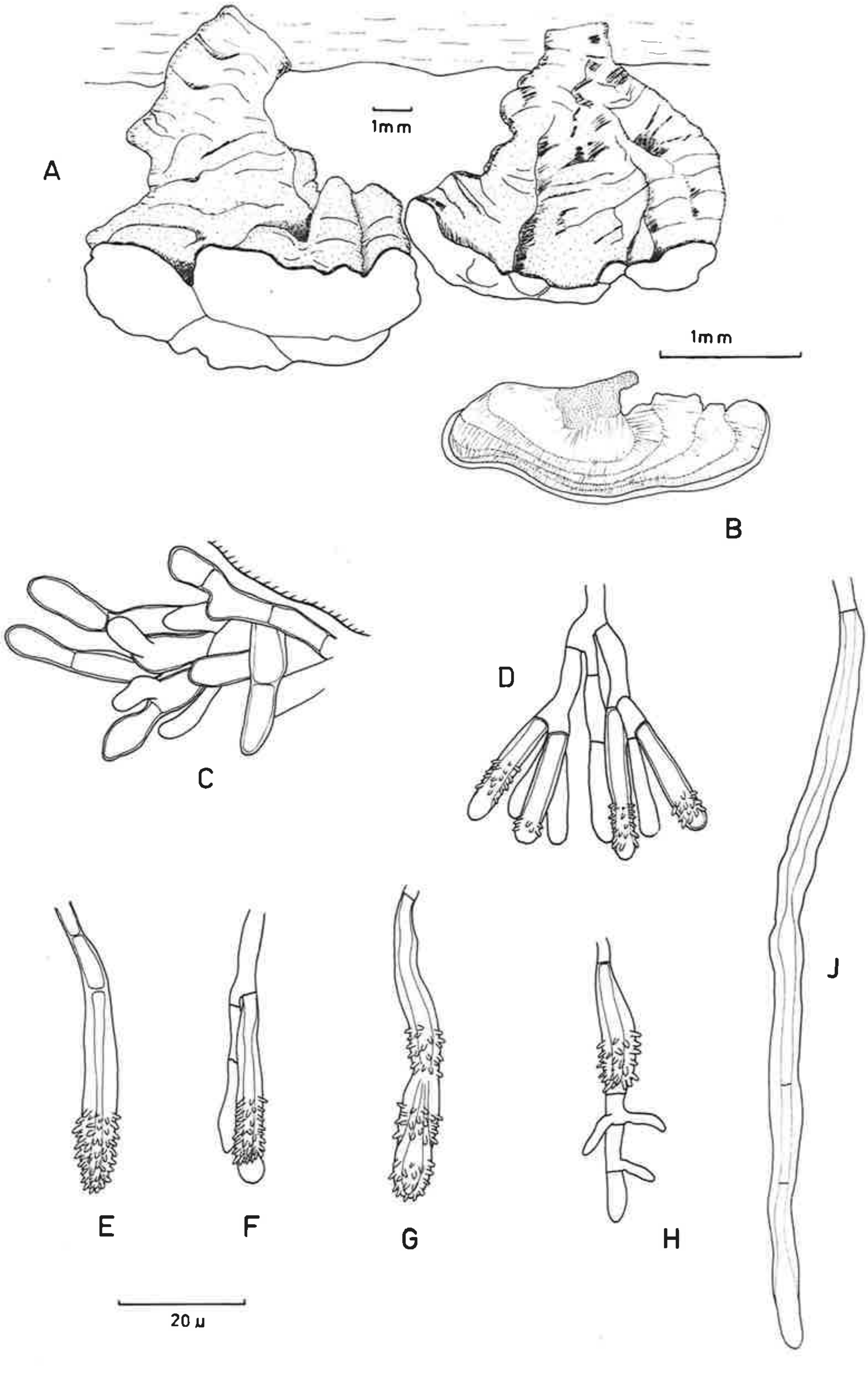
E. A mature acanthohyphidium.

F. Renewed growth from the apex of an acanthohyphidium.

G. An acanthohyphidium showing a series of growth stages.

H. Apical growth from an acanthohyphidium developing into undifferentiated thin-walled hyphae.

J. A long thick-walled skeletal-like hypha with secondary septa.


A
1mm
1mm
B
C
D
J
E
F
G
H
20 µ

Xylobolus illudens (Berk.) Boidin (1958b:341)

Syn.: *Stereum illudens* Berkeley (1845:59)

For further synonyms see Cunningham (1963).

The fructification in this species has a dimitic hyphal system with dark, thick-walled skeletal hyphae and hyaline to pale-colored generative hyphae, lacking clamp connexions and sometimes becoming relatively thick-walled, thus not always easy to differentiate from the skeletal hyphae. The context is composed mainly of skeletal hyphae partly bound together by fewer generative hyphae.

The growing margin is composed mainly of the ends of repent skeletal hyphae of the basal layer, whose apices are thin-walled and often slightly inflated (fig.43:A). The distal ends of some of these hyphae become abruptly deflected and continue growing more or less vertically, at the same time becoming surrounded by vertical branches of the generative hyphae. Eventually a basidiferous layer, and basidia and acanthohyphidia, are differentiated from the generative hyphae. A considerable number of skeletal hyphae curve downward into the hymenium, their apices reaching about the same level as the apices of the hymenial structures. The apical portion of such skeletal hyphae is smooth, thin-walled to moderately thick-walled, occasionally somewhat inflated and with more deeply-staining contents than usual (fig.43:B). They form a distinctive structure which has sometimes been termed a pseudocystidium (Cunningham, 1963; Lentz, 1960) but, as a modified skeletal hypha is more appropriately termed a skeletocystidium. It is clear that the skeletocystidia are formed from basal or context skeletal hyphae and have no close developmental association with the hymenium.

In many specimens, the generative hyphae are not as numerous as the skeletal hyphae and are only distinguished with ease in the basidiferous layer. Acanthohyphidia are formed from the generative hyphae before the basidia, those formed first being produced among the apices of the skeletocystidia. As the hymenium matures, it overgrows some of the skeletocystidia and acanthohyphidia. The young acanthohyphidia are short and thin-walled, with few aculeate processes from the apex (fig.43:D). As they age, they become quite long, thicker-walled and colored, and the number of aculeate processes increases (fig.43:E). Acanthohyphidia may occur as modified branches of the basidial fascicles and are probably homologous with basidia; structures occasionally occur which can be interpreted as basidia with aculeate processes along their sides, or as acanthohyphidia with the apices modified into fertile basidia (fig.43:C). Bourdot & Galzin (1928) state that acanthohyphidia are present in inverse relation to the activity of the fructification. Acanthohyphidia form before the basidia and continue to be formed after basidia develop; there is a close relationship between these structures but the question as to whether it is inverse was not studied.

FIG. 43 *Xylobolus illudens*

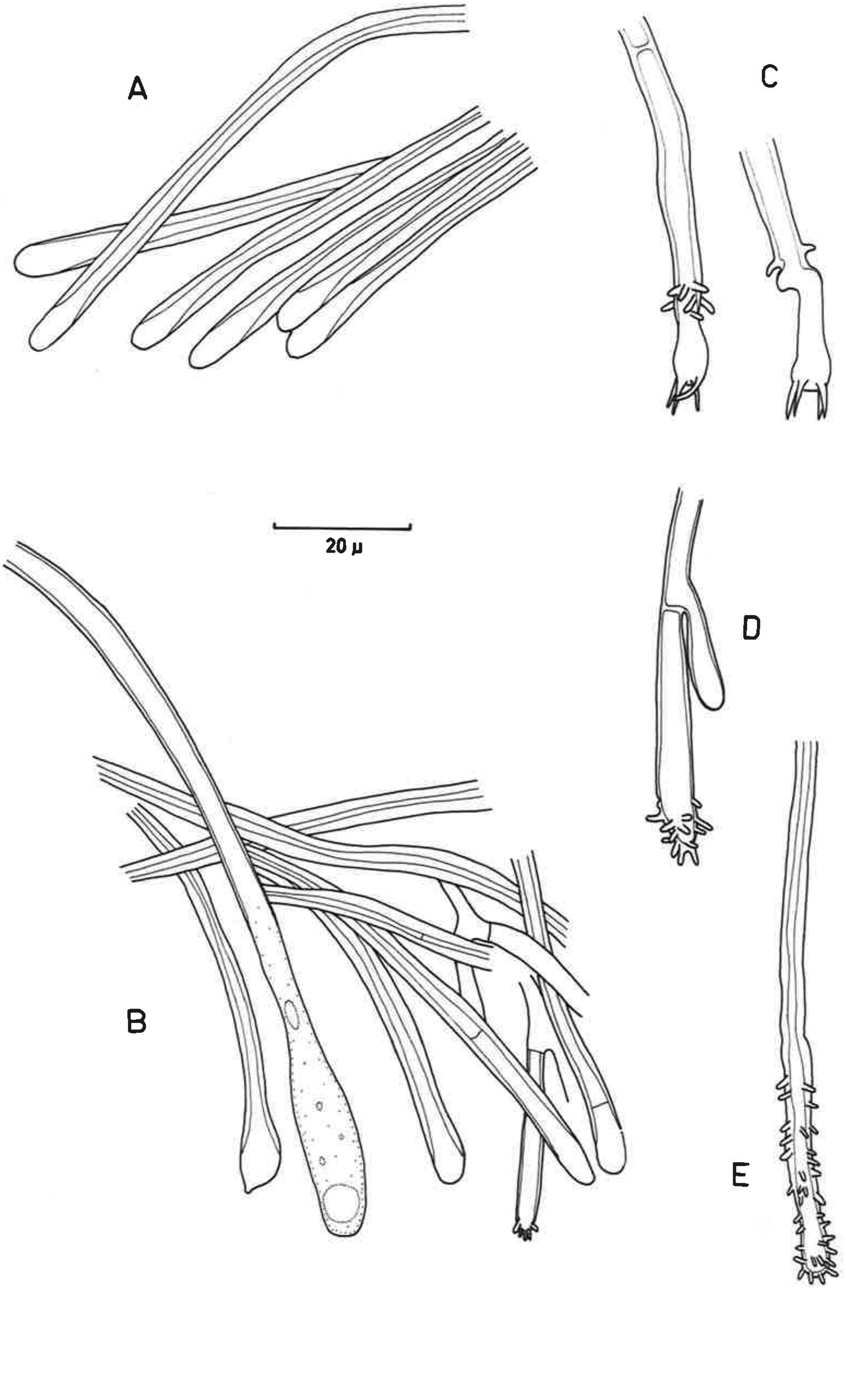
A. Growing edge consisting of skeletal hyphae with thin-walled apices.

B. A portion of the young hymenium showing skeletal hyphae with thin-walled apices, a skeletal hypha with a swollen apex and vascular contents, and an acanthohyphidium.

C. Basidia with aculeate processes.

D. A young acanthohyphidium.

E. A mature acanthohyphidium.


A
C
20 µ
D
B
E

APPENDIX II

Table 2. Comparison of the developmental and microscopic features of the species studied and their current grouping in families and sub-families.

m - clamps in the margin only

r - rare

n.d. - no data available

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Species	Development Types					Cystidial Types							Hyphal system			Clamps		Amyloid spores	Hyphidia			Basidia	Family	Sub-family
	1	2a	2b	3	other	Skeleto-	Radicate	Metuloid	Gloeo-	Lepto-	Hypho-	Other	Monomitic	Dimitic	Dubious	Fructification	Culture (Boidin 1958a)		Simple	acantho-	dendro-			(for the Corticiaceae only)
Stereum hirsutum	x					x								x		–	x	x		x		clavate	Stereaceae	
S. fasciatum	x					x								x		–	x	x		x		"	"	
S. vellereum	x					x								x		–	x	x		x		"	"	
Haematostereum sanguinolentum	x					x								x		–	x	x		x		"	"	
Amylostereum chailletii	x					x								x		x	x	x				"	"	
Lopharia cinerascens	x					x		x						x		x	n.d.	–			x	"	"	
L. crassa	x					x									x	–	n.d.	–				"	"	
Xylobolus illudens	x					x									x	–	x	x		x		"	"	
X. frustulatus					x										x	–	–	x		x		"	"	
Chondrostereum purpureum	x								x				x			x	x	–				"	"	
Punctularia strigoso-zonata	x												x			x	n.d.	–			x	"	Punctulariaceae	Peniophoroideae
P. species	x												x			x	n.d.	–			x	"	"	"
Laxitextum bicolor	x			x					x				x			x	x	x			x	"	Hericiaceae	Tubulicrinoideae
Duportella tristicula	x					x			x					x		x	n.d.	–				"	Corticiaceae	"
D. fulva	x					x								x		x	n.d.	–				"	"	"
Tubulicrinis calothrix		x					x						x			x	n.d.	–				"	"	
T. umbracula		x					x						x			x	n.d.	–				"	"	
Tubulicium vermiferum		x					x						x			x	n.d.	–	x			podobasidia	"	
Xenasma rimicolum		x					x						x			–	n.d.	–				pleurobasidia	Xenasmataceae	
X. pulverulentum		x					x						x			x	x	–				pleurobasidia	"	Repetobasidioideae
Litschauerella abietis		x					x						x			x	n.d.	–	x			"	"	Aleurodiscoideae
Oliveonia pauxilla		x					x						x			–	n.d.	–				obovoid	Ceratobasidiaceae	"
Repetobasidium mirificum		x										x	x			x	n.d.	–				repetobasidia	Corticiaceae	"
Gloeocystidiellum lactescens		x							x				x			–	–	x				clavate	"	Phlebioideae
G. leucoxanthum		x							x				x			x	x	x	x			± utriform	"	"
Aleurodiscus species		x							x				x			x	n.d.	x	x	x		"	"	Peniophoroideae
Phlebia gigantea		x						x					x			xm	xr	–				small clavate	"	"
P. hydnoides		x						x			x		x			m	x	–				"	"	"
Peniophora cinerea		x				x		x							x	x	x	–	x			clavate	"	Hyphodermoideae
P. nuda		x						x	x				x			x	x	–	x			"	"	"
P. incarnata		x						x	x				x			x	x	–	x			"	"	"
Hyphoderma setigerum			x	x							x		x			x	x	–				utriform	"	"
H. pubera			x					x	x				x			x	x	–				"	"	"
H. tenue			x						x	x			x			x	x	–				"	"	"
H. species			x							x			x			x	n.d.	–				"	"	"
Hypochnicium punctulatum			x							x			x			x	x	–				"	"	"
Corticium patricium			x							x			x			x	n.d.	–				clav. to utri	"	"
Hyphodontia alutaria				x							x	x	x			x	n.d.	–				"	"	
Amphinema byssoides				x							x		x			x	x	–				"	"	Corticioideae
A. tomentellum				x							x		x			x	n.d.	–				"	"	Phlebioideae
Coniophorella oliveacea				x							x		x			–	n.d.	–				utriform	Coniophoraceae	
Peniophora longispora				x								x	x			x	n.d.	–				clavate	Corticiaceae	
Peniophora cremea				x								x	x			xm	xr	–				"	"	