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STUDIES OF 'PELLICULARIA' AND ASSOCIATED GENERA OF HYMENOMYCETES

P. H. B. TALBOT
Waite Agricultural Research Institute, Adelaide, South Australia

(With 20 Text-figures)

The generic name *Pellicularia* Cooke is rejected as a *nomen confusum*. Genera and species commonly associated with '*Pellicularia*' are reviewed. *Koleroga* Donk is regarded as a synonym of *Ceratobasidium* Rogers. Two new combinations are made: *Oliveonia atrata* (Bres.) *comb, nov.* and *Thanatephorus sterigmaticus* (Bourd.) *comb. nov.*

The genera dealt with are divided among the Tulasnellaceae and the Corticiaceae, the family Ceratobasidiaceae being regarded as superfluous.

The subclasses Heterobasidiomycetes and Homobasidiomycetes are not recognised, as it is impossible to suggest characters by which they may consistently be delimited. The characters normally used for delimiting these subclasses are, however, still regarded as of great importance for separating lower taxonomic categories.

Generic diagnoses, keys to species and nomenclators of species are provided.

Introduction

As several of the fungi discussed in this paper are important plant pathogens it is a matter of concern that their nomenclature has changed so frequently in recent years. Intensive taxonomic study often brings about change in classification, thus those groups which attract many taxonomists tend to suffer most from nomenclatural change. Yet taxonomy cannot be restrained deliberately when new information becomes available and demands recognition in the system of classification. On the one hand, the task of the taxonomist is eased by judicious splitting of large, unwieldy genera into smaller and perhaps more natural segregates; on the other hand the applied worker, unused to thinking of species in terms of their synonymy, is justifiably disturbed by this process.

This paper is an attempt to trace changes in the taxonomy of the group of fungi loosely and erroneously classed as *Pellicularia* Cooke, to classify them and to provide nomenclators of the more important species.

Rejection of the generic name Pellicularia sensu Rogers

The genus *Pellicularia* Cooke (1876a, 1876b, 1876c, 1881) was originally monotypic, with *P. koleroga* Cooke as its type species. A history of this fungus is given by Donk (1954), who concluded that the name applies to a mixture of a hypothetical gelatinous matrix together with vegetative hyphae of a resupinate Hymenomycete

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and the spores of a mould. Donk therefore rejected *Pellicularia* and *P. koleroga* as *nomina confusa*, illegitimate, impriorable and unable to be used for any taxon whatever. The Code of Nomenclature states that "the name of a taxon must be rejected if the characters of that group are derived from two or more entirely discordant elements, unless it is possible to select one of these elements as a satisfactory type." An Appendix to the Code states that the principal basis for the selection of a type is the original *description* of the taxon and not the type specimen.

In his several articles on *P. koleroga*, Cooke consistently emphasized the gelatinous matrix and the mould spores; the vegetative hyphae present in the specimen received little comment and the presence of basidia was actually denied. On the basis of Cooke's descriptions, therefore, the basidia that were subsequently found in the type specimen and illustrated by Miss Wakefield for Burt (Burt, 1918, 1926) should not be considered when a type for *P. koleroga* is to be selected from the mixture; yet Rogers (1951) attempted to retypify the species by exactly that constituent element of the type specimen. If *P. koleroga* is to be retypified—and it appears to be such a gross example of a *nomen confusum* that this course seems undesirable—the choice should be the mould spore element rather than the vegetative hyphae or basidia. It is, however, quite permissible to select the Basidiomycete element as the type of a new species with characters derived only from that selected part, and that is exactly what Donk (1958a) did in proposing the new genus and species, *Koleroga noxia*. Although Donk and Rogers typify the respective genera *Koleroga* and *Pellicularia* by species based on the same element of the same mixed type specimen, Donk's action has the force of being legitimate under the Code of Nomenclature, while in the opinion of many mycologists Rogers's has not.

Venkatarayan (1949) also rejected *Pellicularia*, reasoning that Cooke did not see the basidial state and gave the name *Pellicularia* to the imperfect state. Others, including Eriksson (1958a, 1958b), Olive (1957), and Christiansen (1959, 1960) have also tacitly rejected the application of the name *Pellicularia* to a Hymenomycete.

The present author is in complete agreement with Donk in considering *Pellicularia* to be illegitimate and impriorable, but presents evidence below showing that *Koleroga noxia* is almost certainly a species of *Ceratobasidium* and that *Koleroga* should lapse into synonymy.

Much of the irritation caused by nomenclatural change in this group centres on the name to be applied to the perfect state of *Rhizoctonia solani* Kühn, a species important as a plant pathogen, as a soil saprophyte, and as a research tool in several biological disciplines. This species is, however, clearly not congeneric with *Pellicularia koleroga* sensu Rogers or *Koleroga noxia* Donk, and acceptance of Rogers's typification of *Pellicularia* would still not permit of its inclusion in *Pellicularia*. The main effect of accepting Rogers's typification would merely be to make *Ceratobasidium* a synonym of *Pellicularia*, which in turn would cause further changes in nomenclature of other species. The fact is that *Pellicularia* as used in Rogers's monograph (Rogers, 1943) is a genus containing many discordant elements, many of which have already been segregated into more natural groupings by Donk.

Historical review of the 'Pellicularia group'

Emphasis on basidial morphology has repeatedly proved useful in the classification of Hymenomycetes ever since Patouillard (1900) proposed the subclasses Heterobasidiomycetes and Homobasidiomycetes on this basis. The systematic position of the genera discussed in this paper will be considered later; for the moment it may be noted that many of the genera appear to fall in a category somewhat intermediate between Heterobasidiomycetes and Homobasidiomycetes in their basidial morphology and were originally proposed as direct or indirect segregates from the genus *Corticium* Fr., a large and unwieldy genus which Bourdot & Galzin (1911) divided into sixteen sections; two of those sections were based on basidial morphology.

Corticium sect. *Urnigera* Bourd. & Galz. includes species with fine hyphae and urniform basidia, i.e. basidia having an inflated base separated by a constriction from the subcylindrical apex bearing a corona of (4–)6–8 sterigmata. In *Corticium* sect. *Botryodea* Bourd. & Galz. the hyphae are wide, with characteristic wide-angled branching, while the broad basidia grouped in discontinuous cymose bouquets have 2–4–6–8 sterigmata; in this section the species have an hypochnoid, pellicular or submembranous texture.

The section *Botryodea* appealed to Donk (1931) as a natural genus for which he proposed the name *Botryobasidium* Donk. At the same time he proposed another genus, *Botryohypochnus* Donk, with *Hypochnus isabellinus* Fr. as its type species; this had been included in *Tomentella* sect. *Botrytes* by Bourdot & Galzin (1924). The clustered arrangement of basidia is similar in these two genera, but they differ in basidial and sporal morphology.

Rogers (1935) merged the genera *Botryobasidium* and *Botryohypochnus*, describing eight species under the former name. He also proposed the genus *Ceratobasidium* Rogers for four species, two of which were transferred from *Corticium* sect. *Botryodea*.

For species with urniform basidia bearing four or more sterigmata Rogers (1935) applied the name *Sistotrema* Fr., but later (Rogers, 1944) reserved *Sistotrema* for pileate forms and used *Trechispora* Karst. for resupinate forms with the same basidial morphology. Following Lundell & Nannfeldt (1947) and Eriksson (1949), the present tendency is to use the name *Sistotrema* for all such fungi whether pileate or resupinate. Rogers (1944) recognised *Galzinia* Bourdot for resupinate Hymenomycetes with basidia consisting of "a basal vesicle and an apical expanded sporiferous portion connected by a neck of variable length"; the neck is slender and often of great length; there are four sterigmata and the spores are not repetitive. The development of basidia in two stages resulting in urniform or utriform (Donk, 1964) metabasidia is apparently widespread and would be unreliable as a generic character unless taken in conjunction with other morphological features. Such development is known *inter alia* in basidia of: *Vuilleminia* Maire (1902); *Botryobasidium* Donk (Eriksson, 1958a, 1958b; Donk, 1958a); *Coniophora* DC. ex Mérat (Lentz, 1957); *Laeticorticium* Donk (Donk, 1956b; Eriksson, 1958a); *Scytinostroma* Donk (1956b); *Waitea* Warcup & Talbot (1962); *Hyphoderma* Wallr. em. Donk, *Hypochnicium*

Eriksson, and *Hyphodontia* Eriksson (Eriksson, 1958a); *Vararia* Karsten (Eriksson, 1958a; Christiansen, 1960).

In 1943 Rogers published a monograph of the genus *Pellicularia* Cooke, comprising fifteen species drawn from several genera mostly with the general aspect of *Botryobasidium*, which name he had previously applied to this group. Rogers regarded *Botryobasidium* as a synonym of *Pellicularia* on the grounds of priority and on the opinion that *P. koleroga*, the type species of *Pellicularia*, was congeneric with the type species of *Botryobasidium*. Typification of *P. koleroga* and its important bearing on the taxonomy of this group has been discussed above.

Again focusing attention on the morphology of basidia and basidiospores, Donk (1956a) segregated two new genera from the '*Pellicularia* group'. These were *Uthatobasidium* Donk (type species: *Hypochnus fusisporus* Schroet. = *Pellicularia flavescens* sensu Rogers) and *Thanatephorus* Donk (type species: *Hypochnus solani* Prill. & Delacr. = *Hypochnus cucumeris* Frank = *Pellicularia filamentosa* sensu Rogers).

Olive (1957) and Pilát (1957) regarded *Uthatobasidium* and *Thanatephorus* as synonyms of *Ceratobasidium*, emphasizing their common possession of repetitive spores but perhaps underrating the fact that the growth habit of the fructification in *Ceratobasidium* is quite different and that the critical basidial morphology is also distinctive. Saksena (1961a, 1961b) recorded his cytological studies of *Corticium praticola* Kotila under *Ceratobasidium*. Discussing nuclear distribution in the lifecycles of various species, Flentje, Stretton & Hawn (1963) recognised the genera *Thanatephorus*, *Ceratobasidium* and *Waitea* as mutually distinct.

Parker-Rhodes (1954) introduced unnecessary confusion into the taxonomy of *Ceratobasidium*; as Donk (1957a, 1958a) has noted, Parker-Rhodes "regarded *Ceratobasidium* . . . a good genus except for its type species (*C. calosporum*) which he excluded as only a form of *Prototremella* [= *Gloeotulasnella*] *calospora* Boud. with 'aseptate basidia' [?]. For the remainder of the genus he introduced the name *Hydrabasidium* with *Corticium atratum* Bres. as its type species. The latter is not an original species of *Ceratobasidium*." Although their spores are similar, there is as yet no proof of intergradation between *Gloeotulasnella calospora* and *Ceratobasidium calosporum*; moreover, the name *Hydrabasidium* was not validly published. In most characteristics except its lack of cystidia, *C. atratum* closely approaches *Oliveonia* Donk and has little in common with typical species of *Ceratobasidium*. *Ceratobasidium calosporum* was perhaps an unfortunate choice of a type species for *Ceratobasidium* as its spores are unlike those of other known species in the genus; however, when obviously anomalous species such as *C. atratum*, *C. terrigenum* and *C. sterigmaticum* are removed from the genus it becomes a satisfactorily homogeneous taxon.

A few other taxa have at some time been considered in the general context of the '*Pellicularia* group'. *Heteromyces* Olive was a preoccupied name which Donk (1958a) replaced by *Oliveonia*; this genus contains species somewhat resembling *Ceratobasidium* but not forming web-blights, differing in the possession of cystidia or gloeocystidia and in having broadly clavate basidia on narrow tapering pedicels instead of abruptly attenuated sphaero- or pyropedunculate basidia.

Cunningham (1953, 1963) described six species of *Pellicularia* in New Zealand, including one (*P. zealandica* G. H. Cunn.) with large, clamped septocystidia arising from basal hyphae. Talbot (1958) noted four species of *Pellicularia* in South Africa, including *P. fodinarum* Talbot & Green with septocystidia from which adventitious clusters of basidia were produced. Such septocystidiate species seem ill-placed in '*Pellicularia*' and may possibly find a place in the genus *Hyphoderma* Wallr. em. Donk. A similar septocystidiate species has already been placed in *Hyphoderma*, namely *H. polonense* (Bres.) Donk (1957b).

The genus *Waitea* Warcup & Talbot (1962) was proposed for a species that could not be fitted without violence into any of the genera mentioned above, but was clearly allied to the '*Pellicularia* group'.

The systematic position of Tulasnellaceae and Ceratobasidiaceae

Although some of the genera considered in this paper (*Botryobasidium*, *Botryohypochnus*) are clearly members of the Corticiaceae, most would be classed in the Tulasnellaceae or Ceratobasidiaceae by those who recognise the need for these families.

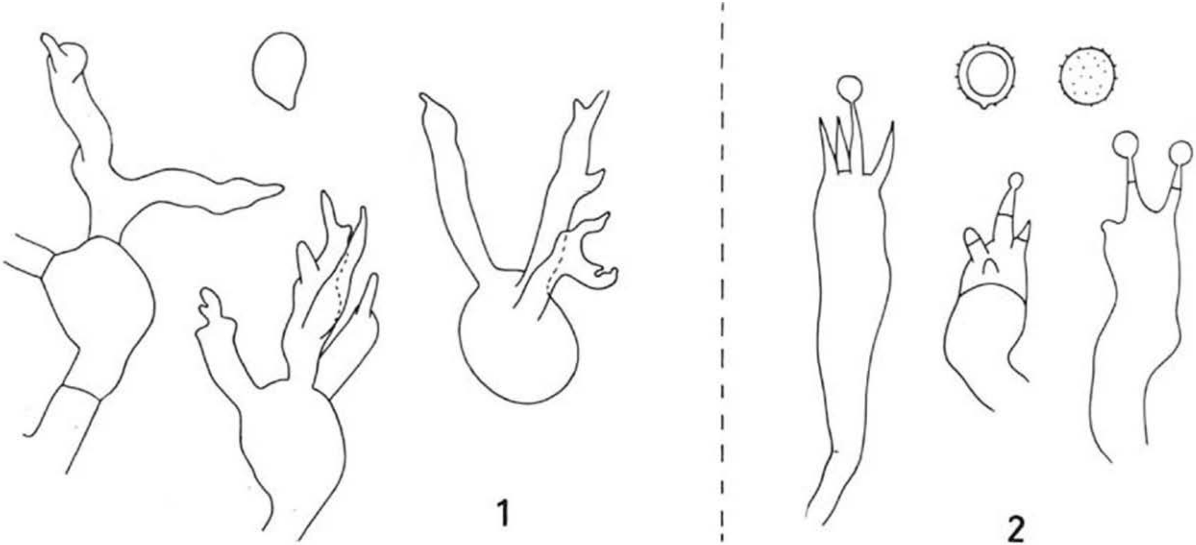
Martin (1945) at first placed *Ceratobasidium* in the Tulasnellaceae but later (Martin, 1948) referred it to a new family, Ceratobasidiaceae, in the Tremellales and maintained this viewpoint still later (Martin, 1952, 1957). Jackson (1949) considered that *Pellicularia* and *Ceratobasidium* were too similar to be placed in separate families and he assigned both to the Ceratobasidiaceae at the base of the Homobasidiomycetes. However, what Jackson had in mind as representing '*Pellicularia*' is in doubt, and could be extremely pertinent. Martin (1957) finds that *Ceratobasidium* is distinctly intermediate between homobasidial and heterobasidial lines, showing strong relationship with the Corticiaceae and Tulasnellaceae but unable to be fitted into either; therefore Martin thinks that there is no alternative but to accept a distinct family for *Ceratobasidium*. Olive (1957, 1958) recognises the Ceratobasidiaceae as a family of Tremellales and includes three genera, *Ceratobasidium*, *Metabourdotia* Olive and *Heteromyces* Olive (= *Oliveonia* Donk). Christiansen (1959, 1960) includes *Uthatobasidium* and *Ceratobasidium* in the Ceratobasidiaceae as Heterobasidiomycetes, but places *Botryohypochnus*, *Botryobasidium* and *Thanatephorus* in Corticiaceae as Homobasidiomycetes.

On the one hand there is a body of opinion which recognises a distinct family, Ceratobasidiaceae, for many members of the '*Pellicularia* group', especially those which seem to show a heterobasidial affinity by possession of repetitive spores and voluminous, sometimes septate, sterigmata. On the other hand, Donk (1956a, 1958a, 1964) and Eriksson (1958a, 1958c) do not recognise the Ceratobasidiaceae, preferring, since their exact systematic position is in doubt, to retain them in the already heterogeneous Corticiaceae.

The Heterobasidiomycetes were originally defined (Patouillard, 1900) as having septate basidia (phragmobasidia) producing secondary basidiospores by repetition, or non-septate basidia (holobasidia) associated with repetitive spores. In contrast, the Homobasidiomycetes were defined as having holobasidia with spores that germinate directly into mycelium. The emphasis in Patouillard's separation of the subclasses therefore lies on spore repetition or its lack, and not primarily on septation of the basidium. This curious situation, which is surely the reverse of current opinion, was possibly unintentional and no doubt arose from the fact that Patouillard found it desirable to include the Caloceraceae (= Dacrymycetaceae) and Tulasnellaceae in the Heterobasidiomycetes; in their gelatinous texture and pigmentation the Dacrymycetaceae resemble well-known types of Tremellales, while in shape the basidia of *Tulasnella* are somewhat similar to those of *Tremella* but lack septation of the metabasidium.

As generally conceived, the Heterobasidiomycetes are phragmobasidial with the notable exceptions of Dacrymycetaceae, Tulasnellaceae and Ceratobasidiaceae. But as Donk (1964) has pointed out, many phragmobasidial species are apparently incapable of spore repetition. There are also both phragmobasidial and holobasidial species known to be capable of spore repetition but highly variable in this respect. It would thus appear that rigid application of the character of spore germination can only result in blurring the two subclasses. Yet if, instead, emphasis is laid solely on the septation of the metabasidium, the Dacrymycetaceae must be excluded from the Heterobasidiomycetes.

With the development of the concept of an 'epibasidium' (Neuhoff, 1924) the presence of stout, variable sterigmata was also introduced gradually into the definition of a Heterobasidiomycete. As many such sterigmata may become adventitiously or secondarily septate at the base (*Tulasnella*) or at a variable position within the sterigma (*Dacrymyces* and *Ceratobasidium*) this feature has been taken by many, the author (Talbot, 1954) included, as indicative of a phragmobasidium, and hence of a Heterobasidiomycete. Donk (1958b, 1964) maintains that secondary septation of the sterigma should have no place in the definition of a phragmobasidium; recent experience has convinced the author of the justness of this attitude. An interesting case is that of a South Australian species of *Phellodon* (Hydnaceae or Bankeraceae), in which the sterigmata are mostly secondarily septate and whose basidia often become secondarily septate shortly below the apex (see Fig. 2); by no stretch of imagination could these basidia be said to be phragmobasidia, or *Phellodon* placed in the Heterobasidiomycetes. In *Thanatephorus praticola* (Fig. 13) and several species of *Ceratobasidium* the sterigmata become secondarily septate far more often than would be supposed from literature records. This occurs with *Ceratobasidium* species on their natural substrata and particularly with *C. cornigerum* in culture. In *C. atratum* (Fig. 20) it is not uncommon to find two septa in a single sterigma. In addition, the sterigmata of most species of *Ceratobasidium* are able to branch; this, too, occurs particularly in culture. Warcup & Talbot (unpublished data) have found that over-watered soil-cultures of *C. cornigerum* are especially liable to produce basidia with branched sterigmata (Fig. 1) and they believe that the presence of free water on the basidia, or perhaps merely excessive humidity, may



Figs. 1–2. — 1. *Ceratobasidium cornigerum*. Basidia with abnormally branched sterigmata in overwatered soil-culture. — 2. *Phellodon* sp. from South Australia. Metabasidia and sterigmata with or without secondary septation.

be responsible. Secondary septation of the metabasidium is also seen in *Corticium terrigenum* Bres. (Fig. 19), and has been reported in *Clavulina* (Corner, 1950). The basidiospores themselves may be septate in certain species; this occurs in *Waitea circinata* (Warcup & Talbot, 1962) and is found very markedly in *Corticium terrigenum* (Fig. 19) where the septa show typical septal pores and are almost certainly formed as a result of nuclear division.

In the opinion of the author, the Ceratobasidiaceae can be distinguished from the Tulasnellaceae only on trivial characters. In Tulasnellaceae the sterigmata are characteristically swollen and spore-like, usually separated by a basal septum from the metabasidium, and sometimes deciduous; in Ceratobasidiaceae the sterigmata, though stout, are subcylindrical or subfusoid and the septa that sometimes form within the sterigmata are probably never basal in position. There seems little merit in maintaining two families on such slight differences. Yet it must also be remembered that equally slight basidial characters serve to differentiate the well-established family Dacrymycetaceae, in which the undivided metabasidium bears two stout sterigmata which may occasionally (Rogers, 1934, 1935) develop adventitious septa. In the Dacrymycetaceae, however, associated characters such as texture and pigmentation, as well as basidial shape, suggest that this is a distinct family.

The author adopts the view that the Ceratobasidiaceae cannot be maintained as distinct from the Tulasnellaceae, while the Dacrymycetaceae form another distinctive family. The problem of classifying these families in higher taxa still remains.

The fact that many phylogenetic schemes have been proposed for Basidiomycetes shows that in our present state of knowledge phylogeny is inconclusive and unreliable as a basis for taxonomy; taxonomy must be based primarily on the visible or detectable properties of the material actually before the taxonomist. Our taxonomic system demands that one should be able to recognise and separate taxa; it succeeds when there is discontinuity in the properties and fails when they vary continuously from one taxon to the next. It is against the principles of orthodox taxonomy to create taxa for intermediate forms. At the same time it is realized that evolution implies that there should be some taxa with intermediate properties—that is the dilemma of taxonomy when related, as it ideally should be, to phylogeny.

Looking for discontinuities, therefore, it has been shown above that the most constant basidial feature that would separate the Heterobasidiomycetes and Homobasidiomycetes is primary septation of the metabasidium, or its lack. Yet even here intermediate examples are known, as in *Metabourdotia* (Olive, 1957) and *Pseudotulasnella* (Lowy, 1964), where the metabasidia are divided by incomplete cruciate primary septa. To accept the phragmobasidial or holobasidial characters for separation of subclasses would result in the Dacrymycetaceae and Tulasnellaceae (including Ceratobasidiaceae) being placed, by definition as Homobasidiomycetes. Yet this is not altogether acceptable, for members of these families have many features which, though not constant in Heterobasidiomycetes, are far more characteristic of that subclass than of Homobasidiomycetes. Heretical though it may seem, experience with the fungi forming the subject of this paper has convinced me that the primary division of Basidiomycetes into Heterobasidiomycetes and Homobasidiomycetes cannot stand. As morphological evidence fails to achieve a satisfactory separation of these subclasses, and as non-morphological evidence appears to be lacking, there is no alternative but to abandon the subclasses and place all orders under the single class "Basidiomycetes". It is to be hoped that this may provide a stimulus to look for non-morphological features which may give a clearer picture of taxonomic groupings and phylogeny at this level. There is no reason why basidial morphology should not continue to be used for the delimitation of lower taxonomic categories and continue to contribute to the enormous advances in the taxonomy of Basidiomycetes initiated by Patouillard.

In the generic types discussed in this paper much variation can occur in such features as: the stoutness and number of sterigmata per basidium; the septation of sterigmata and occasionally of spores; the branching of sterigmata; the repetition of spores or their direct germination to form mycelium.

In species of *Thanatephorus* a septum may occur in the sterigma and the spores are sometimes repetitive, but the metabasidia are undivided. *Waitea circinata* has spores that may or may not become transversely septate; the sterigmata are relatively small and the spores are apparently not repetitive. Species of *Ceratobasidium* have undivided metabasidia, repetitive spores, and stout sterigmata which sometimes become septate or forked. In *Tulasnella* a septum at the base of the sterigma is well established and the sterigmata are sometimes deciduous. In *Metabourdotia* the cruciate septa of the metabasidium are incomplete; if they were complete this fungus would undoubtedly be considered a species of *Sebacina* sensu lato. In *Oliveonia*, cystidia or gloeocystidia are present and the spores are repetitive but the metabasidia are undivided; however, in *O. fibrillosa* (Burt) Donk some basidia appear to have a partial or complete annulus, though possibly this is an artefact.

Synopsis of systematic arrangement

Class Basidiomycetes: Order Tulasnellales: Family Tulasnellaceae: Examples: *Tulasnella* Schroet. and *Gloeotulasnella* Höhn. & Litsch. em. Rogers (not considered further); *Metabourdotia* Olive; *Oliveonia* Donk; *Ceratobasidium* Rogers; *Thanatephorus* Donk; *Uthatobasidium* Donk.

Class Basidiomycetes: Order Aphyllophorales: Family Corticiaceae: Examples: *Waitea* Warcup & Talbot; *Botryobasidium* Donk; *Botryohypochnus* Donk.

The systematic treatment that follows is based on personal knowledge of generic types and the majority of species mentioned, a notable exception being many species of *Botryobasidium*. In order to classify and key out those species of which he has no experience the author has drawn heavily on published descriptions and illustrations, especially those of Donk, Rogers, Eriksson and Christiansen cited below.

KEY TO GENERA

1. Fructification hypochnoid, the basal hyphae giving rise to a relatively thick layer of ascending hyphae which branch at a wide angle and terminate in cymose clusters of basidia or in a semi-palisade hymenium. 2

Fructification usually relatively thin, waxy to reticulate-pruinose or pellicular, with basidia arising directly from the repent basal hyphae or terminally in cymose or racemose clusters from short, discontinuous tufts of ascending hyphae which in some cases branch at a wide angle. 4

2. Basidia urniform or suburniform with (4–)6(–8) very small, curved sterigmata; (Basidia little wider than the supporting hyphae; spores smooth, not repetitive; sclerotia absent; saprobic on rotten wood; conidial state, if present, a species of *Oidium* emend. Linder) *Botryobasidium*

Basidia subcylindrical, subclavate, not developing urnigerously nor constricted about the middle; sterigmata 2–4, relatively large; (Basidia little wider than the supporting hyphae; sclerotia absent; saprobic on rotten wood; conidial states not known, or dubious) . . . 3

3. Spores not repetitive (ornamented, hyaline to yellowish); hymenial branching cymose *Botryohypochnus*

Spores repetitive (smooth, hyaline to yellowish); hymenial branching less regularly cymose and tending to form a palisade . . . . *Uthatobasidium*

4. Basidia little wider than the supporting hyphae 5

Basidia 2–3 times the width of the supporting hyphae 6

5. Basidia suburniform; sterigmata 4, small and horn-like, about one-fifth to one-quarter the length of the metabasidium; (Spores sometimes becoming transversely septate and possibly repetitive as suggested by marked variation in spore size; sclerotia present; saprobic in soil; no known conidial state) . . . . *Waitea*

Basidia not constricted about the middle, subcylindrical or barrel-shaped; sterigmata (2–)4(–7), large, subcylindrical, about as long as or longer than the metabasidium; (Spores repetitive; sclerotia often present; saprobic in soil or on wood, or parasitic on plant parts in or near soil; no known conidial state) . . . . *Thanatephorus*

6. Metabasidia divided apically by incomplete cruciate septa; sterigmata 4; (Gloeocystidia present; spores repetitive; saprobic) . . . . *Metabourdotia*

Metabasidia not septate 7

7. Basidia subglobose or obpyriform, abruptly narrowed at the attachment; gloeocystidia and cystidia absent; (Sterigmata commonly 4, sometimes fewer or more; spores repetitive; sclerotia present or absent; commonly forming reticulate-pruinose web-blights on aerial parts of plants, but also saprobic in soil and rotten wood; no known conidial state) . *Ceratobasidium*

Basidia broadly clavate on a tapering narrow attachment; gloeocystidia and/or cystidia usually present; (Sterigmata 4; spores repetitive; sclerotia absent; saprobic, forming waxy to arid fructifications with basidia arising almost directly from repent basal hyphae; no known conidial state) . . . . *Oliveonia*

METABOURDOTIA

Metabourdotia Olive (1957: 429, f. 1–24).

The genus is at present monotypic, with *M. tahitiensis* Olive as its designated type species (Fig. 3).

Fructification sebacinoid, resupinate, thin, waxy-pruinose. Basidia arising from the basal hyphae, broadly clavate with a tapering base or rarely obovate, divided apically by incomplete cruciate septa and bearing 4 stout subcylindrical sterigmata nearly the same length as the metabasidium and tapering at their apices. Basidiospores smooth, hyaline, not amyloid, repetitive. Gloeocystidia present, with yellowish contents when mature. Dendrophyses present, some with enlarged bases. Hyphae hyaline, without clamp connexions.

OLIVEONIA

Oliveonia Donk (1958a: 20).
Heteromyces Olive (1957: 432, f. 25–30).
Hydrabasidium Parker-Rhodes (1954: 325, 338), nom. nud.

Olive typified the genus *Heteromyces* by *Sebacina fibrillosa* Burt (Fig. 4). As the generic name *Heteromyces* was preoccupied, Donk replaced it by *Oliveonia* with the same type species.

Fructification sebacinoid, resupinate, thin, waxy to arid. Basidia arising from the basal hyphae, broadly clavate with a long tapering base or rarely obovate, with an undivided metabasidium bearing (2–)4(–5) stout tapering sterigmata about half as long as the metabasidium or rarely about the same length. Basidiospores smooth, hyaline, not amyloid, repetitive. Cystidia and/or gloeocystidia present or absent. Hyphae hyaline with or without clamp connexions.

In material of the type species some of the probasidia had what appeared to be a partial or complete annulus of variable position, as indicated by a line of less intense staining; their presence was confirmed by colleagues but their nature remains in doubt.

The type species and *O. pauxilla* (Fig. 5) possess cystidia and/or gloeocystidia. However, *Corticium atratum* Bres. (Fig. 20) lacks cystidiform organs but in all other respects appears to fit the diagnosis of *Oliveonia*, which has been emended accordingly. The genus is still distinguishable by its broad basidia with long tapering bases that arise from a scanty layer of basal hyphae.

KEY TO SPECIES

1. Spores (3–)4–5.5 × 7–9(–12) μ, cylindric-oblong or broad ellipsoid; submerged gloeocystidia and emergent cystidia (often with a denser apex) present; clamp connexions present . . . *O. fibrillosa*

Spores 3–4(–5) × 7–10(–12) μ, ellipsoid or slightly sigmoid; gloeocystidia (or cystidia—the evidence is not clear) mostly emergent; clamp connexions absent . . . . *O. pauxilla*

Spores 5.5–6 × 7.5–10.5 μ, uniguttulate, subglobose with a long attenuated apiculus, or pyriform; cystidiform organs absent; clamp connexions present; basidia becoming deeply pigmented . . . . *O. atrata*

NOMENCLATOR OF INCLUDED SPECIES

Oliveonia atrata (Bres.) *comb. nov.*

Corticium atratum Bresadola (1896: 290). — *Ceratobasidium atratum* (Bres.) Rogers *apud* Martin (1941: 262); Rogers & Jackson (1943: 272); Wakefield (1952: 64, f. 36).
Tulasnella metallica Rick (1934: 169).
Ceratobasidium plumbeum Martin (1939: 513, f. 21–27).

OLIVEONIA FIBRILLOSA (Burt) Donk (1958a: 20).

Sebacina fibrillosa Burt (1926: 335). — *Heteromyces fibrillosus* (Burt) Olive (1957: 433, f. 25-30). — *Ceratobasidium fibrillosum* (Burt) Rogers & Jackson (1943: 327); Martin (1948: 113, f. 1). *Peniophora heterobasidioides* Rogers (1935: 30, f. 15).

OLIVEONIA PAUXILLA (Jacks.) Donk (1958a: 20); Warcup & Talbot (1962: 500, f. 2).

Corticium pauxillum Jackson (1950: 724, f. 9). — *Heteromyces pauxillus* (Jacks.) Olive (1957: 433).

CERATOBASIDIUM

Ceratobasidium Rogers (1935: 4); Martin (1952: 11); Donk (1958a: 17); Flentje, Stretton & Hawn (1963).

Pellicularia Cooke sensu Rogers (1943: 95-118; 1951: 111), pro parte.

Koleroga Donk (1958: 35).

By original designation the type species of *Ceratobasidium* is *C. calosporum* Rogers. The typification of *Pellicularia* has been discussed above: *Koleroga noxia* and *Pellicularia koleroga* sensu Rogers are based on the same part of the same type specimen.

Fructification resupinate, thin, arid to waxy, reticulate-pruinose to pellicular, consisting mostly of repent hyphae forming superficial webs with the hyphae branching at a wide angle, hyaline or dilutely coloured, sometimes with laminated walls, lacking clamp connexions. Basidia undivided, subglobose or obpyriform, abruptly narrowed at the attachment, 2–3 times the width of the supporting hyphae, arising directly from repent hyphae or at the apices of short discontinuous tufts of hyphae; sterigmata commonly 4, sometimes fewer or more, stout, subcylindrical, about the same length as the metabasidia, occasionally forking and sometimes developing a transverse septum away from the base. Basidiospores smooth, hyaline, not amyloid, repetitive. Saprobic or parasitic, some with sclerotial states.

KEY TO SPECIES

1. Parasitic as web-blights on aerial parts of vascular plants 2
Saprobic on rotten wood, soil or parts of plants in contact with soil 3

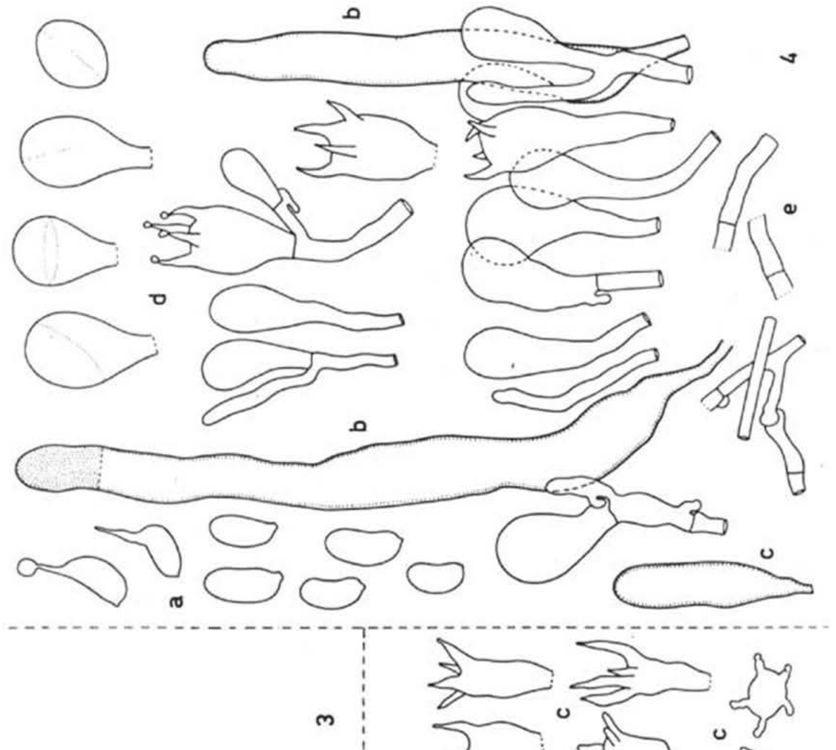
2. Producing brown sclerotia; spores asymmetrically ellipsoid with a flattened side, 9–13 × 5–7.5 μ . . . . *C. anceps*
Sclerotia present or absent; spores various (*Pellicularia koleroga* sensu Rogers; *Koleroga noxia* Donk; *Corticium stevensii* Burt; probably also *Corticium areolatum* Stahel, *Corticium invisum* Petch and *Corticium pervagum* Petch: see note below).

3. Spores under 12 μ long 4
Spores 23–36 × 3–3.5 μ, flexuous-cylindrical . . . . *C. calosporum*

4. Fructifications waxy-pruinose; metabasidia under 18 μ long 5
Fructifications subgelatinous drying to a film; metabasidia over 18 μ long; (Spores broad ellipsoid often with one side flattened, 7.5–9.6 × 5–7 μ, the length less than 1.5 times the breadth) . . . . *C. obscurum*

EXPLANATION OF FIGURES 3–5

Figs. 3–5. — 3. *Metabourdotia tahitiensis*. Basidia and spores from the type specimen. — 4. *Oliveonia fibrillosa*. a. Spores. b. Cystidia. c. Gloeocystidium. d. Basidia and some annulate probasidia (see text). e. Hyphae. From the type of *Sebacina fibrillosa* Burt, New York Bot. Gdn Herb. (NY). — 5. *Oliveonia pauxilla*. a. Spores. b. Cystidia. c. Basidia. d. Hyphae.



Figs. 3–5

5. Spores broad fusiform to ovate-ellipsoid with one side flattened, 6.5–10 × 3.5–6 μ, the length usually 1.5–2 times the breadth . . . . *C. cornigerum*
Spores oblong-cylindrical, 8–11 × 3.5–4 μ, the length more than twice the breadth *C. pseudocornigerum*

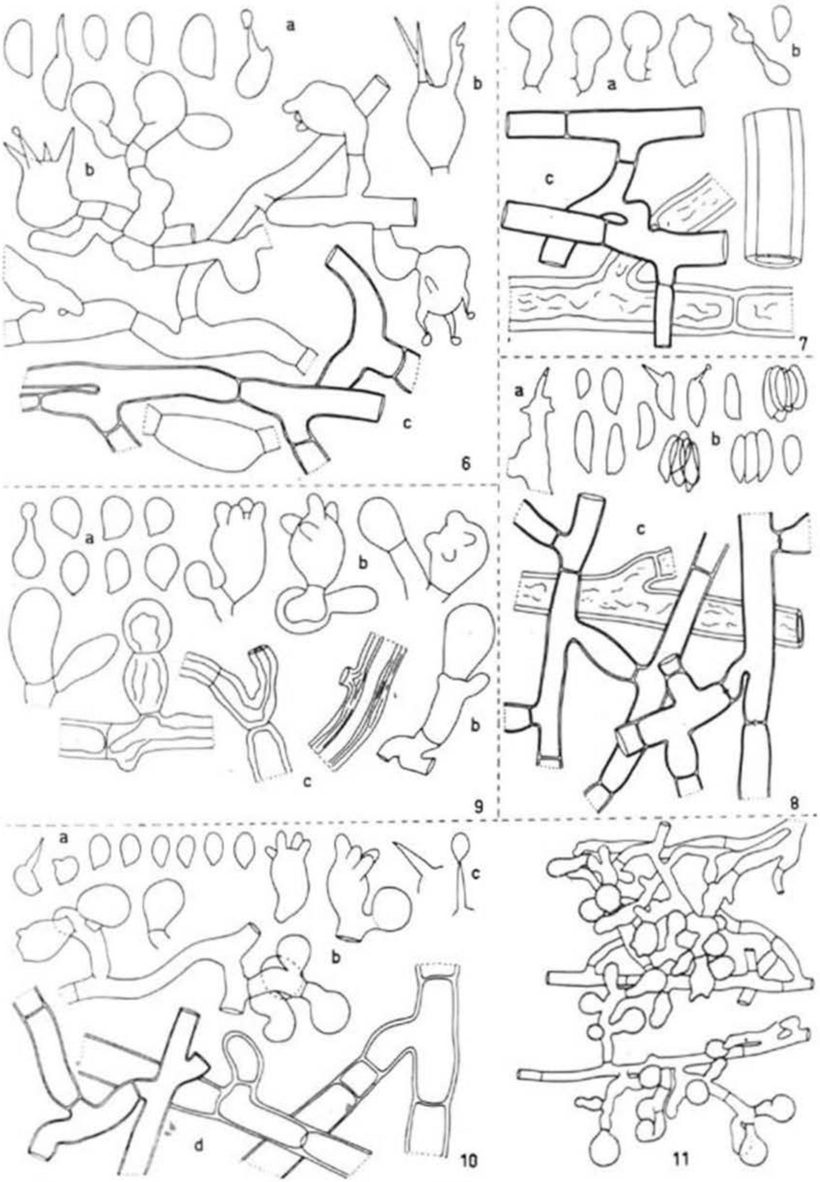
The aerial parts of a number of plants, particularly coffee, citrus, pomes and fig, are attacked by thread-blights or web-blights whose perfect states require re-examination before their classification can be discussed with confidence. Among these are *Corticium microsclerotia* Weber (1939; 1951), *C. areolatum* Stahel (1940), *C. invisum* Petch and *C. pervagum* Petch (1925). Donk (1958a) has tentatively placed the first two of these species and *Hypochnus sasakii* Shirai under *Thanatephorus*. The description and published figures of *C. areolatum* suggest *Ceratobasidium* to the present author, as also do Petch's two species.

Burt (1926) distinguished two species, *Corticium koleroga* (Cooke) Höhn. (on coffee in Mysore, Porto Rico, Colombia and Venezuela) and *Corticium stevensii* Burt (on apple, pear, quince and *Codiaeum* in Brazil, Trinidad and southern U.S.A.). Donk (1958a) maintained the separation of these two species under the genus *Koleroga*. Wolf & Bach (1927) and Rogers (1943) considered these as one species, which Rogers treated under *Pellicularia koleroga* Cooke. The writer has examined two specimens filed in Kew Herbarium as *Corticium koleroga* on coffee leaves from Colombia and South India respectively and considers that Miss Wakefield was correct in stating on one of the herbarium sheets that the species from Colombia and Mysore were distinct.

The Colombia material (Fig. 8) collected by M. T. Dawe in 1916, was cited by Burt as *Corticium koleroga* and corresponds well with his description and illustrations of Cooke's type and other material. Marked variation in spore size suggested that some of the spores were repetitive, and unmistakable repetition was confirmed in two spores after a prolonged search. The basidia were all collapsed but in some instances sterigmata were found to be transversely septate. The spores were found to adhere frequently in groups of six, which would indicate that some basidia probably have six sterigmata. These features, together with the web-like fructification, are characteristic of *Ceratobasidium*, while the uncollapsed basidia shown in illustrations by Burt (1926), Wolf & Bach (1927) and Rogers (1943) are in my opinion no different from those of both *Ceratobasidium* and *Koleroga*. The other Kew specimen, on coffee leaves from South India, shows uncollapsed basidia typical of *Ceratobasidium*

EXPLANATION OF FIGURES 6–11

Figs. 6–11. — 6. *Ceratobasidium anceps*. a. Spores. b. Basidia. c. Hyphae. On *Pteridium aquilinum* leaves, E. M. Wakefield, Sept. 1931, Herb. R. Bot. Gdns Kew (K). — 7. As *Corticium koleroga* on leaves of coffee, Anamalais, South India, 1921, Herb. R. Bot. Gdns Kew (K). a. Probasidia. b. Spores. c. Hyphae. — 8. As *Corticium koleroga* (cited by Burt) on coffee leaves, M. T. Dawe, Colombia, 1916, Herb. R. Bot. Gdns Kew (K). a. Collapsed basidium showing septate sterigma. b. Spores. c. Hyphae. — 9. *Ceratobasidium obscurum*. a. Spores. b. Basidia. c. Hyphae, some with laminated walls. From the type specimen on *Ulmus*, D. P. Rogers 291, New York Bot. Gdn Herb. (NY). — 10, 11. *Ceratobasidium cornigerum*. — 10. a. Spores. b. Basidia, c. Sterigmata. d. Hyphae. From bark of *Ulmus*, D. P. Rogers 220, New York Bot. Gdn Herb. (NY). — 11. Plan view of basidia and hyphae in culture.



Figs. 6–11

but spores of a different shape and size from those in the Colombia material (Fig. 7).

It is considered that Donk differentiated *Koleroga* from *Thanatephorus* for very sound reasons, but apparently kept it distinct from *Ceratobasidium* largely because spore repetition had not been reported in the coffee blights. My conviction is that *Koleroga* should be placed in synonymy under *Ceratobasidium* and that the perfect states of the various web-blights need re-investigation with fresh collections before some species can be satisfactorily classified. The saprobic species of *Ceratobasidium* are better known. *Ceratobasidium obscurum* Rogers (1935) was correctly described as having hyphae with multilamellate walls; this feature is also found in some cultural strains of *C. cornigerum* (Warcup & Talbot, unpublished data) and is therefore not a satisfactory differential character.

NOMENCLATOR OF INCLUDED SPECIES

CERATOBASIDIUM ANCEPS (Bres. & Syd.) Jackson (1949: 243, f. 1., pl. 1–3); Wakefield (1952: 63); Boidin (1958: 103). (See Fig. 6).

Tulasnella anceps Bres. & Syd. *apud* Sydow (1910: 490). — *Corticium anceps* (Bres. & Syd.) Gregor (1932: 464; 1935: 401, f. 1–11).
Ceratobasidium vagum (B. & C.) Pilát sensu Pilát (1957: 81).
Sclerotium deciduum Davis (1919: 689), nom. anam.

CERATOBASIDIUM CALOSPORUM Rogers (1935: 5, f. 1); Martin (1952: 14).

CERATOBASIDIUM CORNIGERUM (Bourd.) Rogers (1935: 5, f. 2); Martin (1952: 13, f. 1); Boidin (1958: 102); Christiansen (1959: 48, f. 42). (See Figs. 10, 11).

Corticium cornigerum Bourdot (1922: 4); Bourdot & Galzin (1928: 241, f. 74).

CERATOBASIDIUM OBSCURUM Rogers (1935: 6, f. 3). (See Fig. 9).

CERATOBASIDIUM PSEUDOCORNIGERUM Christiansen (1959: 46, f. 41).

THANATEPHORUS

Thanatephorus Donk (1956a: 376; 1958a: 28); Eriksson (1958c); Christiansen (1960); Warcup & Talbot (1962: 500); Flentje, Stretton & Hawn (1963).
Pellicularia Cooke sensu Rogers (1943), pro parte.

Donk typified the genus *Thanatephorus* by *Hypochnus solani* Prill. & Delacr., which he regards as synonymous with *Hypochnus cucumeris* Frank; this same species is commonly known as *Pellicularia filamentosa* (Pat.) Rogers, though Donk has suggested that *Hypochnus filamentosus* Pat. may not be the the same species as *Hypochnus cucumeris*. The mycelial state is *Rhizoctonia solani* Kühn.

Typically parasitic on plant parts in or near soil but often saprobic in soil or on rotten wood, forming a rhizoctonia-state and often forming sclerotia. Fructification resupinate, pruinose-pellicular, flaky to somewhat tufted or almost hypochnoid. Hyphae wide (sometimes up to 17 μ), branching at a wide angle and often forming cruciform cells, monomitic; basal hyphae longer-celled and often coloured and thick-walled; ascending hyphae shorter-celled, thin-walled, barrel-shaped, bearing basidia in discontinuous clusters of small asymmetrical cymes or less typically racemes; clamp connexions absent. Basidia short, barrel-shaped to subcylindrical or obovoid, not urniform or constricted about the middle, about the same diameter as the supporting hyphae; sterigmata (1–)4(–7), straight, stout, reaching the same length as the metabasidia or longer, rarely becoming septate. Basidiospores capable of repetition, not amyloid, smooth, hyaline. No known conidial states.

Donk (1956a, 1958a) differentiated *Uthatobasidium* as comprising saprobic species without a rhizoctonia-state, while *Thanatephorus* species were said to be parasitic with a rhizoctonia-state and often sclerotia as well. In habit, both have the general aspect of *Botryobasidium*, with the system of ascending hyphae less well developed in *Thanatephorus*; the basidial features are alike in *Thanatephorus* and *Uthatobasidium*. It is questionable whether these distinctions are of generic value; *Thanatephorus cucumeris* is often on soil or on dead twigs lying on the ground. The presence or absence of a rhizoctonia-state is perhaps not as significant as it may seem to be; several described species of *Rhizoctonia*, on being induced to fruit, are known to produce perfect states belonging in a variety of genera in which the presence of a rhizoctonia-state has never been emphasized and is probably not common to all species. The whole question of the relationship between species of *Rhizoctonia* and perfect states requires intensive investigation before the mycelial features can be considered useful in taxonomy. The type species of *Uthatobasidium* (Fig. 15), it is true, approaches the hypochnoid habit of *Botryobasidium* and develops a semi-palisade hymenium, but this is definitely not so in *Corticium sterigmaticum* Bourd. (Fig. 14) which Donk has associated with *Uthatobasidium*; its basidia are in small cymes arising directly from the repent mycelium and, apart from having regularly 2-spored basidia, its structure is that of a typical *Thanatephorus*. *Corticium sterigmaticum* is accordingly transferred here to *Thanatephorus*.

Despite these reasons for hesitation in segregating *Thanatephorus* and *Uthatobasidium* it is considered that no useful purpose would be served at present by merging the two. Species of *Uthatobasidium* can usually be distinguished by their more hypochnoid habit and by the spores, which become pale yellow at maturity and are mostly biapiculate.

Donk (1958a) notes that *Hypochnus filamentosus* Pat. apud Pat. & Lagerh. is a nomen dubium and is not equivalent to *Pellicularia filamentosa* sensu Rogers; he points out that the former is not known to occur in soil but is found on leaves of *Dianthus* and *Amaryllis* in Ecuador, forming a *pinkish* fructification.

Exner (1953) recognised four special forms of *Pellicularia filamentosa* sensu Rogers (= *Thanatephorus cucumeris*), on the basis of cultural characters and the diseases produced, not on morphological differences in the perfect states. These were: *P. filamentosa* f. sp. *solani* (Kühn) Exner, *P. filamentosa* f. sp. *microsclerotia* (Matz) Exner, *P. filamentosa* f. sp. *sasakii* (Shirai) Exner and *P. filamentosa* f. sp. *timsii* Exner.

Flentje (1956, 1957) and Flentje & Saksena (1957) have recorded the development in culture of the perfect states of a number of strains of *Pellicularia filamentosa* sensu Rogers and *P. praticola*, derived from several hosts and differing in pathogenicity and cultural characters. The features differentiating *P. filamentosa* and *P. praticola* were enumerated. The combination *Thanatephorus praticola* was subsequently proposed in Flentje, Stretton & Hawn (1963), where nuclear behaviour in species of *Thanatephorus*, *Ceratobasidium* and *Waitea* was described. Saksena (1961a, 1961b) has also investigated nuclear phenomena in *Ceratobasidium praticola.*

Doubt has been expressed as to whether *Thanatephorus cucumeris* and *T. praticola* are different species (Luttrell, 1962; Whitney & Parmeter, 1963; Whitney, 1964). In *T. praticola* (Fig. 13) the sterigmata are considerably longer than in *T. cucumeris* (Fig. 12) when both are grown under similar cultural conditions. Reports on the fructifications of *T. praticola* have usually been drawn up from artificial cultures and it is certain that cultural conditions may cause the formation of abnormally long sterigmata in some species (e.g. *Ceratobasidium cornigerum* on maize-meal agar). Nevertheless, Kotila (1929) originally described *T. praticola* as it occurred naturally on alfalfa plants and also in agar culture and on potted alfalfa plants, and stated that the basidia, sterigmata and basidiospores were identical in all cases; very humid conditions were necessary for fructifications to develop. Flentje (1956), who was well aware of the cultural differences between *T. cucumeris* and *T. praticola*, had one strain of *T. cucumeris* in which the sterigmata could be lengthened experimentally to a maximum of 46.8 μ long by using different substrates and by increasing the relative humidity, and he concluded that sterigmatal length was of little value as a distinguishing character. However, Flentje (1952, 1956) has indicated differences between *T. cucumeris* and *T. praticola* in growth rate, colour and appearance of mycelium, hyphal width, subhymenial branching and spore size, which strongly suggest that two species are involved. Boidin (1958) found that these species differ in enzyme activity, while Saksena & Vaartaja (1961) were able to distinguish them by cultural behaviour and by the morphology of the 'chlamydospores' produced in their mycelia.

According to Donk (1958a) the majority of orchid mycorrhizal fungi would appear to be mycelial states of *Thanatephorus*. Some of these are described by Bernard (1909) under *Rhizoctonia* and others by Burgeff (1909) under "Orcheomyces"; this work is reviewed by Ramsbottom (1923). Curtis (1939) also deals with orchid mycorrhizal fungi and presents figures showing monilioid hyphae of the kind used by Saksena & Vaartaja (1960, 1961) for differentiating *Rhizoctonia* species.

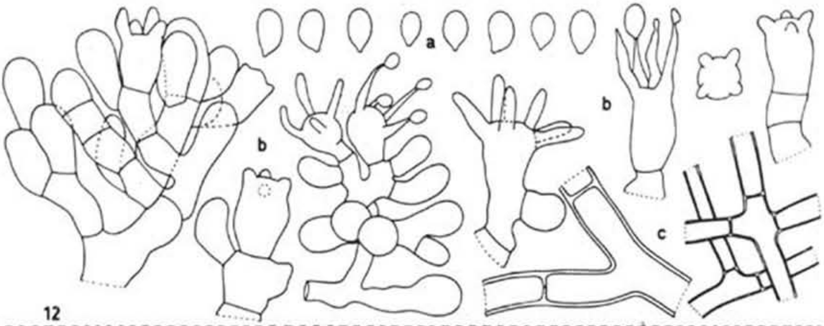
KEY TO SPECIES

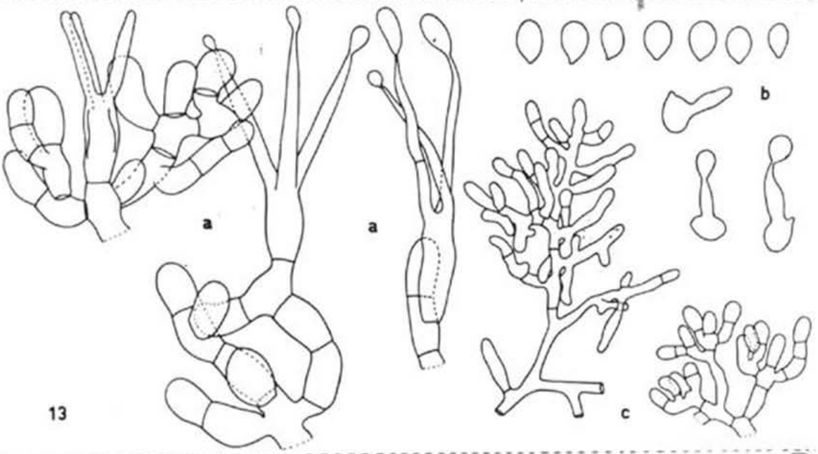
1. Sterigmata constantly 2 in number; (Spores subcylindrical, curved, 12–17 × 4.5–6 μ) *T. sterigmaticus*

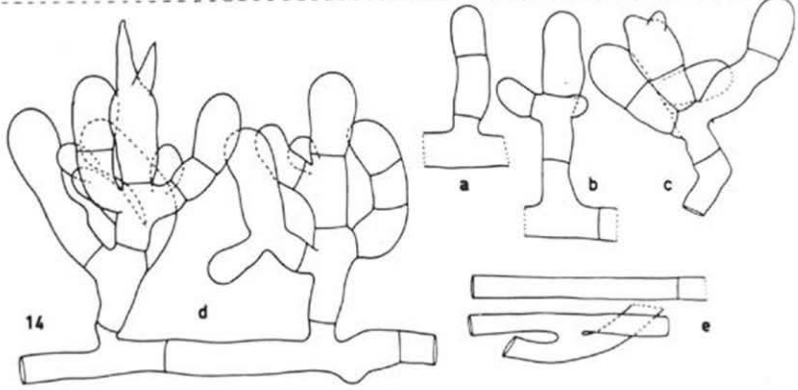
Sterigmata (1–)4(–7) in number; spores oblong-ellipsoid to broad obovate, usually widest at the distal end 2

EXPLANATION OF FIGURES 12–14

Figs. 12–14. — 12. *Thanatephorus cucumeris*. Culture a. Spores. b. Basidia. c. Hyphae. — 13. *Thanatephorus praticola*. Culture. a. Basidia. b. Spores. c. Two types of hymenial branching. — 14. *Thanatephorus sterigmaticus*. a–c. Stages in the formation of basidia. d. Two mature basidial clusters arising from a repent hypha. e. Hyphae. From material of *Ceratobasidium sterigmaticum*, D. P. Rogers 101, New York Bot. Gdn Herb. (NY).







Figs. 12–14

2. Hyphae up to 9 μ wide; mycelium in culture white, mealy, later greyish-brown; sterigmata (1–)3(–4), usually very much longer than the metabasidia; spores 7–9 × 4–6 μ; subhymenial branching often racemose. . . . . *T. praticola*

Hyphae up to 12(–17) μ wide; mycelium in culture felt-like, cinnamon-brown; sterigmata usually 4, about the same length as the metabasidia or shorter; spores 7–10(–12) × 4–7 μ; subhymenial branching mostly cymose . . . . *T. cucumeris*

NOMENCLATOR OF INCLUDED SPECIES

THANATEPHORUS CUCUMERIS (Frank) Donk (1956a: 376; 1958a: 28–34); Christiansen (1960: 68, f. 48); Warcup & Talbot (1962: 500, f. 3); Flentje, Stretton & Hawn (1963: 450–467).

Hypochnus cucumeris Frank (1883: 62).

Hypochnus solani Prillieux & Delacroix (1891: 220, f. 1). — *Botryobasidium solani* (Prill. & Delacr.) Donk (1931: 117); Rogers (1935: 18). — *Ceratobasidium solani* (Prill. & Delacr.) Pilát (1957: 81).

Rhizoctonia solani Kühn (1858: 224), nom. anam. — *Pellicularia filamentosa* f. sp. *solani* (Kühn) Exner (1953: 716).

Pellicularia filamentosa (Pat.) Rogers sensu Rogers (1943: 113, f. 11), pro parte; Cunningham (1953: 328, f. 3); Boidin (1958: 99); Flentje (1956: 343, f. 1–3); Talbot (1958: 136, f. 8). — *Ceratobasidium filamentosum* (Pat.) Olive sensu Olive (1957: 431).

THANATEPHORUS PRATICOLA (Kotila) Flentje *apud* Flentje, Stretton & Hawn (1963: 451).

Corticium praticola Kotila (1929: 1065, f. 5, 6); Rogers (1943: 115); Flentje (1952: 892); Boidin (1958: 100). — *Pellicularia praticola* (Kotila) Flentje (1956: 353, f. 2). — *Ceratobasidium praticola* (Kotila) Olive (1957: 431); Saksena (1961a: 717; 1961b: 749); not validly recombined.

Rhizoctonia praticola Saksena & Vaartaja (1961: 637), nom. anam.

Thanatephorus sterigmaticus (Bourd.) *comb. nov.*

Corticium sterigmaticum Bourdot (1922: 4); Bourdot & Galzin (1928: 240, f. 73) — *Ceratobasidium sterigmaticum* (Bourd.) Rogers (1935: 7, f. 4).

Uthatobasidium sect. *Ypsilonidium* Donk (1958a: 21)—type species; no combination formally made.

UTHATOBASIDIUM

Uthatobasidium Donk (1956a: 376; 1958a: 21); Eriksson (1958a: 58); Christiansen (1959: 48).

The genus is typified by *Hypochnus fusisporus* J. Schroet. which, according to Donk, has been identified by modern authors as *Hypochnus flavescens* Bonord., which he regards as a nomen dubium. For practical purposes material reliably determined as "*Pellicularia flavescens* (Bonord.) Rogers" (Fig. 15) corresponds with the generic type.

Saprobic on decaying wood and humus. Fructification pruinose-arachnoid then becoming floccose to hypochnoid, the basal hyphae giving rise to a relatively thick ascending layer of hyphae which branch at a wide angle and terminate in discontinuous to semi-palisaded clusters of basidia. Hyphae mostly hyaline but some basal ones becoming coloured, monomitic, lacking clamp connexions. Basidia cylindric-clavate, not constricted about the middle, about the same width as the supporting hyphae; sterigmata (2–)4(–5), stout, straight. Basidiospores smooth, hyaline to yellowish, repetitive, not amyloid, commonly biapiculate and broadly ellipsoid or fusoid to citriform in shape. Conidial states, rhizoctonia-states and sclerotia not recorded.

Uthatobasidium fusisporum and *U. ochraceum* have been merged by several authors under the specific epithet '*flavescens*' in the genera *Pellicularia* (Rogers, 1943) and *Ceratobasidium* (Olive, 1957). Donk separates them largely on the distinctive spores, as do Eriksson and Christiansen.

Corticium sterigmaticum Bourd. was placed in *Ceratobasidium* by Rogers (1935) and by some subsequent authors. This species was made the type of *Uthatobasidium* sect. *Ypsilonidium* Donk (1958a); it is here regarded as a species of *Thanatephorus*.

KEY TO SPECIES

1. Spores subglobose to obovate with a single apiculus, 8–10 × 5–6.5 μ . . . *U. ochraceum*
Spores broad fusiform to asymmetrically limoniform, usually biapiculate 2

2. [Spores 4.5–5.5 × 4–4.5 μ . . . . *U. citriforme*, see Species inquirendae]
Spores 8–16 × 5–10 μ . . . . *U. fusisporum*

NOMENCLATOR OF INCLUDED SPECIES

UTHATOBASIDIUM FUSISPORUM (Schroet.) Donk (1958a: 22).

Hypochnus fusisporus Schroeter (1888: 416).

Hypochnus flavescens Bonord. sensu Fuckel (1871: 291). — *Corticium flavescens* (Bonord.) Winter sensu auctt.; Bourdot & Galzin (1928: 239). — *Botryobasidium flavescens* (Bonord.) Rogers sensu Rogers (1935: 13, f. 8), pro parte; Eriksson (1958a: 59, f. 12). — *Pellicularia flavescens* (Bonord.) Rogers sensu Rogers (1943: 105), pro parte; Boidin (1958: 95). — *Ceratobasidium flavescens* (Bornord.) Olive sensu Olive (1957: 431).

UTHATOBASIDIUM OCHRACEUM (Massee) Donk (1958a: 23).

Coniophora ochracea Massee (1889: 137, pl. 47, f. 13). — *Botryobasidium ochraceum* (Massee) Donk *apud* Rogers (1935: 16, f. 7); Eriksson (1958a: 59, f. 12f–e).

Pellicularia flavescens (Bonord.) Rogers sensu Rogers (1943: 105), pro parte.

WAITEA

Waitea Warcup & Talbot (1962: 503, f. 4); Flentje, Stretton & Hawn (1963).

The genus is at present monotypic, with *W. circinata* Warcup & Talbot as its type species (Fig. 16).

Saprobic in soil. Fructifications composed of wide rhizoctonia-like basal hyphae giving rise to narrower, erect hyphae which produce irregular cymose clusters of basidium initials that are typically involute, circinate or coiled. Hyphae hyaline, without clamp connexions. Basidia little wider than the supporting hyphae, subcylindrical, frequently but not constantly constricted about the middle; sterigmata 4, curved, 1/4 to 1/5 the length of the metabasidium. Basidiospores hyaline, smooth, thin-walled, not amyloid, not repetitive (see note below), sometimes developing

1 or 2 transverse septa, widest at the distal end. Sclerotia produced in culture, pinkish or orange, sometimes turning brown. No conidial state known.

In general aspect *Waitea* is culturally similar to *Thanatephorus* but differs in its irregular and contorted hymenial branching, its suburniform basidia, small sterigmata and non-repetitive spores. The presence of marked variation in spore size in some preparations suggests that the spores of *Waitea* might be repetitive, but this has never been confirmed directly and the sterigmata are not of a type usually associated with spore repetition. The suburniform basidium is reminiscent of *Botryobasidium*, whose basidia, however, bear 6–8 small sterigmata and whose spores are fusoid to navicular or broadest towards the proximal end. Because *Waitea* has holobasidia without large sterigmata, and spore repetition has not been observed, it is here regarded as a member of the Corticiaceae.

BOTRYOBASIDIUM

Botryobasidium Donk (1931: 116; 1956a: 369; 1958a: 26); Rogers (1935: 10); Eriksson (1958a: 47; 1958b: 3); Christiansen (1960: 69).

Corticium sect. *Botryodea* Bourdot & Galzin (1911: 247; 1928: 238), pro parte.

Pellicularia Cooke sensu Rogers (1943: 95) pro parte.

The lectotype species of this genus is *Corticium subcoronatum* Höhn. & Litsch. (Fig. 17).

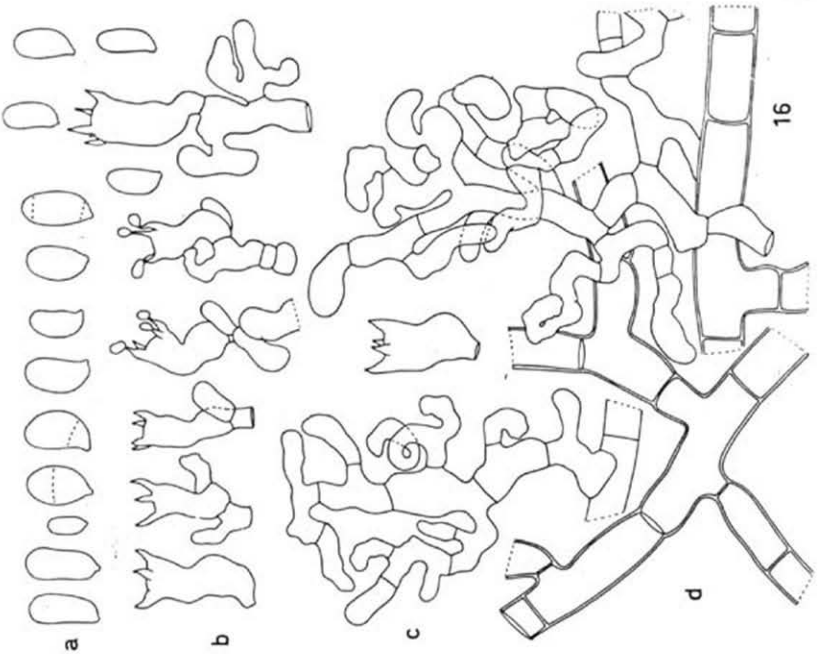
Saprobic on rotten wood and humus. Fructification arachnoid-pruinose becoming byssoid to hypochnoid. Hyphal system monomitic; basal hyphae long-celled with somewhat thickened yellowish walls, or hyaline; superior hyphae suberect, hyaline, thin-walled, staining strongly, with or without clamp connexions, branching at a wide angle, bearing terminal clusters of basidia usually cymosely. Basidia subcylindrical and typically constricted about the middle; sterigmata (4–)6(–8), small, curved. Basidiospores amygdaliform, widest at the proximal end, or fusoid or subnavicular, not amyloid, not repetitive, smooth (minutely ornamented in some species doubtfully placed in this genus). Cystidia present or absent. No rhizoctonia-state formed. Sclerotia absent. Conidial states of the form-genus *Oidium* (emend. Linder, 1942).

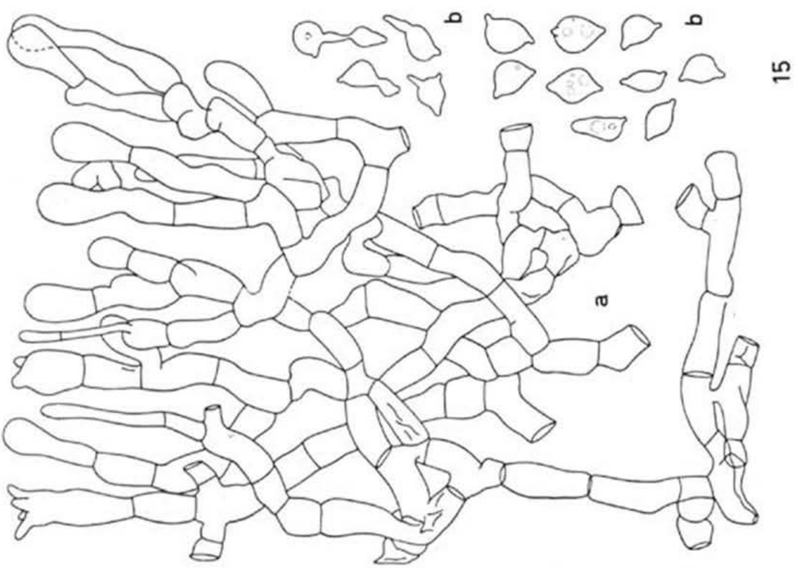
Eriksson (1958a; 1958b) has distinguished the following subgenera:

1. Subgenus *Botryobasidium*. Type: *Botryobasidium subcoronatum* (Höhn. & Litsch.) Donk. — Basal hyphae not notably different from the subhymenial ones. Basidium eventually suburniformly constricted about the middle, subventricose at the base.
2. Subgenus *Brevibasidium*. Type: *Botryobasidium botryosum* (Bres.) Erikss. — Basal hyphae not notably different from the subhymenial ones. Basidia short and proportionately wider than in subgenus *Botryobasidium*. Conidial states connected with this subgenus only and belong in the form-genus *Oidium* emend. Linder.

EXPLANATION OF FIGURES 15, 16

Figs. 15, 16. — 15. *Uthatobasidium fusisporum*. a. Vertical section through fructification. b. Spores. — 16. *Waitea circinata*. Culture. a. Spores. b. Basidia. c. Circinate basidium initials. d. Hyphae.





Figs. 15, 16

3. Subgenus *Dimorphonema*. Type: *Botryobasidium pruinatum* (Bres.) Erikss. — Basal hyphae much thicker-walled, darker and wider than the subhymenial ones. Subhymenial hyphae thin-walled, hyaline. Hyphae asperulate or smooth. Basidia more or less constricted.

KEY TO SUBGENERA AND SPECIES

1. Basal hyphae not notably different from the subhymenial ones (some may be thicker and slightly but not notably pigmented) 2
Basal hyphae much wider than the subhymenial ones and notably pigmented. Subhymenial hyphae hyaline, thin-walled. Basidia more or less urniform . Subgen. *Dimorphonema* . . . 12

2. Basidia suburniform; clamp connexions common . . . Subgen. *Botryobasidium* . . 3
Basidia not constricted, short, wide; mostly lacking clamp connexions
Subgen. *Brevibasidium* . . . 6

3. Simple, aseptate cystidia present 4
Cystidia absent 5

4. Cystidia 8–12.5 μ wide. Spores broad fusiform or subnavicular, 8–9 × 4–5 μ. Basal hyphae up to 15 μ wide . . . . *Pellicularia ansosa*
Cystidia 4–9 μ wide. Spores navicular, 5.5–6 × 2.5–3 μ. Basal hyphae up to 7 μ wide
B. pilosellum

5. Clamps present at all septa. Spores slender fusoid, 6.5–8.5(–15) × (2–)3–4(–5) μ. Conidial state *Oidium* sp., with conidia fusoid, 15–20 × 6–9 μ . . . . *B. subcoronatum*
Clamps present at some septa only. Spores narrow, navicular, 7–9 × 1.5–2.5 μ
B. angustisporum

6. Clamps present at all septa 7
Clamps absent 8

7. [Septocystidia 6–10 μ wide, with clamped septa, little encrusted. Clamps usually small. Spores fusiform, (8–)11–13(–16) × 3.5–4.5 μ . . *B. cystidiatum*, see Species inquirendae]
No cystidia. Clamps not small. Spores broadly navicular, biapiculate, 9–11 × 5–6 μ
B. medium

8. Septocystidia 9–11 μ wide, with coloured incrustation. Basal hyphae up to 19 μ wide. Spores subreniform or depressed-oblong, (5.5–)6–8 × 3–4.5(–6) μ . . *Pellicularia langloisii*
Cystidia absent 9

9. Spores within the limits of 7–9 × 2–3.5 μ, i.e. slender in proportion to length . . . 10
Spores 3–6 μ wide and broad in proportion to length 11

10. Spores narrow, almost allantoid, 8–9 × 2–3 μ; conidial state *Oidium curtisii* (Berk.) Linder; hyphae up to 15 μ wide . . . . *B. vagum*[1]
Spores slender navicular, 7–9 × 2.5–3.5 μ; conidial state *Oidium tomentosum* (B. & C.) Linder; basal hyphae up to 10 μ wide . . . . *B. lembosporum*
Spores slender navicular to subcylindric, 7–9 × 2.5–3.5 μ; conidial state *Oidium conspersum* (Link) Linder; basal hyphae up to 6–7 μ wide . . . . *B. conspersum*

11. Spores obliquely and narrowly ovoid, obtuse at both ends, 7.5–12 × 3.5–5 μ. No known conidial state . . . . *B. obtusisporum*
Spores broad fusiform, narrowed at both ends and biapiculate, 9–11 × 4.5–6 μ. No known conidial state . . . . *B. botryosum*[1]
Spores navicular or amygdaliform, 6–8 × 3–4 μ; conidial state *Oidium candicans* (Sacc.) Linder . . . . *B. candicans*

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[1] *Botryobasidium botryosum* has often been merged under *B. vagum*, but Eriksson (1958a: 54) differentiates them on the spore shapes and the absence of a conidial state in *B. botryosum*.

12 Clamps present at all septa. Basal hyphae up to 10 μ wide, very dark. Spores narrow ellipsoid, 5–6 × 2–3 μ. . . . . *B. heteronemum*
Clamps absent. Basal hyphae up to 20 μ wide, yellow. Spores obliquely ovoid or rarely subglobose, (4.5–)5–8 × (2.5–)3–4 μ 13

13. Hyphae asperulate . . . . *B. pruinatum* var. *pruinatum*
Hyphae smooth . . . . *B. pruinatum* var. *laeve*

NOMENCLATOR OF INCLUDED SPECIES

BOTRYOBASIDIUM ANGUSTISPORUM (Boidin) Eriksson (1958a: 48, f. 6); Donk (1958a: 26); not validly recombined.

Pellicularia angustispora Boidin (1957b: 119, f. a–c).

BOTRYOBASIDIUM BOTRYOSUM (Bres.) Eriksson (1958a: 53, f. 8); Donk (1958a: 26); Christiansen (1960: 70, f. 50).

Corticium botryosum Bresadola (1903: 99).
Pellicularia vaga (B. & C.) Rogers (1943: 110), pro parte.

BOTRYOBASIDIUM CANDICANS Eriksson (1958b: 6, f. 4, 5); Christiansen (1960: 72, f. 51).

BOTRYOBASIDIUM CONSPERSUM Eriksson (1958a: 133, f. 42); Donk (1958a: 26); Christiansen (1960: 75, f. 54, 54A).

BOTRYOBASIDIUM HETERONEMUM Eriksson (1958b: 13, f. 8).

BOTRYOBASIDIUM LEMBOSPORUM (Rogers) Donk (1958a: 26).

Pellicularia lembospora Rogers (1943: 109, f. 8).

BOTRYOBASIDIUM MEDIUM Eriksson (1958a: 54, f. 9, 10); Donk (1958a: 26).

BOTRYOBASIDIUM OBTUSISPORUM Eriksson (1958a: 57, f. 11); Donk (1958a: 26); Christiansen (1960: 73, f. 53).

BOTRYOBASIDIUM PILOSELLUM Eriksson (1958b: 4, f. 2); Donk (1958a: 26).

BOTRYOBASIDIUM PRUINATUM (Bres.) Parker-Rhodes (1956: 258), not validly recombined; Eriksson (1958a: 52, not validly recombined; 1958b: 8, f. 6); Donk (1958a: 26); Christiansen (1960: 76, f. 56).

Corticium pruinatum Bresadola (1903: 99). Not *C. pruinatum* (B. & C.) Speg. 1899. — *Pellicularia pruinata* (Bres.) Rogers *apud* Linder (1942: 170); Rogers (1943: 107), pro parte; Boidin (1958: 96, pl. 3 f. 9); Wakefield (1952: 63, f. 27), pro parte.

BOTRYOBASIDIUM PRUINATUM var. LAEVE Eriksson (1958b: 10, f. 7); Christiansen (1960: 78, f. 57).

BOTRYOBASIDIUM SUBCORONATUM (Höhn. & Litsch.) Donk (1931: 117); Rogers (1935: 12, f. 6); Eriksson (1958a: 50, f. 7); Christiansen (1960: 70, f. 49).

Corticium subcoronatum Höhnel & Litschauer (1907: 822). — *Pellicularia subcoronata* (Höhn. & Litsch.) Rogers (1943: 104, f. 7); Boidin (1958: 93); Cunningham (1953: 324, textf. 1 f. 6, textf. 2 f. 1).

BOTRYOBASIDIUM VAGUM (B. & C.) Rogers (1935: 17), pro parte; Donk (1958a: 26); Eriksson (1958a: 54, f. 8h).

Corticium vagum Berkeley & Curtis (1873: 179); Burt (1926: 295, f. 3) pro parte. — *Pellicularia vaga* (B. & C.) Rogers *apud* Linder (1942: 170); Rogers (1943: 110, f. 9), pro parte; Talbot (1958: 135, f. 6).
Ceratobasidium vagum (B. & C.) Pilát (1957: 81), misapplied.

BOTRYOHYPOCHNUS

Botryohypochnus Donk (1931: 118; 1958a: 24); Eriksson (1958b: 2); Christiansen (1960: 66).
Tomentella sect. *Tomentellastrum* subsect. *Botrytes* Bourdot & Galzin (1924: 137; 1928: 481, f. 121).

By original designation the type species is *Hypochnus isabellinus* Fr. [= *Botryohypochnus isabellinus* (Fr.) Erikss.] (Fig. 18).

Saprobic on rotten wood, humus or soil. Fructification arachnoid-pruinose then granular, thickening later to become loosely hypochnoid, with a monomitic hyphal system of basal and ascending hyphae which are hyaline then coloured especially at the base, wide, short-celled, septate without clamp connexions, branching at a wide angle. Basidia formed in botryose clusters in a thickening, discontinuous hymenium, short, plump to barrel-shaped, subovoid to subclavate, not urniform or constricted about the middle, of about the same diameter as the supporting hyphae; sterigmata (2–)4, stout, small, curved, much shorter than the metabasidium. Basidiospores hyaline to yellow-brown, not amyloid, not repetitive, globose or rarely slightly angular, asperulate with relatively long obtuse-cylindrical or obtuse-conical spines (smooth in one doubtful species). Walls of hyphae, basidia and spores staining strongly with aniline blue. No conidial states known with certainty.

Although *Tomentella* Pat. is somewhat similar to *Botryohypochnus* it differs in having hyphae with longer and narrower cells and especially in having long clavate basidia.

KEY TO SPECIES

1. Spores globose, yellowish, 6.5–10 μ diam. or 6.5–9 × 6.5–7.5 μ, with prominent blunt apiculus and numerous cylindrical-conical spines 1–3 μ long; fructifications isabelline *B. isabellinus*
(Spores globose, smooth, 10 μ diam.; fructification white . . . . *Tomentella granulata*)
(Spores biapiculate, somewhat hemispherical with a short ellipsoid body tapering abruptly into laterally-borne true and false apiculi, 10–11.5 × 6.5–7 μ; spore wall minutely tuberculate, often much thickened; fructification pinkish-buff to cream buff . . *Pellicularia biapiculata*)

NOMENCLATOR OF INCLUDED SPECIES

BOTRYOHYPOCHNUS ISABELLINUS (Fr. ex Schleich.) Eriksson (1958b: 2, f. 1); Christiansen (1960: 68, f. 47).

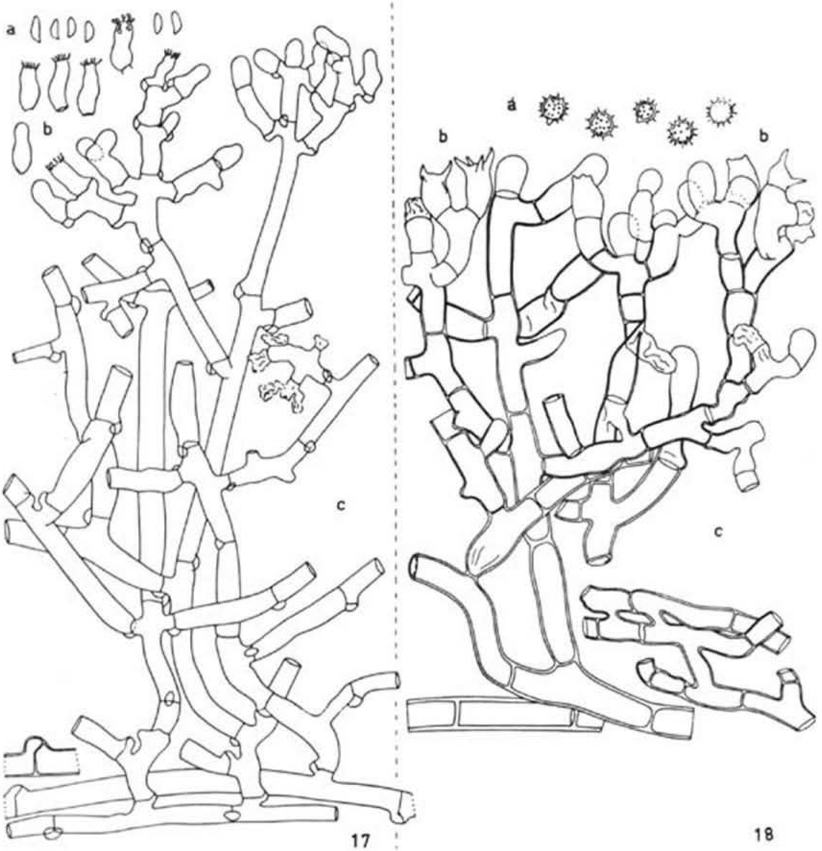
Hypochnus isabellinus Fries (1818: 281, pl. 6 f. 3). — *Hypochnus isabellinus* Fr. ex Schleicher (1821: 58); Fries (1849: 337). — *Botryobasidium isabellinum* (Fr. ex Schleich.) Rogers (1935: 11, f. 5). — *Pellicularia isabellina* (Fr. ex Schleich.) Rogers (1943: 99); Boidin (1957a: 281, f. 3).

SPECIES INQUIRENDAE VEL EXCLUDENDAE

The following species are either insufficiently known or cannot be classified satisfactorily at present.

CERATOBASIDIUM ALBUM Rick (1943: 219).

CORTICIUM ALBUM Dastur (1940: 92, pl. 1), nomen nudum; Rogers (1943: 116), incidental mention. Not *C. album* Britzelm. 1897.



Figs. 17, 18. — 17. *Botryobasidium subcoronatum*. a. Spores. b. Basidia. c. Vertical section through fructification. — 18. *Botryohypochnus isabellinus*. a Spore. b. Basidia. c. Vertical section through fructification.

Pellicularia alba Dastur (1946: 193), "sp. nov." — *Botryobasidium album* (Dastur) Venkatarayan (1950: 81).

PELLICULARIA ANSOSA Jacks. & Rogers *apud* Rogers (1943: 103, f. 6). Both Eriksson (1958b: 4) and Donk (1958a: 26) suggest that this species belongs in the genus *Botryobasidium*.

CORTICIUM AREOLATUM Stahel (1940: 129, fs. 1–7). Not *C. areolatum* Bresadola 1925. The published figures suggest that this is a species of *Ceratobasidium*.

PELLICULARIA ASPERULA Rogers (1943: 100, f. 2); Talbot (1958: 137, f. 37). The basidia are like those of *Botryobasidium* but the spores are asperulate.

PELLICULARIA BIAPICULATA Rogers *apud* Martin (1944: 71, f. 6). Donk (1958a: 24) has associated this with *Botryohypochnus*, while Rogers suggested that it is very close to *Pellicularia flavescens* (i.e. *Uthatobasidium fusisporum*). Although its spores are biapiculate they differ from those of *Uthatobasidium* in being non-repetitive and warted.

PELLICULARIA CHORDULATA Rogers (1943: 98, f. 1). Donk (1958a: 27) suggests that this may perhaps be a species of *Cristella*.

UTHATOBASIDIUM CITRIFORME Christiansen (1959: 49, f. 44).

BOTRYOBASIDIUM CORONATUM (Schroet.) Donk (1931: 117); Rogers (1935: 15, f. 9). Rogers (1943: 107) places this species as a synonym of *Pellicularia pruinata* (= *Botryobasidium pruinatum*). Eriksson (1958b: 7) suggests that *Corticium coronatum* sensu Höhnel & Litschauer could be identical with *Botryobasidium candicans*.

BOTRYOBASIDIUM CYSTIDIATUM (Rogers) Eriksson (1958a: 48; 1958b: 5, f. 3), not validly recombined.

Pellicularia cystidiata Rogers (1943: 101, f. 4). — *Suillosporium cystidiatum* (Rogers) Pouzar (1958: 31).

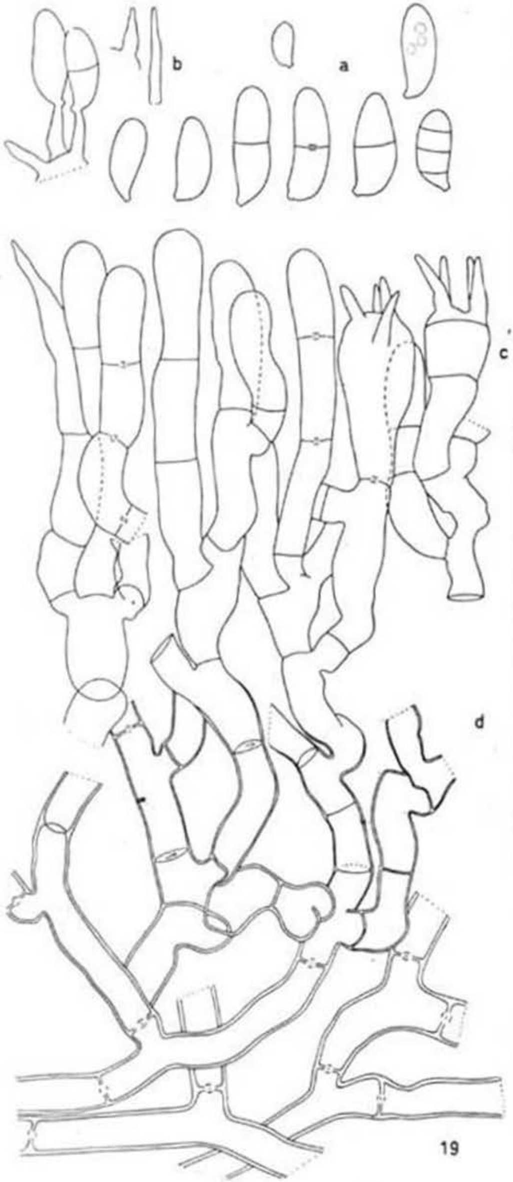
Type of the genus *Suillosporium* Pouzar. Donk (1958a: 27–28) suggests that this species should be placed in *Suillosporium* or better in *Jaapia* (Coniophoraceae) if the latter is emended.

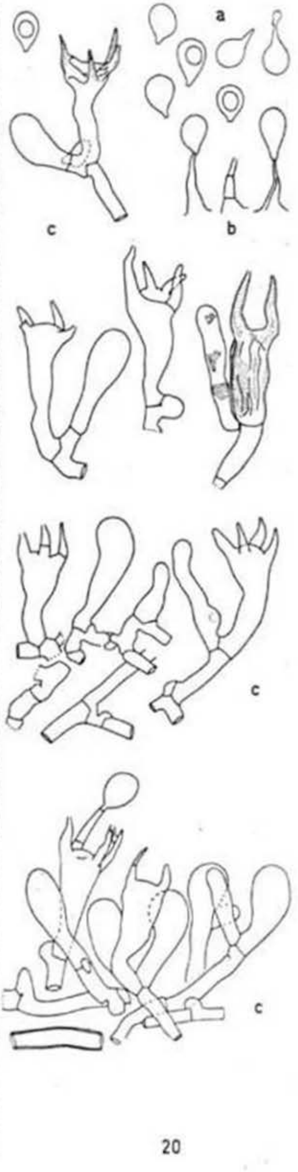
PELLICULARIA DIGITATA Rogers *apud* Martin (1944: 72, f. 10). Donk (1958a: 26) suggests that this might be a 4-spored species of *Botryobasidium*.

PELLICULARIA FODINARUM Talbot & Green *apud* Talbot (1958: 135, f. 7). A septocystidiate species possibly to be referred to the genus *Hyphoderma*.

EXPLANATION OF FIGURES 19, 20

Figs. 19, 20. — 19. *Corticium terrigenum*. a. Spores. b. Sterigmata. c. Basidium with secondary septation. d. Vertical section through fructification (full thickness not shown). From material leg. et det. E. M. Wakefield, as *Ceratobasidium terrigenum*, Herb. R. Bot. Gdns Kew (K). — 20. *Oliveonia atrata*. a. Spores. b. Sterigmata, some secondarily septate. c. Basidia and hyphae. From material of *Ceratobasidium atratum*, Seaver & Rogers 2036, New York Bot. Gdn Herb. (NY).





Figs. 19, 20

CORTICIUM INVISUM Petch (1925: 316). The description strongly suggests a species of *Ceratobasidium*. Type material examined had the general aspect of a *Ceratobasidium* but no satisfactory basidia or spores were found. Donk (1958a: 36) saw a similarity to *Koleroga noxia*.

PELLICULARIA LANGLOISII (Pat.) Rogers (1943: 101, f. 3).

Hypochnus langloisii Patouillard (1908: 3).

A septocystidiate species which Donk (1958a: 27) suggests may belong in *Botryobasidium*.

CORTICIUM MICROSCLEROTIA Weber (1939: 565, nomen nudum; 1951: 726, fs. 1–5).

Rhizoctonia microsclerotia Matz (1917: 117, f. 1–3), nom. anam. — *Pellicularia filamentosa* f. sp. *microsclerotia* (Matz) Exner (1953: 716), nom. anam.?

Tentatively placed by Donk (1958a: 29) as a species of *Thanatephorus*.

CERATOBASIDIUM MYCOPHAGUM Christiansen (1959: 45, f. 39). Apparently not a species of *Ceratobasidium*.

KOLEROGA NOXIA Donk (1958a: 35).

Pellicularia koleroga Cooke sensu Rogers (1943: 112, f. 10); Boidin (1958: 98, f. 25, pl. 3, f. 8). — *Corticium koleroga* (Cooke) Höhnel sensu Höhnel (1910: 395); Burt (1918: 123, f. 1; 1926: 292, f. 1). — *Botryobasidium koleroga* (Cooke) Venkatarayan (1949: 188).

A species of *Ceratobasidium*, but as more than one species seems to be involved fresh collections are necessary to distinguish them.

JAAPIA OCHROLEUCA (Bres.) Nannfeldt & Eriksson (1953: 184, f. 2).

Pellicularia ochroleuca (Bres.) Rogers (1943: 102, f. 5). — *Coniobotrys ochroleuca* (Bres.) Pouzar (1958: 32).

PELLICULARIA OTAGENSIS Cunningham (1953: 324, textf. 1 f. 7, textf. 2 f. 2). Appears from its description to be a species of *Botryobasidium* subgen. *Botryobasidium*.

CERATOBASIDIUM PEARSONII (Bourd.) Christiansen (1959: 46, f. 40).

Corticium pearsonii Bourdot (1921: 52, f. 1); Bourdot & Galzin (1928: 223). — *Paullicorticium pearsonii* (Bourd.) J. Eriksson (1958a: 66, f. 14d–f, j–l); Liberta (1962: 220, f. 1).
Corticium subinvisibile Rogers (1935: 28, f. 13).

CORTICIUM PERVAGUM Petch (1925: 316). The description suggests a species of *Ceratobasidium*. Type material examined had the general aspect of *Ceratobasidium* but the basidia were immature and the spores uncertain. Donk (1958a: 36) saw a similarity to *Koleroga noxia*.

HYPHODERMA POLONENSE (Bres.) Donk (1957b: 15); Christiansen (1960: 202, f. 109).

Kneiffia polonensis Bresadola (1903: 103). — *Peniophora polonensis* (Bres.) Höhnel & Litschauer (1906: 292); Bourdot & Galzin (1928: 315); Wakefield (1952: 61, f. 32); Boidin (1958: 139, f. 47, pl. 7, f. 12). — *Pellicularia polonensis* (Bres.) Boidin (1957b: 121).
Peniophora canadensis Burt (1926: 260).

CORTICIUM ROLFSII Curzi (1931: 306).

Pellicularia rolfsii West (1947: 69, f. 1).
Botryobasidium rolfsii Venkatarayan (1950: 82).
Sclerotium rolfsii Saccardo (1911: 257), nom. anam.

(Reports on a Symposium on *Sclerotium rolfsii* are published in Phytopathology **51**: 107–128. 1961).

CORTICIUM SALMONICOLOR Berkeley & Broome (1873: 71); Talbot (1951: 17, pl. 10).

Pellicularia salmonicolor (B. & Br.) Dastur (1946: 193). — *Botryobasidium salmonicolor* (B. & Br.) Venkatarayan (1950: 82).

This species is regarded as not related in any way to the group under discussion.

CORTICIUM SASAKII (Shirai) Matsumoto (1934: 119).

Hypochnus sasakii Shirai (1906: (319), fs. 1–3); Matsumoto (1934: 116, f. 1B, f. 2). — *Pellicularia filamentosa* f. sp. *sasakii* (Shirai) Exner (1953: 717).

This species is associated with *Thanatephorus* by Donk (1958a: 29).

PELLICULARIA SCABRIDA Cunningham (1953: 326, textf. 1 f. 4, textf. 3 f. 1). Possibly a species of *Botryobasidium* subgen. *Dimorphonema*.

CORTICIUM STEVENSII Burt (1918: 125, f. 2; 1926: 293, f. 2).
Associated with the genus *Koleroga* by Donk (1958a: 35), but here regarded as a species of *Ceratobasidium*; fresh collections are necessary to distinguish this species from other closely related web-blights.

CERATOBASIDIUM STRIISPORUM Rick (1943: 219).

PLEUROBASIDIUM TELAE Arnaud (1951: 194, f. 1B, C), nomen nudum; Donk (1956a: 371).

CORTICIUM TERRIGENUM Bresadola (1903: 99).

Ceratobasidium terrigenum (Bres.) Wakefield (1952: 64, f. 37). — *Hydrabasidium terrigenum* (Bres.) Parker-Rhodes (1954: 325), generic name not validly published.

This species, as represented by Miss Wakefield's collection in Kew Herbarium (Fig. 19), is not a *Ceratobasidium*. The fructification has a fleshy to membranous texture and attains a considerable thickness of ascending hyphae branched at a wide angle, without clamp connexions. The basidia, forming a semi-palisaded hymenium, may become secondarily septate below the apex and are clavate with

3–4 stout, straight sterigmata. The basidiospores, measuring 6.5–7.5(–9) × 16–24 μ, may become 1–3-septate after being shed; spore repetition was not seen.

PELLICULARIA ZEALANDICA Cunningham (1953: 322, textf. 1 f. 3). Possibly referable to *Hyphoderma*.

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ON SPORIDESMIUM TRIGONELLUM SACC.

M. A. Rifai

Botany Department, The University, Sheffield 10, England *

(With five Text-figures)

The genus *Oncopodiella* Arn., which was published without a Latin diagnosis, is validated. Its type species is identified with *Sporidesmium trigonellum* Sacc. and the new combination *Oncopodiella trigonella* (Sacc.) Rifai is proposed. This species is redescribed and illustrated from the type material and from a recent British collection.

During the 1963 Spring Foray of the British Mycological Society which was held at Cambridge, a collection of a hysteriaceous fungus was made on the bark of a fallen tree of *Ulmus* sp. When this collection was scrutinized under a low-power binocular microscope it was noticed that a curious hyphomycete was also present, growing on the innerside of the bark and forming barely visible colonies. It had dark brown dictyospores which were more or less trigonal in outline and each conidium bore 2–4 distinctive hyaline papillae. These conidia were produced singly as blown out ends of the short slender conidiophores which elongate by producing new growing points subapically causing the scars or the short cylindrical pegs left by the previous conidia to be pushed sideways. Therefore the apices of the mature conidiophores can be seen to bear several of these pegs, which are disposed rather irregularly.

It appears that this interesting fungus, which is new to the Hyphomycetes flora of Britain, has quite a wide distribution. Its occurrence in Belgium and Italy was recorded by Saccardo (1882, 1886) and more recently Arnaud (1954) reported it from France. The scarcity of records or collections of this species is probably due to its small size and rather inconspicuous colonies which make it rather difficult to discern in the field.

This species was first described by Saccardo (1882) as *Sporidesmium trigonellum* Sacc., based on a collection made in Belgium by Libert. The type species of the genus *Sporidesmium* Link ex Fr., however, has phragmosporous conidia (Ellis, 1958). Consequently, *S. trigonellum* and many other brown dictyosporous species included in *Sporidesmium* by Saccardo and other mycologists who followed him, cannot be retained here.

In an attempt to disentangle the taxonomic and nomenclatural confusions that exist in this complex of fungi, Moore (1959b) transferred a large number of species formerly classified as *Sporidesmium* to the genus *Piricauda* Bub. In emending the last named genus, however, Moore (1959a, 1959b, 1960) ignored the method of conidial development as well as the structure of the conidiophores of these fungi, two

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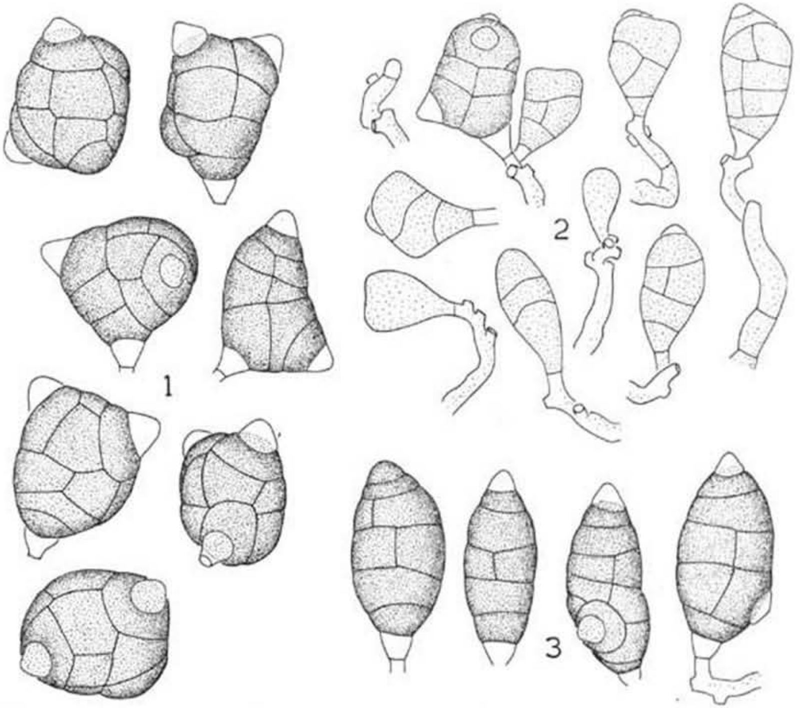
* Permanent address: Herbarium Bogoriense, Bogor (Java), Indonesia.

characters which in recent years have been found to be of paramount importance in the classification of Hyphomycetes (Hughes, 1953; Tubaki, 1958; Subramanian, 1963). Therefore it is not surprising that Moore's emendation of the genus *Piricauda* has not been accepted and most of the species which he transferred to it have subsequently been redistributed in several different genera such as *Monodictys* Hughes (Hughes, 1958; Jones, 1963), *Pithomyces* Berk. & Br. (Ellis, 1960), *Acrodictys* M. B. Ellis (Ellis, 1961) and probably some other genera. *Sporidesmium trigonellum* cannot also be considered to be congeneric with *Piricauda paraguayensis* (Speg.) Moore, the type and only species of the genus *Piricauda* (Hughes, 1960), because the conidia of these two species are produced by morphologically different kinds of conidiophores and in entirely different ways.

In 1954 Arnaud described and illustrated *Oncopodiella tetraedrica* Arn. gen. et spec. nov. which, however, was not validly published since no Latin diagnosis was



Figs. 1–3. *Oncopodiella trigonella*. — 1. Conidia. — 2. Young conidia and conidiophores. — 3. Abnormal conidia (from *Libert 432*, × 1250).

given either for the genus or for the species. The type specimen of this species *(G. Arnaud no. 767)* has not been available for comparison, but except for the slightly longer conidiophore measurement, Arnaud's brief French description and his illustration of its conidiophore and conidia wholly agree with Saccardo's original specimen of *S. trigonellum* and also with the more recent British collection. Since there seems to be noother genus that can accommodate *S. trigonellum*, in the following the generic name *Oncopodiella* is validly published by providing the necessary Latin diagnosis.

The monotypic genus *Oncopodiella* can be easily distinguished from the other brown dictyosporous Hyphomycetes genera by its peculiar type of conidiophore.

Oncopodiella Arn. ex Rifai, *gen. nov.*

Oncopodiella Arn. *in* Bull. Soc. mycol. Fr. **69**: 296. 1954 (sine diagnose latina).

Fungi imperfecti, hyphomycetes, saprophytici. Coloniae effusae vel punctiformes, atro-brunneae. Mycelium immersum ex hyphis septatis, brunneis, ramosis compositum. Conidiophora dispersa vel densa, simplicia, subhyalina vel pallide brunnea, 0–1-septata, gracilia, curta, recta vel flexuosa, per proliferationes successivas subapicales elongascentia. Conidia singula in apice conidiophori oriunda, subtrigona, obovoidea vel subglobosa, levia, breviter hyalino-papillata, sicca. — Species generis typica: [*Oncopodiella tetraedrica* Arn. =] *Sporidesmium trigonellum* Sacc.

Oncopodiella trigonella (Sacc.) Rifai, *comb. nov.*—Figs. 1–5.

Sporidesmium trigonellum Sacc. *in* Michelia **2**: 641. 1882 (ut *Sporodesmium*), basionym.—*Piricauda trigonella* (Sacc.) Moore *in* Rhodora **61**: 105. 1959.

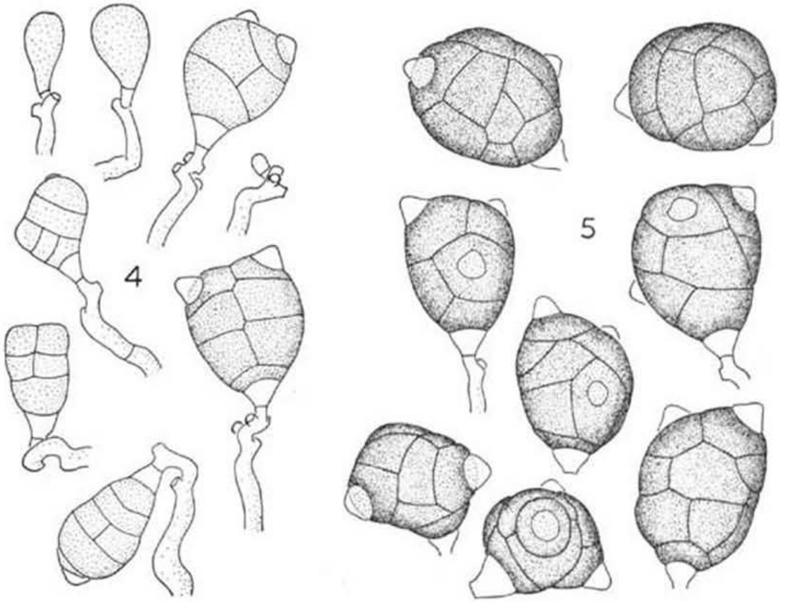
Oncopodiella tetraedrica Arn. *in* Bull. Soc. mycol. Fr. **69**: 296. 1954 (sine diagnose latina).

The colonies are blackish brown, effused but restricted, or minutely punctiform, often inconspicuous or appear only as dispersed black dust.

The mycelium is mostly immersed in the substrate, composed of pale brown to brown, branched, septate and smooth-walled hyphae 1.5–4 μ in diameter.

The conidiophores are solitary and dispersed or rather crowded, arising terminally or occasionally laterally from the immersed hyphae. They are short and delicate, smooth, thin-walled, unbranched, 0–1-septate, mostly flexuous, very rarely also straight, pale brown below, becoming paler to almost hyaline towards their apices, slender, 3–4 μ diameter at the base, gradually diminishing in width to about 1.2–2 μ diameter at the apex, and up to 25 μ long. These conidiophores elongate by subapical proliferation, producing new growing points which develop to one side of the previous conidium-producing apex. Ultimately the apical portion of each conidiophore may bear up to five or more conspicuous flat-topped short subcylindrical pegs, to which formerly conidia have been attached. No noticeable swelling takes place in this conidium-producing area.

The conidia are produced singly as blown out ends of the successively developed growing points of conidiophores. At first an obovoid conidial initial is blown out at the tip of the conidiophore and soon its rounded distal end flattens slightly and the future papillae begin to take their shape. In the meantime 2–5 transverse and longitudinal or oblique septa are formed and often there is a slight constriction at each septum. The originally colourless conidial initials gradually turn darker with



Figs. 4–5. *Oncopodiella trigonella*. — 4. Young conidia and conidiophores. — 5. Conidia (from *Webster & Rifai* s.n., × 1250).

age until ultimately they are dark reddish brown; under reflected light the mature conidia appear blackish brown or opaque and shining. At the distal end of the conidia two or four, mostly three prominent papillae can be observed which unlike the rest of the conidia usually remain hyaline or subhyaline. They are conical, 2.5–4.5 μ wide at the base and up to 4 μ high. The mature conidia are subtrigonal, broadly obovoid, subglobose or subangular, sometimes turbinate with a rounded base and flattened end, smooth-walled and excluding the papillae they measure 13.5–19 × 12–16 μ, occasionally with their width exceeding their length. They become detached rather easily, leaving behind the flat-topped short subcylindrical pegs.

Some abnormal conidia which are broadly fusiform and with only one or two papillae have also been observed.

HABITAT.—On dead bark of *Ailanthus*, *Ulmus*, and other trees.

DISTRIBUTION.—Belgium, France, Great Britain, Italy.

ILLUSTRATIONS.—Arnaud *in* Bull. Soc. mycol. Fr. **69**: fig. 13 Q, R. 1954; Moore *in* Rhodora **61**: pl. 1241, fig. 16. 1959.

SPECIMENS EXAMINED.—BELGIUM: Malmédy, on the bark of *Ailanthus glandulosa*, s. dat., *Libert 432* (PAD, type of *Sporidesmium trigonellum* Sacc.). — GREAT BRITAIN: Cambridgeshire, Devil's Ditch (near Stetchworth), on the innerside of the bark of a fallen tree of *Ulmus* sp., 18 May 1963, *Webster & Rifai s.n.* (Herb. Mycol. Sheff. Univ. no. 2687, IMI, BO).

For making available the type specimen of *Sporidesmium trigonellum* I am indebted to Professor C. Cappelletti (Padua). I would like to thank Drs M. B. Ellis (Kew) and J. Webster (Sheffield) for their most valuable advice and helpful criticism during the preparation of the manuscript and to Mr A. O. Hulton (Sheffield) for kindly correcting the Latin diagnosis. This work was supported by a grant from the British Council (The Colombo Plan Technical Assistance Cooperation Scheme), to which acknowledgement is also made.

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SPORE DEVELOPMENT IN THE FORM-GENUS PHOMA

G. H. Boerema
Plantenziektenkundige Dienst, Wageningen

(With 31 Text-figures)

Diagrams drawn after electron-micrographs of the spore formation in *Phoma* spp. are shown. The manner in which the spores are formed, called here the 'monopolar repetitive budding process', is discussed.

In the present paper a number of diagrams are given of the spore-forming process in *Phoma* spp. drawn after numerous micrographs obtained by Ir. J. G. Brewer (see Brewer & Boerema, 1965[1] in an electron-microscopic study. These diagrams explain the various pictures of the spore formation in the form-genus *Phoma* as seen with the light-microscope.

The sporogenous tissue in the pycnidia of *Phoma*-like fungi is extremely small-celled and hyaline. This explains the differences in interpretation of the light-microscope observations on the spore-forming process in this kind of fungi (Klebahn, 1933; Goidànich & Ruggieri, 1947; Boerema, 1964; Boerema & van Kesteren, 1964; Sutton, 1965). It is rather like the case of a Papua who sees a Western style house for the first time from a distance. In spite of his sharp eyes he must look at it more closely to understand the details he is seeing. In the case of the spore formation in *Phoma*-like fungi such an inspection at close quarters was made possible through the electron-microscope.

As described by Brewer & Boerema (l.c.) the spore-forming process in *Phoma* spp. may be characterized as a monopolar repetitive budding of the small, undifferentiated inner cells of the pycnidial wall. Chains of more than ten spores can be born by a single parent cell (Figs. 24, 28). In the electron-micrographs the spore first produced by the parent cell can always be recognized by the fact that the outer (electron-transparent) layer of the bud is not connected with the slimy coat of the other spores in the pycnidial cavity. The development of the first spore starts as a papilla-like protrusion which gradually acquires the shape of a bud (Figs. 1–10). On abstriction of the first spore, the wall at the top of the parent cell expands into a more or less thick, rim-like fold (Figs. 11–14). The initials of the subsequent spores are shaped like a bud from the start (Figs. 15, 16). With the repetition of the budding process either the apical fold of the wall of the parent cell becomes increasingly thicker or a complex of folds is seen to develop (Figs. 17–23). This structure seen under the light-microscope makes the parent cell often resemble a phialide (Sutton, 1965) or even an annellophore. The gradual thickening of the wall at the top of the parent cell may also be the cause

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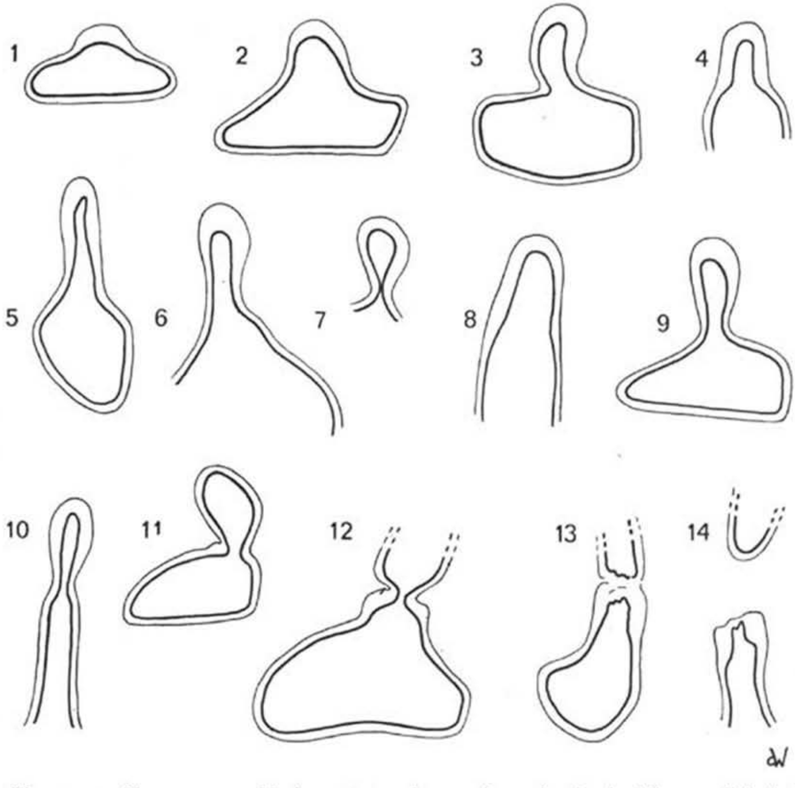
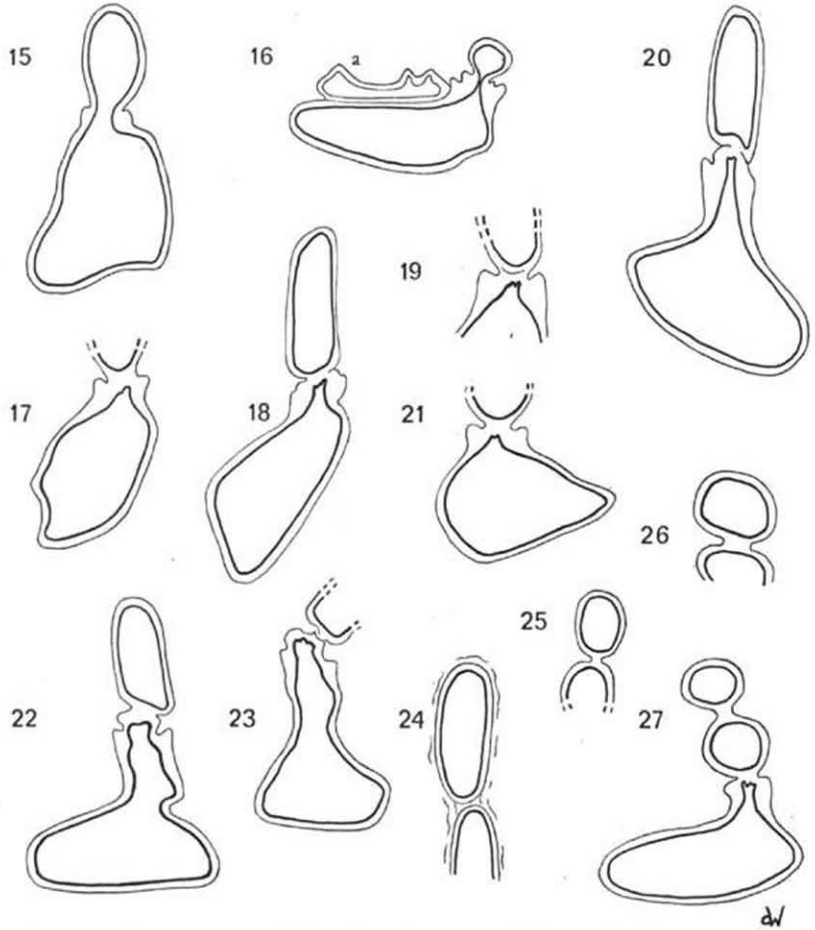
[1] Except in Figures 24, 28, the slimy matter surrounding the spores (the disintegrated electron-transparent layer of the spore-initial + the 'cloudy substance') has not been drawn.



Figs. 1–14. *Phoma* spp. — Various stages of spore formation by budding on "virginal" parent cells.
Diagrams drawn after electron-micrographs; magnification ca. × 2500.

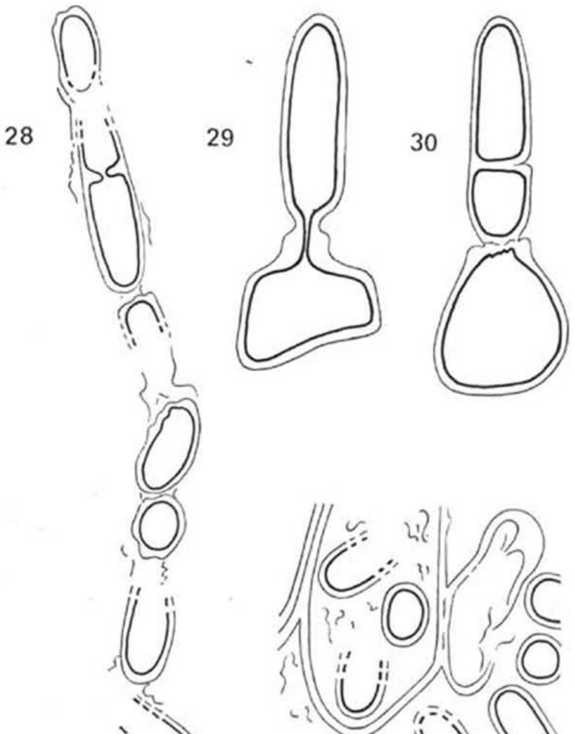
of the phenomenon that a bud, seen under the light-microscope, seems to be connected with the parent cell only by a thin thread of plasm (Figs. 16, 19).

The electron-microscopic study by Brewer & Boerema (l.c.) reveals that the differentiation of the spore-wall during the process of budding takes place in very gradual stages. This may explain why, under the light-microscope, the wall of the spore-initial is often difficult to distinguish. This is particularly true in cases in which the protoplasm has been stained. Under the light-microscope the spore then gives rather the impression of having been produced by an extrusion of a part of the plasm through a small pore in the thickened apex of the parent cell (Goidànich & Ruggieri, 1947; Boerema, 1964: "porogenous").



Figs. 15–27. *Phoma* spp. — Various stages of spore production by budding on parent cells which have previously produced spores. — 16a. Old collapsed parent cell. — 22, 23. Deeply seated parent cells with neck-like outgrowths resembling sporophores. — 24. Two spores connected by a slimy mass. — 20, 21. Deformed "double" spores produced by extremely rapid budding.
Diagrams drawn after electron-micrographs; magnification ca. × 2500.

Spore-forming cells deeply seated in the meristematic tissue develop protuberances (pseudo-sporophores), on which the spores arise by budding (Figs. 22, 23). If spore formation is carried out in rapid succession, a new bud may be produced



Figs. 28–31. *Phoma* spp. — 28. A chain of spores connected by a slimy mass, showing one large, septate spore between smaller, continuous ones. — 29, 30. Production of large spores which on abstriction usually become more-celled by "euseptation". — 31. Central part of a pycnidial primordium, a loose cell containing three (endogenous?) spores.
Diagrams drawn after electron-micrographs; magnification ca. × 2500.

at the top of the parent cell before the former has been detached, which may give rise to deformed "double" spores (Figs. 25–27).

In mature pycnidia of *Phoma* spp. septate spores also often occur.[2] These more-celled spores develop in the same way as the continuous ones (Fig. 28), generally appearing as relatively large buds (Fig. 29) which become septate immediately on abstriction (Fig. 30) or else later: euseptation, see Brewer & Boerema (l.c.).

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[2] The percentage of more-celled spores is influenced by conditions governing the growth, inclusive of the matrix, but specific and racial features are also involved. Some species *in vivo* produce chiefly septate spores, whereas *in vitro* the spores are for the greater part continuous.

Finally, it should be noted that the electron-microscope observations have strengthened the opinion that the first spores in a pycnidium of a species of *Phoma* may be of endogenous origin (Fig. 31; compare Boerema, 1964).

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REVIEW

D. G. Cooney & R. Emerson, *Thermophilic Fungi. An account of their biology, activities and classification.* (W. H. Freeman and Company, San Francisco, London, 1964). Pp. xii + 188, 74 text-figures, 6 plates (4 black and white, 2 in colour), 8 tables. Price 36/–.

This book, written by two distinguished American mycologists, provides an elaborate account of the morphology and biology of all known thermophilic fungi. The authors do this in a most readable form. The book is divided into three parts. Part I includes a brief introduction and a description of the methods used for the isolation and maintenance of thermophiles. More than half of the book consists of Part II, that deals with the occurrence, morphology, cultural characteristics, taxonomy and temperature relations of the investigated fungi. Fifteen taxa are described, including four new species and three new varieties of existing species. A short diagnosis is given of every described species. Illustrations in the form of good line drawings are provided for all species. Macroscopic features of three species are illustrated by excellent colour plates. Part III is devoted to general biology and practical importance of thermophilic fungi. While this book was in the press, several new reports of thermophilic fungi came to the attention of the authors. A short account of these fungi with their references is given in the Addenda.

There are a few debatable points in this very useful monograph, especially in the chapters dealing with taxonomy and nomenclature. For instance it seems rather doubtful to me that the fungus described as *Torula thermophila* really belongs to *Torula*. In the description of *Thermoascus thermophilus* two different species are mixed up. For the perfect stage of *Penicillium duponti* the authors use erroneously the invalid name *Talaromyces duponti* (Griffon et Maublanc) Apinis. Nevertheless this is a most notable book. Its greatest value, however, lies in the very clear descriptions, while the many references at the end of the book make this an excellent reference book. The treatment is a practical and useful one. The book is well produced on good quality paper. In view of the steadily increasing interest in thermophilic fungi there can be no question of the wide usefulness of this book.

A. C. Stolk

INDEX

New names are in bold-face type. Subdivisions of genera are indicated by the sign §, illustrations by an asterisk *.