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# STUDIES OF 'PELLICULARIA' AND ASSOCIATED GENERA OF HYMENOMYCETES

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### (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. — I. 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. 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
4. Basidia little wider than the supporting hyphae
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)
6. Metabasidia divided apically by incomplete cruciate septa; sterigmata 4; (Gloeocystidia present; spores repetitive; saprobic)
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

### 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  $(3-)4-5.5 \times 7-9(-12) \mu$ , cylindric-oblong or broad ellipsoid; submerged gloeocystidia and emergent cystidia (often with a denser apex) present; clamp connexions present O. fibrillosa

Spores  $3-4(-5) \times 7-10(-12) \mu$ , ellipsoid or slightly sigmoid; gloeocystidia (or cystidia—the evidence is not clear) mostly emergent; clamp connexions absent . . . . . . O. pauxilla Spores  $5.5-6 \times 7.5-10.5 \mu$ , uniguttulate, subglobose with a long attenuated apiculus,

## 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

I. Parasitic as web-blights on aerial parts of vascular plants	2 3
2. Producing brown sclerotia; spores asymmetrically ellipsoid with a flattened side	.,
$9-13 \times 5-7.5 \mu$	s a h
3. Spores under 12 $\mu$ long	4 n
4. Fructifications waxy-pruinose; metabasidia under 18 $\mu$ long	5 d

#### **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.

382

TALBOT: On 'Pellicularia'



Figs. 3-5

383

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 reexamination 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. TALBOT: On 'Pellicularia'



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.

386

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  $\mu$ ), 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 semipalisade 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. 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  $\mu$  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

I.	Sterigmata	cor	ısta	ntl	y 2	in	n	um	ber	;; (	Sp	ore	es	sub	cyl	lin	dri	ica	1,	cu	rve	d,	19	21	7	×	4.5	;–6	μ	)
																									Γ.	ste	rig	mat	icu	s
	Sterigmata	. (1–	)4(	-7)	in	nu	mb	er;	sp	ore	\$ C	oble	ong	g-el	lips	soi	d 1	to	br	oad	l o	bo	vat	te,	usi	ual	ly '	wie	les	t
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). TALBOT: On 'Pellicularia'



Figs. 12-14

### 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

390

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

I.	Spores	subglo	bose to	obo	vat	e w	ith	a si	ingl	e a	pic	ահ	18, I	3-10	УX	5-(	5.5 J	u.	•		U.	ochr	ace	um
	Spores	broad	fusifor	m to	as	ym	me	tric	ally	lir	mo	nife	orm	1, U	sual	<b>ly</b> 1	biap	icu	late	:.	•		•	2
2. [	[Spores Spores	4·5-5· 8-16 2	5 × 4- × 5-10	-4·5 μ.	μ	•••	•	•	•••	•	•	•	. U	. cit	rifor	-me,	see	SF •	ecio	es :	inqu U.	ıirer fusisj	nda port	e] um

### 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 rhizoctoniastate 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. TALBOT: On 'Pellicularia'



Figs. 15, 16

393

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

<b>1.</b> Basal hyphae not notably different from the subhymenial ones (some may be thicker and slightly but not notably pigmented)
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 $8-12.5 \mu$ wide. Spores broad fusiform or subnavicular, $8-9 \times 4-5 \mu$ . Basal hyphae up to $15 \mu$ wide
5. Clamps present at all septa. Spores slender fusoid, $6.5-8.5(-15) \times (2-)3-4(-5) \mu$ . Conidial state Oidium sp., with conidia fusoid, $15-20 \times 6-9 \mu$ B. subcoronatum Clamps present at some septa only. Spores narrow, navicular, $7-9 \times 1.5-2.5 \mu$ B. angustisporum
6. Clamps present at all septa
7. [Septocystidia 6-10 $\mu$ wide, with clamped septa, little encrusted. Clamps usually small. Spores fusiform, (8-)11-13(-16) × 3.5-4.5 $\mu$ . B. cystidiatum, see Species inquirendae] No cystidia. Clamps not small. Spores broadly navicular, biapiculate, 9-11 × 5-6 $\mu$ B. medium
8. Septocystidia 9-11 $\mu$ wide, with coloured incrustation. Basal hyphae up to 19 $\mu$ wide. Spores subreniform or depressed-oblong, (5.5-)6-8 $\times$ 3-4.5(-6) $\mu$ . Pellicularia langloisii Cystidia absent
<b>9.</b> Spores within the limits of $7-9 \times 2-3.5 \mu$ , i.e. slender in proportion to length 10 Spores $3-6 \mu$ wide and broad in proportion to length
<b>10.</b> Spores narrow, almost allantoid, $8-9 \times 2-3 \mu$ ; conidial state Oidium curtisii (Berk.) Linder; hyphae up to 15 $\mu$ wide
<b>II.</b> Spores obliquely and narrowly ovoid, obtuse at both ends, $7.5-12 \times 3.5-5 \mu$ . No known conidial state

<sup>1</sup> 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.
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. Hyphae asperulate
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 obtuseconical 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,  $6.5-10 \mu$  diam. or  $6.5-9 \times 6.5-7.5 \mu$ , with prominent blunt apiculus and numerous cylindrical-conical spines  $1-3 \mu$  long; fructifications isabelline

B. isabellinus (Spores globose, smooth, 10  $\mu$  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  $\times$  6.5–7  $\mu$ ; 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).

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).

398

TALBOT: On 'Pellicularia'



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).

400

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

402

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

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

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