

## STUDIES OF 'PELICULARIA' 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 nomenclatures 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 nomenclatures 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

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.

Venkataraman (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, 1954) 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 *Uthatabasidium* 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 *Uthatabasidium* 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.

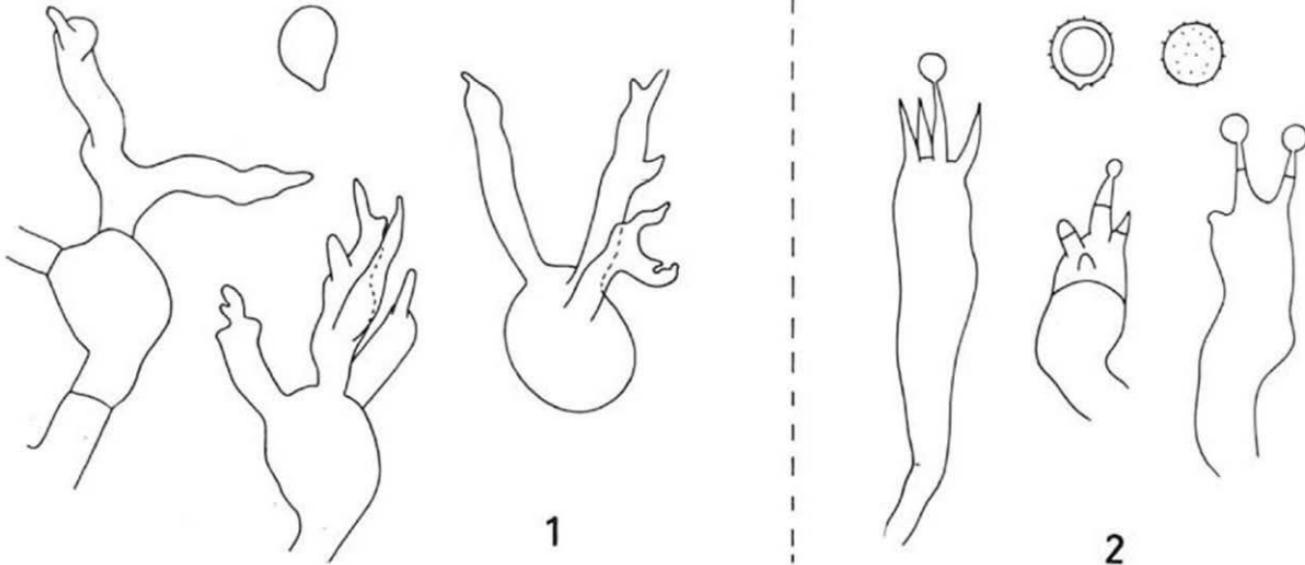
On the one hand there is a body of opinion which recognises a distinct family, Ceratobasidiaceae, for many members of the '*Pellicularia* group', especially those which seem to show a heterobasidial affinity by possession of repetitive spores and voluminous, sometimes septate, sterigmata. On the other 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 Bunkeraceae), 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. *Wailea 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 gloecystidia 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; *Uthalobasidium* Donk.

Class Basidiomycetes: Order Aphylophorales: Family Corticiaceae: Examples: *Wailea* 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 *Botryohyphochnus*
- Spores repetitive (smooth, hyaline to yellowish); hymenial branching less regularly cymose and tending to form a palisade . . . . . *Uthatabasidium*
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.

### O L I V E O N I A

*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.

### K E Y T O S P E C I E S

I. Spores (3-)4-5.5 × 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) × 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 × 7.5-10.5  $\mu$ , uniguttulate, subglobose with a long attenuated apiculus, or pyriform; cystidiform organs absent; clamp connexions present; basidia becoming deeply pigmented . . . . . *O. atrata*

### N O M E N C L A T O R O F I N C L U D E D S P E C I E S

#### ***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 fibrillum* (Burt) Rogers & Jackson (1943: 327); Martin (1948: 113, f. 1). *Peniophora heterobasidioides* Rogers (1935: 30, f. 15).

## OLIVEONIA PAUXILLA (Jacks.) Donk (1958a: 20); Warcup &amp; 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.

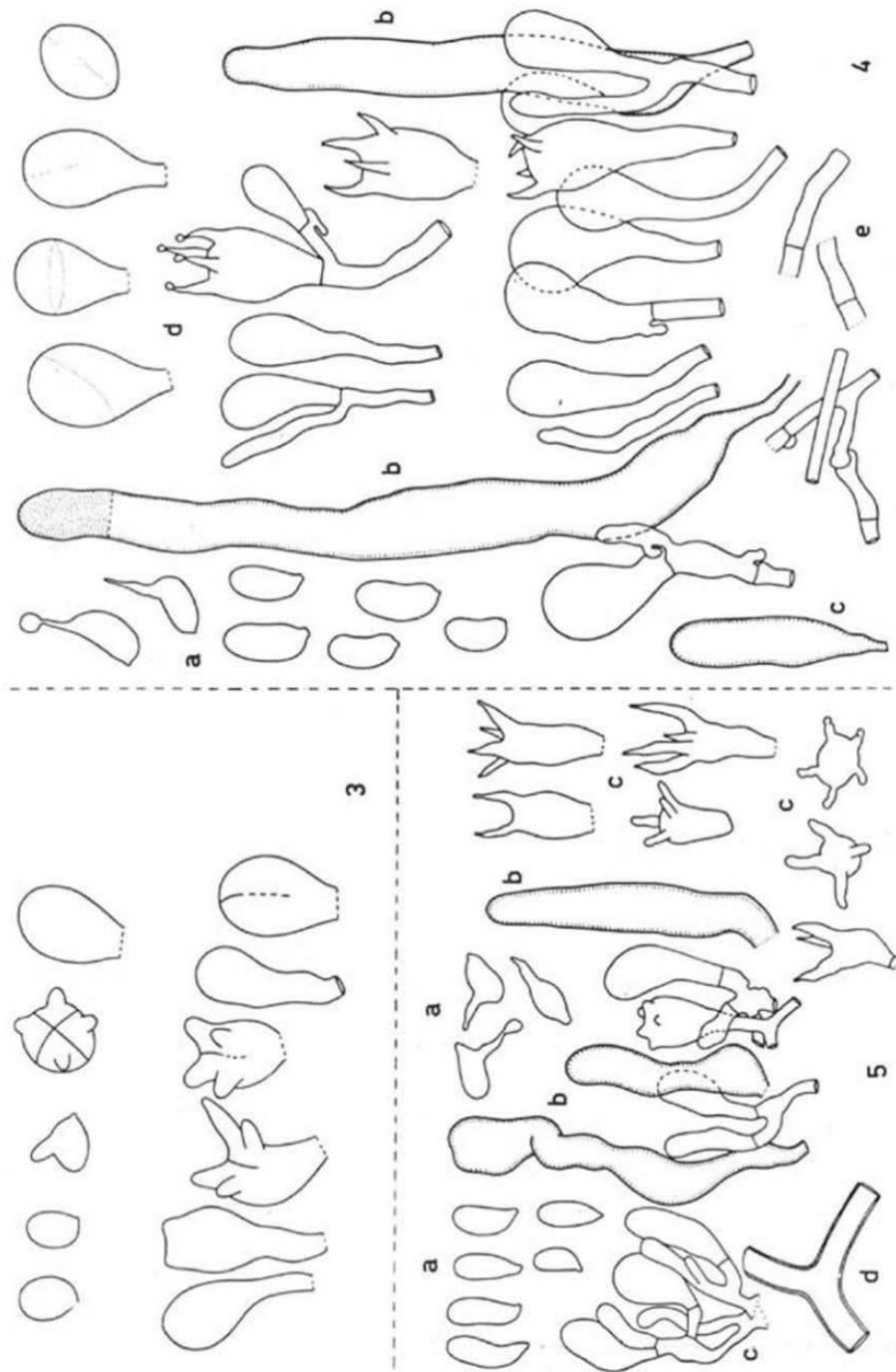
Fructification resupinate, thin, arid to waxy, reticulate-pruinose to pellicular, consisting mostly of repent hyphae forming superficial webs with the hyphae branching at a wide angle, hyaline or dilutely coloured, sometimes with laminated walls, lacking clamp connexions. Basidia undivided, subglobose or oboviform, 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,  $9-13 \times 5-7.5 \mu$  . . . . . *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 pveragum* Petch: see note below).
3. Spores under  $12 \mu$  long . . . . . 4  
Spores  $23-36 \times 3-3.5 \mu$ , flexuous-cylindrical . . . . . *C. calosporum*
4. Fructifications waxy-pruinose; metabasidia under  $18 \mu$  long . . . . . 5  
Fructifications subgelatinous drying to a film; metabasidia over  $18 \mu$  long; (Spores broad ellipsoid often with one side flattened,  $7.5-9.6 \times 5-7 \mu$ , 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. Gloecystidium. 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,  $6.5-10 \times 3.5-6 \mu$ , the length usually 1.5-2 times the breadth . . . . . *C. cornigerum*

Spores oblong-cylindrical,  $8-11 \times 3.5-4 \mu$ , the length more than twice the breadth  
*C. pseudocornigerum*

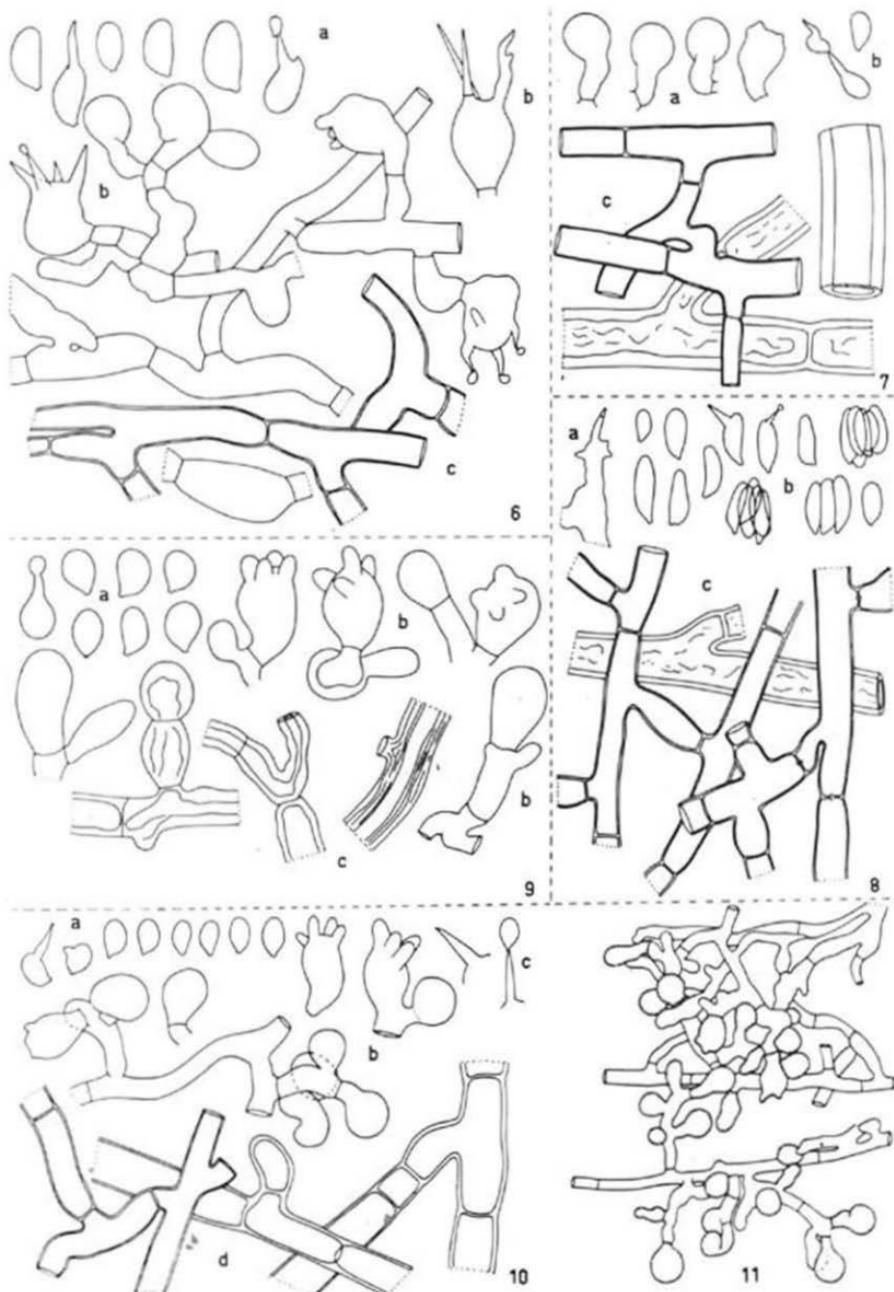
The aerial parts of a number of plants, particularly coffee, citrus, pomes and fig, are attacked by thread-blights or web-blights whose perfect states require re-examination before their classification can be discussed with confidence. Among these are *Corticium microsclerotia* Weber (1939; 1951), *C. 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 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 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  $46.8\ \mu$  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.

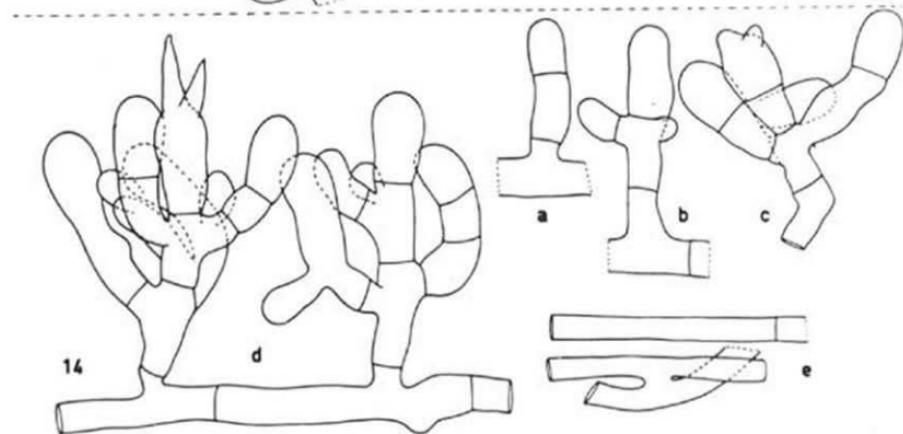
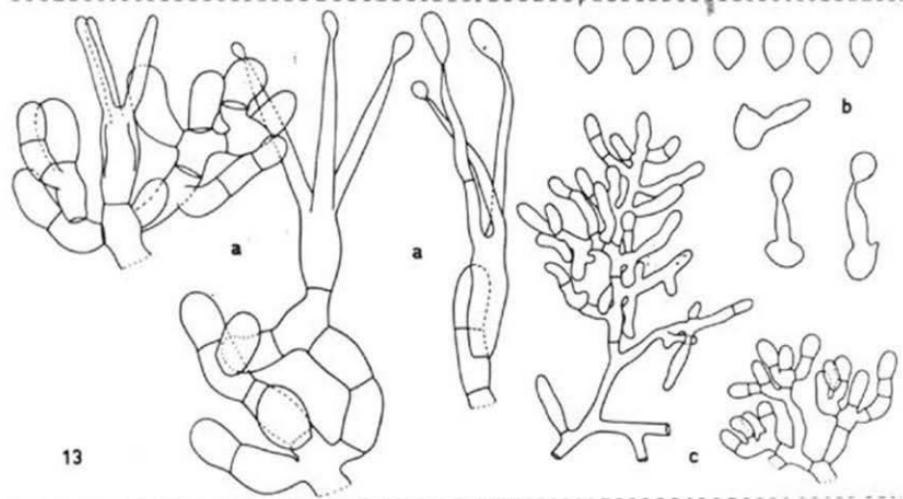
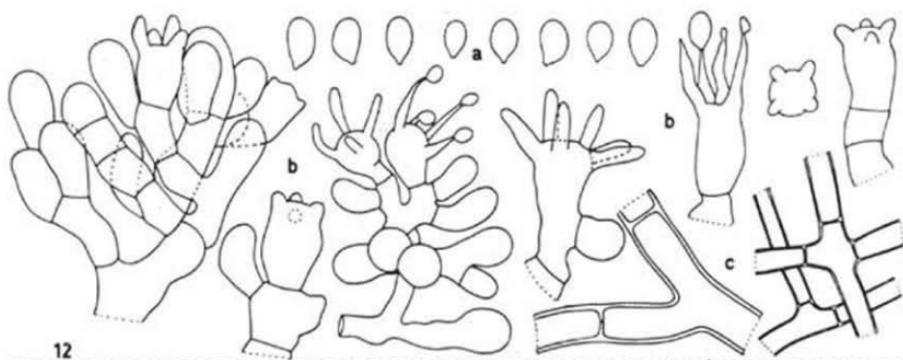
According to Donk (1958a) the majority of orchid mycorrhizal fungi would appear to be mycelial states of *Thanatephorus*. Some of these are described by Bernard (1909) under *Rhizoctonia* and others by Burgeff (1909) under "Orchomycetes"; this work is reviewed by Ramsbottom (1923). Curtis (1939) also 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,  $12-17 \times 4.5-6 \mu$ )  
*T. sterigmaticus*

#### EXPLANATION OF FIGURES 13-14

- 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  $9\ \mu$  wide; mycelium in culture white, mealy, later greyish-brown; sterigmata (1–)3(–4), usually very much longer than the metabasidia; spores  $7\text{--}9 \times 4\text{--}6\ \mu$ ; subhymenial branching often racemose. . . . . *T. praticola*

Hyphae up to  $12\text{--}17\ \mu$  wide; mycelium in culture felt-like, cinnamon-brown; sterigmata usually 4, about the same length as the metabasidia or shorter; spores  $7\text{--}10\text{--}12 \times 4\text{--}7\ \mu$ ; 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); Saksema (1961a: 717; 1961b: 749); not validly recombined.

*Rhizoctonia praticola* Saksema & 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. Schröet. 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-arachnidoid 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, rhizoconidia-states and sclerotia not recorded.

*Uthatobasidium fusicolor* 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. *Ypsilonionium* Donk (1958a); it is here regarded as a species of *Thanatephorus*.

#### KEY TO SPECIES

- 1. Spores subglobose to obovate with a single apiculus,  $8-10 \times 5-6.5 \mu$  . . . . *U. ochraceum*  
Spores broad fusiform to asymmetrically limoniform, usually biapiculate . . . . . 2
- 2. [Spores  $4.5-5.5 \times 4-4.5 \mu$  . . . . . *U. citrifome*, see Species inquirendae]  
Spores  $8-16 \times 5-10 \mu$  . . . . . *U. fusicolor*

#### NOMENCLATOR OF INCLUDED SPECIES

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

*Hypochnus fusicolor* 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* (Bonord.) Olive sensu Olive (1957: 431).

**UTHATOBASIDIUM OCHRAEUM** (Massee) Donk (1958a: 23).

*Comiophora 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.

#### W A I T E A

*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 rhizoconidia-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).

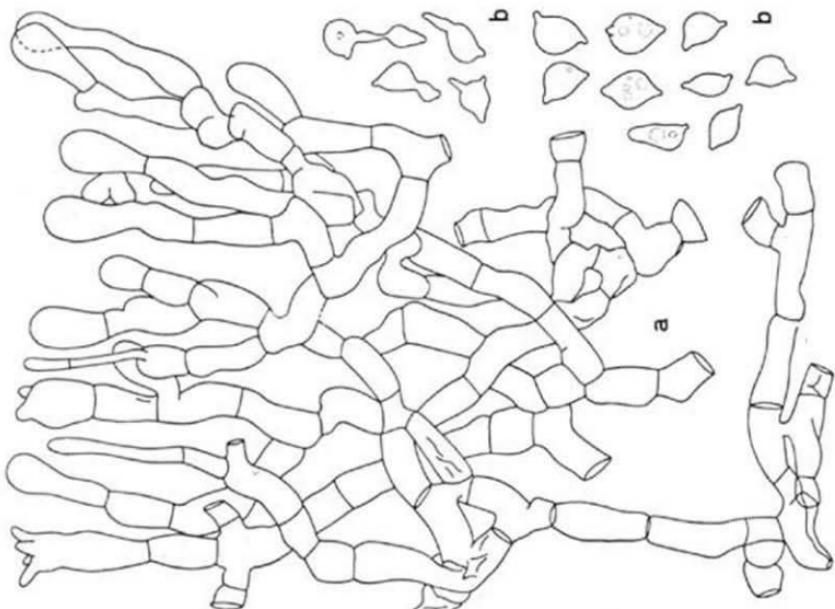
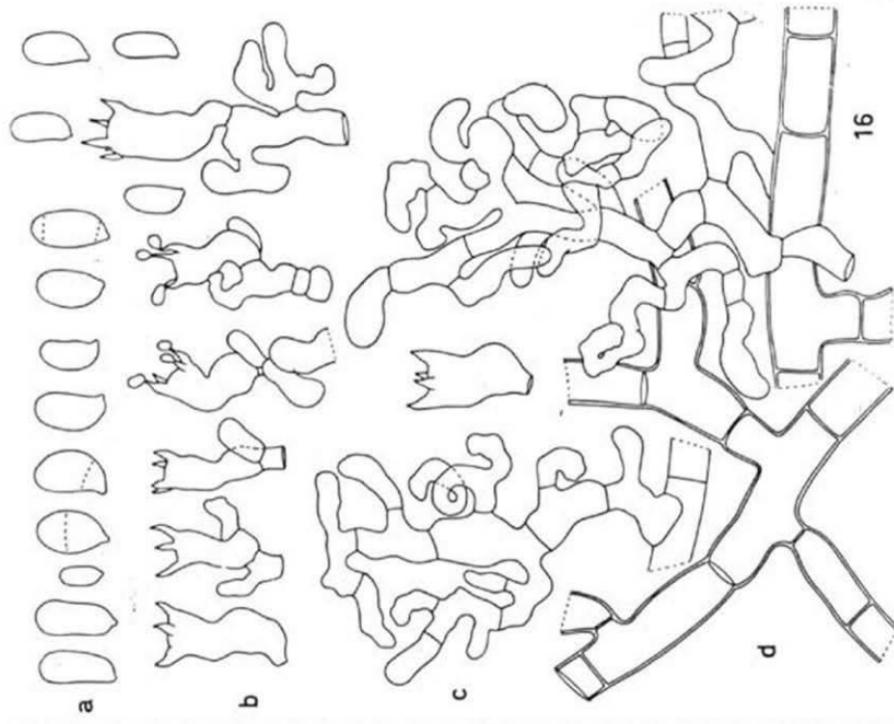
Eriksson (1958a; 1958b) has distinguished the following subgenera:

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.

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#### EXPLANATION OF FIGURES 15, 16

- Figs. 15, 16. — 15. *Uthatobasidium fusicporum*. 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. <i>Dimorphonema</i> . . . . .	12
2. Basidia suburniform; clamp connexions common . . . . .	Subgen. <i>Botryobasidium</i> . . . . . 3
Basidia not constricted, short, wide; mostly lacking clamp connexions . . . . .	Subgen. <i>Brevibasidium</i> . . . . . 6
3. Simple, aseptate cystidia present . . . . .	4
Cystidia absent . . . . .	5
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 . . . . .	<i>Pellicularia ansosa</i>
Cystidia 4–9 $\mu$ wide. Spores navicular, 5.5–6 $\times$ 2.5–3 $\mu$ . Basal hyphae up to 7 $\mu$ wide . . . . .	<i>B. pilosellum</i>
5. Clamps present at all septa. Spores slender fusoid, 6.5–8.5(–15) $\times$ (2–)3–4(–5) $\mu$ . Conidial state <i>Oidium</i> sp., with conidia fusoid, 15–20 $\times$ 6–9 $\mu$ . . . . .	<i>B. subcoronatum</i>
Clamps present at some septa only. Spores narrow, navicular, 7–9 $\times$ 1.5–2.5 $\mu$ . . . . .	<i>B. angustisporum</i>
6. Clamps present at all septa . . . . .	7
Clamps absent . . . . .	8
7. [Septocystidia 6–10 $\mu$ wide, with clamped septa, little encrusted. Clamps usually small. Spores fusiform, (8–)11–13(–16) $\times$ 3.5–4.5 $\mu$ . . . . .	<i>B. cystidiatum</i> , see Species inquirendae]
No cystidia. Clamps not small. Spores broadly navicular, biapiculate, 9–11 $\times$ 5–6 $\mu$ . . . . .	<i>B. medium</i>
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) $\mu$ . . . . .	<i>Pellicularia langloisii</i>
Cystidia absent . . . . .	9
9. 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 . . . . .	11
10. Spores narrow, almost allantoid, 8–9 $\times$ 2–3 $\mu$ ; conidial state <i>Oidium curtisii</i> (Berk.) Linder; hyphae up to 15 $\mu$ wide . . . . .	<i>B. vagum</i> <sup>1</sup>
Spores slender navicular, 7–9 $\times$ 2.5–3.5 $\mu$ ; conidial state <i>Oidium tomentosum</i> (B. & C.) Linder; basal hyphae up to 10 $\mu$ wide . . . . .	<i>B. lembosporum</i>
Spores slender navicular to subcylindric, 7–9 $\times$ 2.5–3.5 $\mu$ ; conidial state <i>Oidium conspersum</i> (Link) Linder; basal hyphae up to 6–7 $\mu$ wide . . . . .	<i>B. conspersum</i>
11. Spores obliquely and narrowly ovoid, obtuse at both ends, 7.5–12 $\times$ 3.5–5 $\mu$ . No known conidial state . . . . .	<i>B. obtusisporum</i>
Spores broad fusiform, narrowed at both ends and biapiculate, 9–11 $\times$ 4.5–6 $\mu$ . No known conidial state . . . . .	<i>B. botryosum</i> <sup>1</sup>
Spores navicular or amygdaliform, 6–8 $\times$ 3–4 $\mu$ ; conidial state <i>Oidium candidans</i> (Sacc.) Linder . . . . .	<i>B. candidans</i>

<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  $\mu$  wide, very dark. Spores narrow ellipsoid, 5–6  $\times$  2–3  $\mu$ . . . . . *B. heteronemum*  
 Clamps absent. Basal hyphae up to 20  $\mu$  wide, yellow. Spores obliquely ovoid or rarely subglobose, (4.5–)5–8  $\times$  (2.5–)3–4  $\mu$  . . . . . 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

*Botryohyphochnus* 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. [= *Botryohyphochnus isabellinus* (Fr.) Erikss.] (Fig. 18).

Saprobic on rotten wood, humus or soil. Fructification arachnid-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 *Botryohyphochnus* 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).

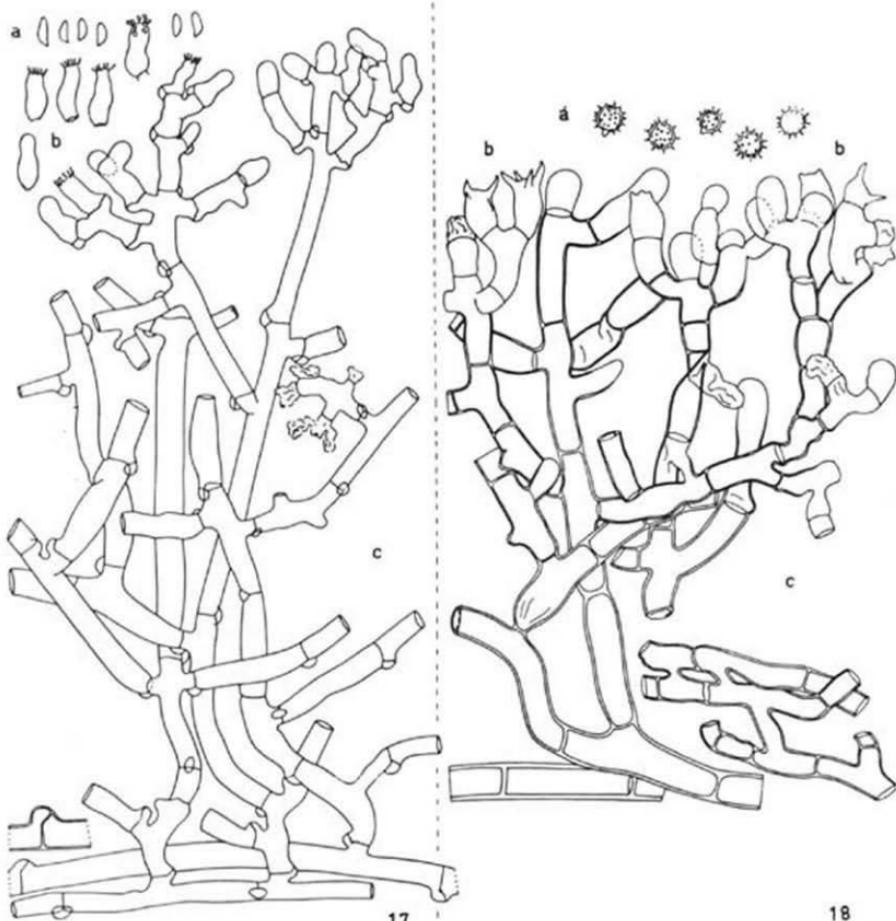
*Hypochnus isabellinus* Fries (1818: 281, pl. 6 f. 3). — *Hypochnus isabellinus* Fr. ex Schleicher (1821: 58); Fries (1849: 337). — *Botryobasidium isabellinum* (Fr. ex Schleich.) Rogers (1935: 11, f. 5). — *Pellicularia isabellina* (Fr. ex Schleich.) Rogers (1943: 99); Boidin (1957a: 281, f. 3).

## 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) Venkata-rayan (1950: 81).

PELICULARIA 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*.

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

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

PELICULARIA 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 flavescent* (i.e. *Uthatobasidium fusisporum*). Although its spores are biapiculate they differ from those of *Uthatobasidium* in being non-repetitive and warted.

PELICULARIA 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 candidans*.

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).

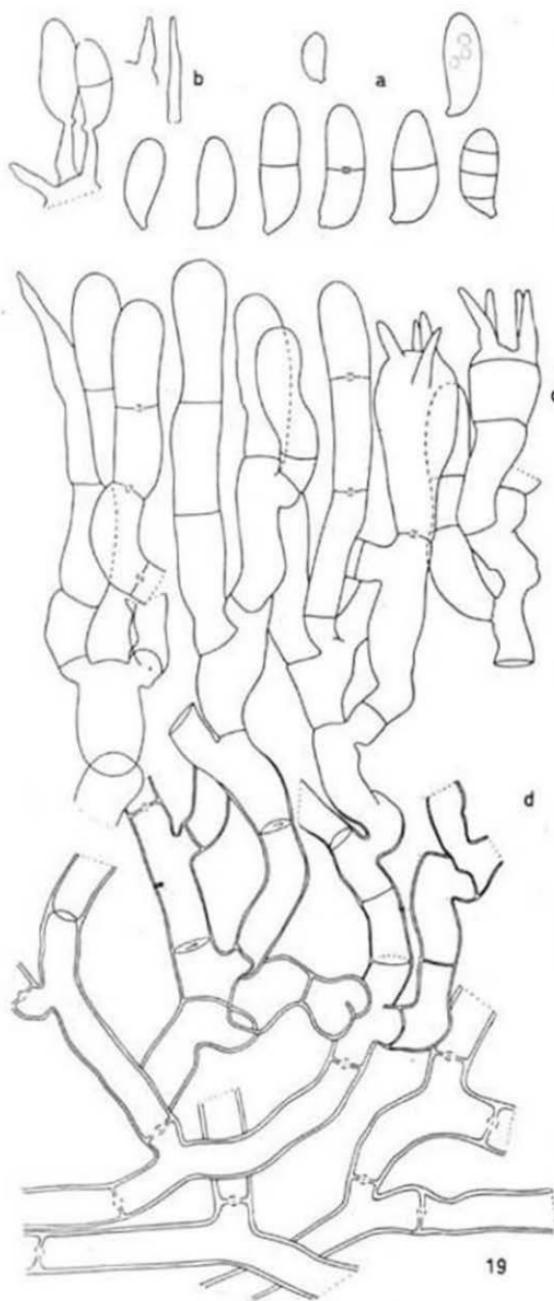
Type of the genus *Suillosporium* Pouzar. Donk (1958a: 27-28) suggests that this species should be placed in *Suillosporium* or better in *Jaapia* (Coniophoraceae) if the latter is emended.

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

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

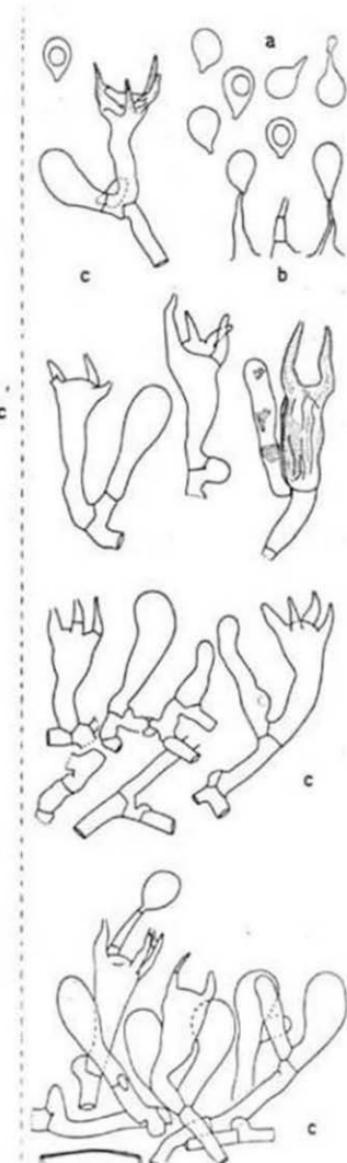
#### EXPLANATION OF FIGURES 19, 20

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).



19

Figs. 19, 20



20

CORTICUM 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*.

PELICULARIA LANGLOISHII (Pat.) Rogers (1943: 101, f. 3).

*Hypochnus langloisii* Patouillard (1908: 3).

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

CORTICUM 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) Höhnlel sensu Höhnlel (1910: 395); Burt (1918: 123, f. 1; 1926: 292, f. 1). — *Botryobasidium koleroga* (Cooke) Venkatarayyan (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).

PELICULARIA 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). — *Paulli-corticium pearsonii* (Bourd.) J. Eriksson (1958a: 66, f. 14d-f, j-l); Libert (1962: 220, f. 1).

*Corticium subinvisibile* Rogers (1935: 28, f. 13).

CORTICUM 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.) Höhn & 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* Venkatarayyan (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.) Venkatarayyan (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).

PELPLICULARIA 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-brights.

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  $\mu$ , may become 1–3-septate after being shed; spore repetition was not seen.

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

#### ACKNOWLEDGEMENTS

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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 histeriaceous 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 inner side 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.

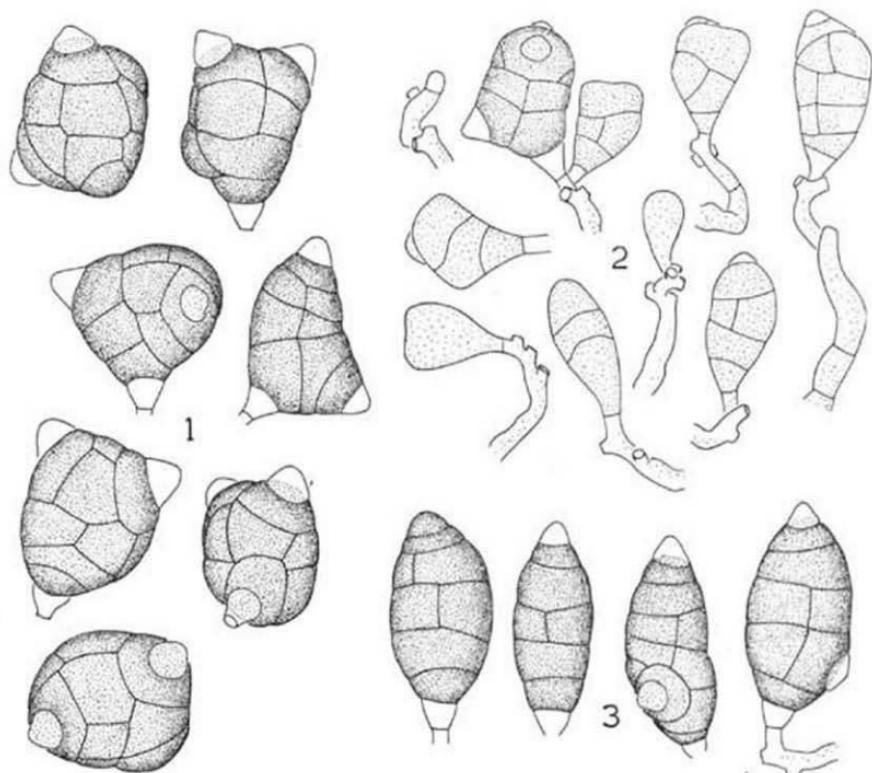
This species was first described by Saccardo (1882) as *Sporidesmium trigonellum* Sacc., based on a collection made in Belgium by Libert. The type species of the genus *Sporidesmium* Link ex Fr., however, has phragmosporous conidia (Ellis, 1958). Consequently, *S. trigonellum* and many other brown dictyosporous 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

\* 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,  $\times 1250$ ).

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 no other 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.

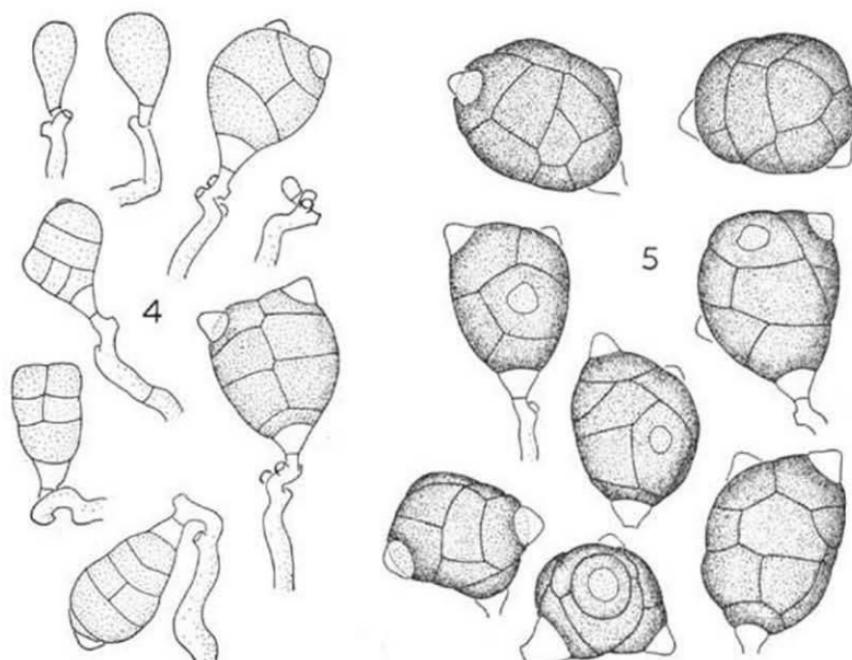
*Oncopodiella tetraedrica* Arn. in Bull. Soc. mycol. Fr. **69**: 296. 1954 (sine diagnose latina).

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  $\mu$  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  $\mu$  diameter at the base, gradually diminishing in width to about 1.2-2  $\mu$  diameter at the apex, and up to 25  $\mu$  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 ovoid 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.,  $\times 1250$ ).

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  $\mu$  wide at the base and up to 4  $\mu$  high. The mature conidia are subtriangular, 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  $\times$  12–16  $\mu$ , 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 *Ailanthes*, *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 *Ailanthes glandulosa*, s. dat., Libert 432 (PAD, type of *Sporidesmium trigonellum* Sacc.). — GREAT BRITAIN: Cambridgeshire, Devil's Ditch (near Stetchworth), on the innervise 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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PERSOONIA

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SPORE DEVELOPMENT IN THE FORM-GENUS PHOMA

G. H. BOEREMA

Plantenziektenkundige Dienst, Wageningen  
(With 31 Text-figures)

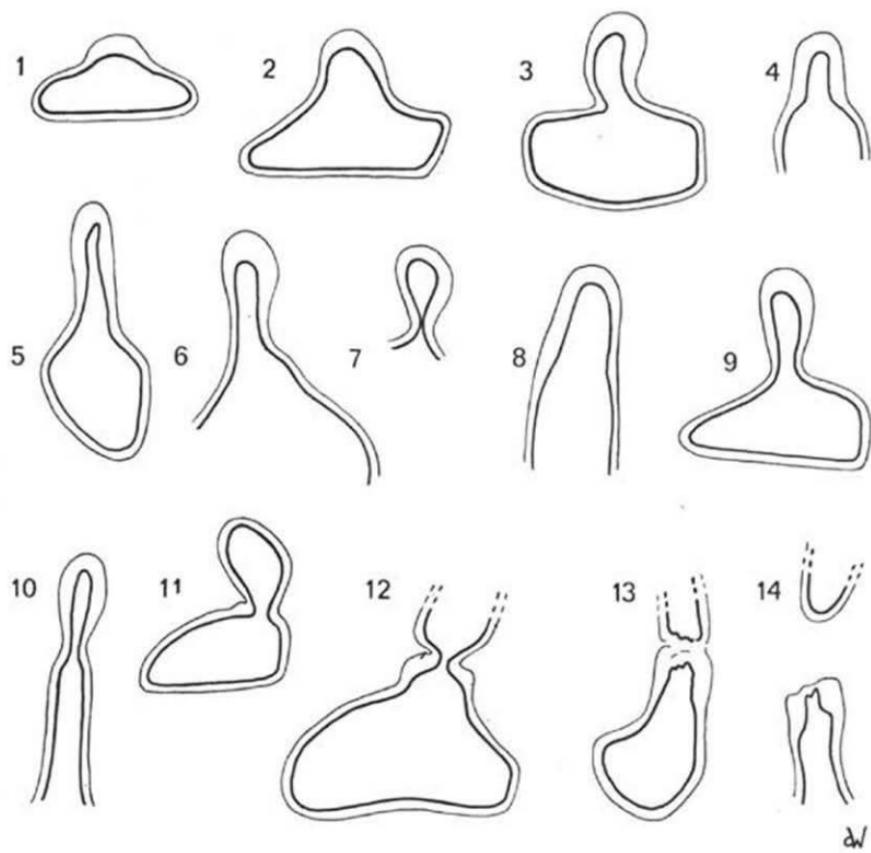
Diagrams drawn after electron-micrographs of the spore formation in *Phoma* spp. are shown. The manner in which the spores are formed, called here the 'monopolar repetitive budding process', is discussed.

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<sup>1</sup>) 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; Goidanich & 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 abstraction 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

<sup>1</sup> 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.

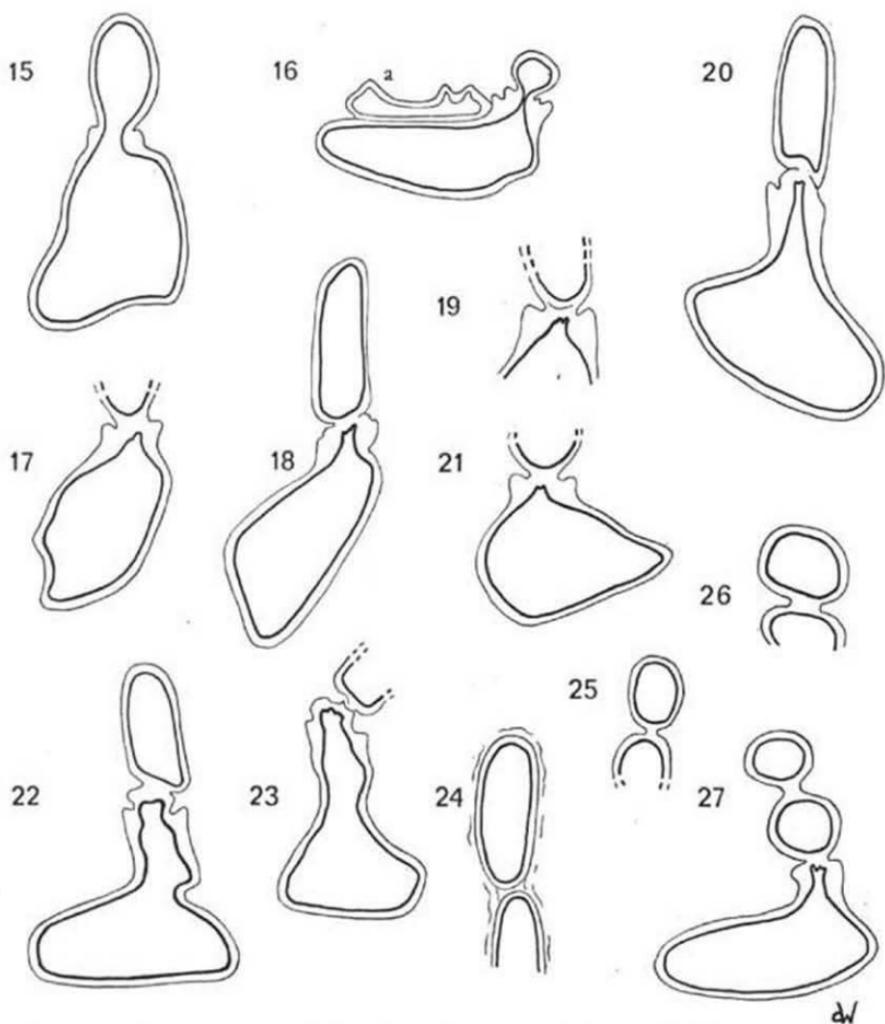


Figs. 1-14. *Phoma* spp. — Various stages of spore formation by budding on "virginal" parent cells.

Diagrams drawn after electron-micrographs; magnification ca.  $\times 2500$ .

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).

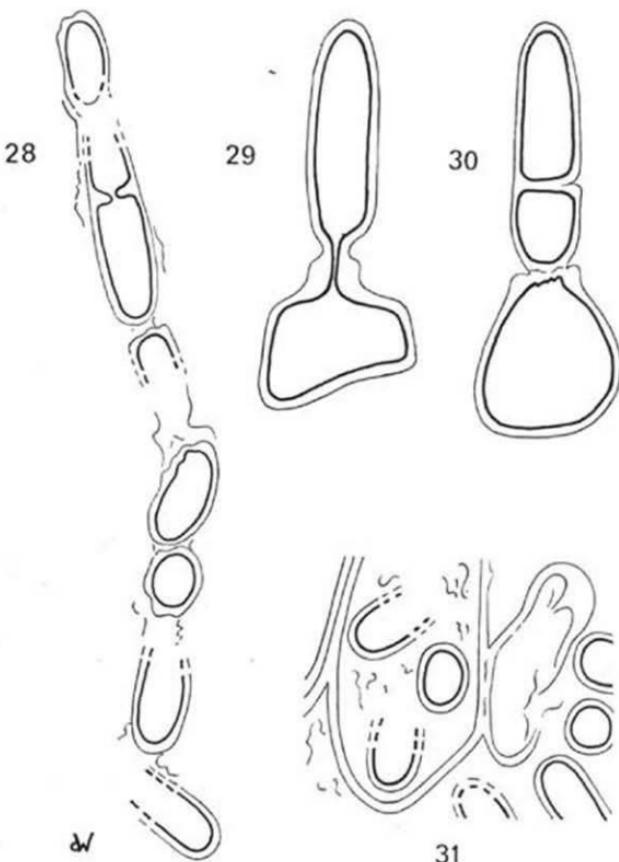
The electron-microscopic study by Brewer & Boerema (l.c.) reveals that the differentiation of the spore-wall during the process of budding takes place in very gradual stages. This may explain why, under the light-microscope, the wall of the spore-initial is often difficult to distinguish. This is particularly 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 (Goidanich & 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.  $\times 2500$ .

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 abstraction 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.  $\times 2500$ .

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.<sup>2</sup> 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 abstraction (Fig. 30) or else later: euseptation, see Brewer & Boerema (l.c.).

<sup>2</sup> 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 \*.

- Abies* 120
- Abortiporus biennis* 206
- Acacia* 75
- Acanthophysium* 304; *biapiculatum* 366; *fasciculatum* 366; *pulvinatum* 367
- Acer* 57, 108, 152
- Achroomyces* 243
- Acia* 304, 314
- Aciella* 304
- Aconitum* 69, 72; *napellus* 32
- Acrodictys* 408
- Acrotamnium* 300, 304
- Actiniceps* 252, 291, 304, 309
- Actiniopsis* 6
- Actinostroma* 304
- Acurtis* 301, 304
- Adenostylis* 72
- Aesculus* 47, 64, 65; *hippocastanum* 64, 69
- Agaricus* 212, 279
- Agrocybe* 303
- Ailanthus* 410; *glandulosa* 410
- Albatrellus* 205, 219, 241, 279, 281, 286, 287; *confluens* 286
- Aldridgea* 300, 304
- Aldridgiella* 300, 304
- Alectotorophoides* 304
- Aleurocorticum* 365, 367; *acerinum* 365; *incrustans* 366; *maculatum* 367; *mexicanum* 367; *microsporum* 367; *pachysterigatum* 367
- Aleurocystidium* 258, 304
- Aleurocystis* 290, 304
- Aleurodiscus* 210, 216, 217, 222, 229, 230, 232-234, 239, 256, 258, 259, 261, 271, 272, 299, 294, 304, 305, 308, 310, 315, 365; § *Dendrophysium* 365; § *Rigidodiscus* 365; *acerinus* 365; *macrodens* 366; *moquinianum* 367; *nivosus* 367; *oakesii* 234
- Allantula* 252, 305
- Alliaria* 21; *officinalis* 21
- Allophylaria* 51, 56; *macrospora* 51, 52; ***myricariae*** 55\*, 56; ***ogrensis*** 57, 59\*
- Alnus* 69, 99, 100, 102, 103, 112, 117, 142, 152; *glutinosus* 99, 102; *incana* 142
- Alternaria* 20; *brassicae* 20
- Alytosprium* 300, 305
- Amanita* 332, 340, 352, 354, 356, 357; *echinocephala* 338; *porphyria* 341; *strobiliformis* 338
- Amanitopsis umbonata* 336
- Amauroderma* 265, 266
- Amaurodon* 259, 305
- Ampelopsis* 57
- Amphinema* 259, 305
- Amylaria* 208, 247, 252, 258, 270, 305
- Amylocorticium* 222, 259, 305
- Amylocystis* 281
- Amylostereum* 222, 294, 305, 313, 320
- Anaphysmene* 197
- Antennaria plantaginifolia* 58
- Anthriscus silvestris* 51
- Antrodia* 281, 285
- Aphelia* 251, 294, 295, 305; *dendroides* 305; *tuberosa* 319
- Aporpium* 282
- Apospheria brassicae* 20, 25; *violacea* 10, 12, 14
- Apus* 305
- Aracocoryne* 252, 305
- Armillaria* 336; *umbonata* 334
- Armillariella ditopa* 355
- Arrhenia* 208, 248, 290, 301, 305
- Arrhytidia* 306
- Artemisia* 51; *campestris* 51; *vulgaris* 51
- Ascocorynium* 85
- Astrochaete* 284
- Asterocyphella* 135, 289, 305
- Asterodon* 234, 273, 276, 304, 305
- Asteroma brassicace* 18, 19
- Asteromella* 17, 19; ***brassicae*** 17, 18, 20; *brassicina* 18; *ovata* 19
- Asterosolenia* 135
- Asterostroma* 234, 260, 271, 274-278, 305
- Asterostromatoideae*** 275
- Asterostromella* 274, 305, 320
- Athelia* 214, 222, 257-259, 282, 305; *bispora* 209
- Aurantioporus* 281
- Aureobasidium* 301
- Auricula* 305
- Auricularia* 224, 292, 293
- Auriculariopsis* 222, 258, 259, 262, 290, 291, 294, 305
- Aurifilaria* 276
- Auriscalpium* 232, 244-246, 272, 286, 305, 316; *vulgare* 246
- Bagnisimitrula saccardoa* 95
- Bankera* 222, 246, 247, 272, 297, 305
- Baumannella* 302, 305
- Beccaria* 305
- Beccariella* 305
- Beenakia* 239, 268, 273, 305
- Belonioscypha* 60; *lactea* 48
- Betula* 77, 120, 142, 151, 152; *lutea* 152
- Biannularia* 357
- Boletochaete* 234

- Boletopsis 185, 219, 222, 247, 282, 296, 297, 305  
 Boletus 274; byssinus 148; fimbriatus 148; ignarius 274; pezizoides 148  
 Bondarzewia 247, 270, 282, 286  
 Bonia 301, 305  
 Boninohydnum 305; pini 168, 187, 189\*, 190  
 Botryobasidium 214, 228, 238, 257-259, 305, 315, 373-375, 379, 380, 387, 392, 393, 400; § Botryobasidium 392, 394, 400; § Brevibasidium 392, 394; § Dimorphonema 394, 401; album 398; angustisporum 238, 394, 395; botryosum 392, 394, 395; candidans 394, 395, 398; conspersum 394, 395; coronatum 398; cystidiatum 394, 398; flavescens 391; heteronemum 395; isabellinum 396; koleroga 400; lembosporum 394, 395; medium 394, 395; obtusisporum 394; ochraceum 391; 395; pilosellum 394, 395; pruinatum 394, 395, 398; pruinatum var. laeve 395; pruinatum var. pruinatum 395; rollsi 401; salmonicolor 401; solani 390; subcoronatum 392, 395, 397\*; vagum 394, 396  
 Botryohypothrix 228, 258, 297, 306, 319, 373, 375, 379, 380, 396, 398; isabellinum 396, 397\*  
 Bovista 236  
**Brachybasidiales 243**  
 Brachybasidium 243  
 Brassica 9, 13, 14, 16-18, 21-23, 27; oleracea 13, 18  
 Bresadolina 205, 260, 294, 295, 306, 308  
 Briardia carneopallida 36  
 Buglossum 306  
 Bulgaria 32; agaricicola 32  
 Byssocorticium 259, 306  
 Byssonectria 312  
  
**Calathella 122**, 290, 301, 306; **davidii** 127\*-129\*; **erucaeformis** 121\*, 123-126, 129\*, 140  
 Caldesiella 296, 297, 306, 311, 315  
 Calodon 297, 306; ridleyi 177  
 Calonectria 6  
 Caloporia 306  
 Caloporus 278, 280, 282, 306  
 Calycella 42; **strumosa** 67\*, 68; subconfluens 68; subpallida 68; sulfurina 68  
 Calycellina 39, 46, 52, 61, 70; **castanea** 37\*, 38; populina 70, 71\*; **pulviscula** 61, 63\*; **spiraeae** 66, 67\*  
 Calycina castanea 38; episphaerica 43; limonium 51; maculosa 52; montaniensis 54; propinquua 60  
 Calypella 135, 222, 289, 290, 301, 306; capula 135; gibbosa 135; goldbachii 131; lactea 131; ochroleuca 131; pallida 135  
 Camarosporium 21  
 Campanella 142, 248, 249, 282, 290, 291, 301, 306, 313  
 Cantharellula 248, 302  
 Cantharellus 209, 212, 214, 222, 241, 242, 245, 248-250, 254, 267, 273, 286, 296, 297, 304, 306, 314; § Gomphus 310; § Polyozellus 316; cibarius 209, 248; crispus 150; fasciculatus 116, 117; muscigenus 145; reticulatus 144, 146; umbonatus 302  
 Carduus 69  
 Carex 134, 138  
 Caripia 249, 252, 294, 306, 312, 315, 316  
 Castanea 57  
 Catathelasma 357, 358; imperiale 357  
 Catilla 290, 301, 306  
 Cedrus deodora 152  
 Cellypha 131, 134, 290, 301, 306; caricina 134; goldbachii 129\*, 131, 133\*-135, 138; griseopallida 138; lactea 131, 134; malbranchei 134  
 Cephalosporium 5  
 Ceraceae 301, 306  
 Ceratella 306  
 Ceratellopsis 251, 306  
 Ceratobasidium 224, 225, 227/228, 257, 258, 261, 262, 306, 372-376, 379, 380, 382, 384, 386, 388, 391, 398, 400, 401; atratum 374, 376, 381, 399\*; anceps 382, 385\*, 386; album 397; calosporum 374, 382, 386; cornigerum 376, 377\*, 384, 385\*, 386, 388; fibrillosum 382; filamentosum 390; flavescens 391; mycophagum 400; obscurum 382, 385\*, 386; pearsonii 400; plumbeum 381; praticola 388, 390; pseudocornigerum 384, 386; solani 390; sterigmaticum 374, 389\*, 390; striisporum 401; terrigenum 374; 399\*, 401; vagum 386, 396  
 Cercis 57  
 Cerefolium 51  
 Cerinomyces 227, 243, 258, 301, 306  
 Ceriporus 278  
 Ceriporia 281  
 Cerocorticium 3, 259, 306  
 Cerrenella 306  
 Chaetocalathus 106  
 Chaetocarpus 306  
 Chaetocypha 300, 306; albissima 123; bloxamii 135; dumetorum 131; erucaeformis 123; lactea 131; malbranchei 132; ochroleuca 131; pallida 135; rubi 131  
 Chaetomella brassicaceae 17  
 Chaetoporellus 281  
 Chaetoporia 294  
 Chaetoporus 281  
 Chaetotyphula 306  
 Chamaecnemum 51, 52; angustifolium 51,  
 52

Chamaerion angustifolium 21  
 Chanterel 248, 306  
*Chlorocyphella* 299, 301, 306  
*Chloroneuron* 249, 268, 307  
*Chlorophyllum* 307  
*Chloroscypha* 34; **alutipes** 33\*, 34; *jacksonii* 51; **limonicolor** 50  
*Chlorosplenium* 79  
*Chondrostereum* 222, 294, 295, 307; *pureum* 295  
*Chromocreopsis* 1; *bicolor* 3; *cubispora* 2; *hirsuta* 2  
*Chromocyphella* 244, 290, 301, 307, 308, 315  
*Cibalocoryne* 91  
*Ciboria* 57; *cerea* 76; *coracina* 39; *nyssogena* 55\*, 56; *velhaensis* 74  
*Ciboriella* 29, 78; **griseolinae** 78; *rufescens* 78; **subcinnabarina** 78  
*Ciboriopsis* 29, 79; *advenula* 79; *bramleyi* 79; *cecropiae* 79; *lenta* 79; *microspora* 79; *phlebophora* 79; **simulata** 65, 67\*, 79; *uleana* 79  
*Cilicia* 307  
*Cirsium spinosissimum* 69  
*Cistella* 38, 39, 46; *trabinella* 38, 68  
*Cladaria* 307  
*Cladodendron* 280  
*Cladoderris* 293, 307  
*Cladomeris* 280  
*Clavaria* 222, 236, 238, 242, 250-252, 254, 298, 299, 306, 307, 311; *bourdotii* 312; *corniculata* 240; *coronilla* 253, 299; *falcata* 214, 222, 251, 253, 299; *fossicola* 299; *helicoidea* 226, 299; *himantia* 312; *laciniata* 207; *mucida* 298, 299; *surculus* 253  
*Clavariachae* 252, 276, 307  
*Clavariadelphus* 222, 240, 249, 250, 252, 268, 307  
*Clavariella* 307  
*Clavicorona* 206, 249, 252, 269, 270, 307; *pyxidata* 270  
*Clavulicum* 213, 215, 222, 227, 243, 258, 307  
*Clavulina* 213, 215, 222, 231, 243, 249, 252-254, 307, 319, 378  
*Clavulinopsis* 222, 252, 254, 299, 307, 309, 317, 320; *hastula* 253, 299; *septentrionalis* 253  
*Clematis vitalba* 138  
*Climacocystis* 281  
*Climacodon* 273, 307  
*Clitocybe* 248  
*Cnazonaria* 307  
*Collinsonia canadensis* 62  
*Coltricia* 242, 276  
*Coltriciella* 276  
*Columnocystis* 237, 294, 306, 307  
*Coniobotrys* 255, 259, 307; *ochroleuca* 400

*Coniophora* 216, 220, 222, 254, 255, 259, 307, 373; *mustialaensis* 312; *ochracea* 391  
*Coniophorafomes* 300, 307  
*Coniophorella* 255, 259, 307  
*Comiothecium* 193, 197  
*Coolia* 331, 333, 356; *odorata* 342; *odorata f. bispora* 342; *schreieri* 331, 337  
*Coprinus* 229, 231  
*Cora* 298, 299, 307, 311; *pavonia* 307  
*Coraemyces* 307  
*Corallium* 307  
*Corella* 299, 307  
*Coriolellus* 281  
*Coriolopsis* 281  
*Coriolus* 222, 280, 281, 285  
*Cornicularia* 307  
*Corniola* 142, 302, 307  
*Cornus* 57, 60; *florida* 46  
*Corticirama* 207, 258, 259, 307  
*Corticium* 208, 214, 221, 222, 242, 247, 252, 256, 258, 259, 294, 307, 308, 310, 311, 317, 319, 355, 373; § *Botryodea* 373, 392; § *Urnigera* 373; *album* 397; *alliaceum* 366; *anceps* 386; *arcuatum* 382, 384, 398; *atratum* 374, 381; *bombycinum f. ramulosum* 207; *botryosum* 395; *ceraceum* 306; *cornigerum* 386; *coronatum* 398; *flavescens* 391; *griseocanum* 366; *invisum* 382, 384, 400; *koleroga* 384, 385\*, 400; *macrosporum* 366; *microsclerotia* 384, 400; *pauxillum* 382; *pearsonii* 400; *pervagum* 382, 384, 400; *pilati* 307; *praticola* 374, 399; *pruinatum* 395; *rollisi* 401; *salmonicolor* 401; *sasakii* 401; *sterigmaticum* 387, 390, 391; *stevensi* 382, 384, 401; *subcoronatum* 392, 295; *subinvisibile* 400; *terrigenum* 378, 399\*, 401; *tulasnelloideum* 211; *vagum* 396  
*Corynella prasinula* 34  
*Corynetes* 81, 85, 89-91; *arenarius* 89-91; *geoglossoides* 91; *globosus* 89, 90\*, 91, 94, 95  
*Coryneum* 194  
*Corynites* 89, 91  
*Corylus* 138, 152  
*Cotylidia* 205, 294, 295, 308; *pallida* 306  
*Crataegus* 99; *oxyacantha* 99, 102  
*Craterella* 308  
*Craterellus* 222, 248, 249, 308, 319, 320; *cornucopioides* 220, 248; *pogonati* 144  
*Creolophus* 269, 270, 273, 308  
*Creopus* 2, 5  
*Crepidotus* 135, 290  
*Crinipellis* 106, 290  
*Cristella* 222, 257-259, 273, 282, 308, 316, 318, 319, 398; *fastidiosa* 207, 258  
*Cryptochaete* 308  
*Cryptomela* 197  
*Cryptotorpus* 279-281

- Crystallocystidium 300, 308  
 Cucurbita 42  
 Cudonia 81, 86; acicularis 73; queletii 72, 73; stagnalis 72  
 Cudoniella 29, 72, 73; acicularis 41, 42, 72, 73; aquatica 72; **clavus** 73; clavus var. **grandis** 73; javanica 77; **rubicunda** 73  
 Cyathula 30, 79; coronata 30  
 Cyclomyces 276  
 Cylindrocarpion 6  
 Cylindrocladum 6  
 Cymatella 248, 294, 301, 308, 309  
 Cymatoderma 294, 304, 305, 307, 308  
 Cymbella 301, 308, 315  
 Cyphella 138, 242, 255-257, 271, 289, 290, 308; albissima 123; albocarnea 123; alboviolascens 126; bloxamii 135, 138, 139; bloxamii var. disciformis 136; caricina 131; citrispora 98-100, 102-105; citrispora f. crataegi 98-101\*, 102-104; citrispora f. lobata 98-101\*, 102-104; conglobata 140, 142; disciformis 133\*, 136, 138, 139; dumetorum 131; cruciformis 123; erucaeformis var. albocarnea 123; eumorpha 123; fasciculata 116; goldbachii 131, 134; goldbachii var. lactea 131; involuta 133\*, 136, 137\*-139; janchenii 98, 99, 101\*, 102-105; lactea 131, 135; lactea var. rubi 131; lloydiana 138; malbranchei 131; mellea 114; membranacea 138; musaecola 144; muscicola 144, 147; ochroleuca 131, 134; pallida 135, 138; porioides 148; punctiformis var. corticola 98, 99, 103; rosicola 98, 99, 102, 104, 107\*; rubi 131, 134; sorthamni 133\*, 136, 137\*-139; sessilis 133\*, 136, 138, 316; tiliæ 106; velenovskyi 134, 135  
 Cyphellina 300, 308  
 Cyphelloid fungus, sterile 152, 143\*  
 Cyphellopsis 108-110, 113, 114, 140, 222, 289, 290, 301, 308, 314, 317; anomala 109, 113, 114, 140; **confusa** 110, 111\*-113, 115\*, 117, 140  
 Cystidioidendron 273, 300, 308  
 Cystoderma 332, 352, 358; § Dissoderma 333; paradoxum 332, 333, 348  
 Cystostereum 294, 308  
 Cytidia 258, 259, 289-291, 294, 308, 313  
 Cytidiella 258, 259, 262, 290, 291, 294, 308  
 Dacrina 308  
 Dacrymyces 213, 376  
 Dacryobolus 222, 258, 259, 273, 308, 310  
 Dacryopsella 308  
 Daedalea 278, 279, 283  
 Daedaleopsis 281  
 Dasyscypha lactea 48  
 Dasyscyphus 70; **aconiti** 31, 33\*; grevillei 32, 39, 47; pygmaeus 35  
 Deflexula 179, 252, 308; fascicularis 179; pennata 179; **sprucei** 179\*; subsimplex 179; vanderystii 179  
 Delicatula 294, 301, 308  
 Dendrocladium 308  
 Dendrocyphella 290, 302, 308  
 Dendrothele 259, 308, 365, 366; **acerina** 365, 366; **alba** 366; **alliacea** 366; **biapiculata** 366; **candida** 366; **dryina** 366; **duthiae** 366; **fasciculata** 366; **griseo-cana** 365, 366; **incrassata** 366; **lepra** 366; **macrodens** 366; **macrospora** 366; **maculata** 367; **mexicana** 367; **microspora** 367; **moquinia** 367; **nivosa** 367; **pachysterigmata** 367; **papillosa** 365, 366; **pulvinata** 367; **seriata** 367; **strumosa** 367  
 Dentinum 191, 309; **crocidens** 158  
 Dentipellis 260, 269, 273, 309  
 Depazea 19; brassicace 18, 19; brassicacola 19-21, 25; brassicicola 25, 26; vagans 25; vagans var. brassicac 20  
 Dianthus 387  
 Diaporthe 20; **incrassata** 20  
 Diceillomyces 243, 309  
 Dichaena strumosa 68  
 Dichonema 309  
 Dichostereum 309  
 Dictyolus 142, 249, 302; **juranus** 147; **retirugis** 144, 146  
 Dictyonema 298, 299, 307, 309, 311, 313, 317, 320  
 Dictyonematomyces 309  
 Dictyopanus 234, 244, 282  
 Digitatispora 213, 222, 225, 243, 259, 309; marina 225  
 Dimorphocystis 252, 304, 309  
 Discinella 29, 50, 79; boudieri 79; **maragarita** 79; menziesi 79; terrestris 79  
 Discocycphella 294, 300-302, 309  
 Discohainesia 38, 57; **oenotherae** 57, 59\*  
 Discorrhiza hyalina 77  
 Donkella 240, 309  
 Donkia 162, 273, 309; pulcherrima 162, 186, 239  
 Dothidea brassicace 17, 18  
 Dozya 5  
 Drosophila 215  
 Dryodon 309  
 Duchesnia 57  
 Duportella 258, 259, 262, 294, 309; **tristicula** 172  
 Echinochaete 281, 284  
 Echinodontium 262, 263, 273, 309, 311  
 Echinotrema 258, 259, 282, 309  
 Elfvingia 265, 266  
 Elmerina 281  
 Entoloma abortivum 304  
 Eoagaricus 302, 309

- Eomycenella 294, 302, 309  
 Epicnaphus 294, 302, 309  
 Epilobium 21, 57; angustifolium 99, 100, 102, 103  
 Episphaeria 290, 302, 309  
 Epithele 258, 259; typhae 309  
 Erigeron 56; canadense 46  
 Erinacea maculosa 52  
 Eriocladus 309  
 Eriopeziza poroidea 148  
 Eschscholtzia californica 44  
 Etheirodon 309  
 Eucalyptus 38, 57; globulus 46  
 Eugeoglossum 91  
 Eupatorium 98, 103  
 Eutypa hydnoides 303  
 Exobasidiellum 243
- Fagus 152, 193; orientalis 104; sylvatica 195, 197  
 Favolaschia 142, 254, 282, 290, 291, 302, 309, 317  
 Favolus 280, 281, 283; alveolarius 280  
 Fibricium 258, 259, 309  
 Fibuloporia 279  
 Filipendula ulmaria 66  
 Filoboletus 244, 282  
 Fistulina 222, 263, 264, 290, 291, 306, 309, 312; hepatica 264  
 Flagelloscypha 97, 103, 105, 290, 302, 309; abieticola 105; **citriscpora** 98, 100, 101\*, 102, 104; faginea 104; trachychaeta 104  
 Flaviporellus 276  
 Flaviporus 281, 285  
 Floccularia 357, 358; luteovirens 357, 358  
 Fomes 205, 266, 267, 279-281; ellisianus 266; fomentarius 265; fraxinophilus 266; juniperinus 266  
 Fomitopsis 281  
 Fragaria 57  
 Fraxinus 138  
 Friesites 309  
 Friesula 300, 310  
 Fusarium 6
- Galerina 360, 363; § **Tubariopsis** 363; clavata 363; dimorphocystis 363; graminea 360, 361, 363; heterocystis 363; laevis 360, 361, 363; marginata 360; **propinqua** 360, 362\*, 363; unicolor 360  
 Galzinia 216, 218, 257, 259, 310, 373; pedicellata 216  
 Ganoderma 157, 222, 226, 236, 264-267; applanatum 266; rivulosum 157  
 Gaultheria 57  
 Gaura 57  
 Genista scorpiaria 47  
 Geoglossum 86, 91; § **Corynetes** 89; § **Leptoglossum** 89; alveolatum 91; hookeri 89; irregularare 85; littorale 91; luteum 82; microsporum 89; rufum 82; viride 82; vitellinum 85  
 Geopeltalum 231, 248  
 Geotus 290, 302, 310  
 Geranium 57  
 Gibberella 6  
 Glabrocyphella 289, 310  
 Gliocoryne 310  
 Globifomes 281  
 Glocoasterostroma 300, 310  
 Gloecantharellus 249, 268, 310  
 Gloecystidiellum 222, 232, 233, 257-259, 269, 271, 278, 310  
 Gloecystidium 257, 259, 308, 310  
 Gloeocanophora 310  
 Gloeopeniophorella 300, 310  
 Gloeophyllum 279-281  
 Gloeoporus 256-259, 261, 262, 282, 310  
 Gloeocladulum 310  
 Gloeosoma 290, 310  
 Gloeostereum 293, 294, 310  
 Gloeotulasella 224, 227, 258, 310, 379; calospora 374  
 Gloiocephala 244, 253, 294, 302, 310  
 Gliodon 166, 244-246, 272, 310, 313, 318; **nigrescens** 166; strigosus 165\*, 166  
 Gloiothele 258, 259, 310  
 Glyceria 153  
 Gomphora 310  
 Gomphus 222, 239, 249, 267, 268, 310, 315, 320  
 Goossenia 248, 310  
 Grammothele 258, 259, 310  
 Grandinia 258, 259, 273, 300, 310  
 Grandiniella 310  
 Grandiniochaete 273, 301, 310  
 Grandinoides 310  
 Grifola 222, 281, 286  
 Guepiniopsis buccina 44  
 Gunnera scabra 66  
 Gymnomitrula 85, 87, 88  
 Gyrodontium 157, 163, 187, 255, 272, 305, 310; **boveanum** 157, 163; henningsii 187, 190; serpuloides 187, 190, 191, 310; **versicolor** 163, 168, 190, 191, 310  
 Gyroladium 311  
 Gyrophana 220, 254, 255, 311, 318  
 Gyrophora 311  
 Gyroporus 287
- Haematostereum 311  
 Hainesia 57; lythri 57  
 Hapalopilus 281  
 Haplocybe 72  
 Hebeloma sacchariolens 342-344  
 Helicogloea 212  
 Helote 91  
 Helotiella lactea 48  
 Helotium 29-31, 35, 43, 72, 294, 302, 311; aciculare 42, 72; agaricicola 31, 32;

- airae 76; albidum 76; albovirens 33\*, 34; allantosporum 79; alutaceum 34; ampulum 35; arenicola 35; atrosubiculatum 74; aurantiacum 36; belisense 36; bodeni 36; brevisporum 75; calyculus 30; cameronunse 74; caracasensis 76; castaneum 38; caudatum 64, 65; cejpi 76; chlorosplenoides 79; citrinum 54; citrinum subsp. turfaceum 50; consanguineum 39; conscriptum 35; coracinum 39; craginianum 40; crastophilum 40; cudo-noides 42; cupreum 77; cyathoideum 31, 51; dakotense 42; dearnessii 43; destructor 43, 68; eichleri 43, 45\*; epiphyllum 36, 50; episphaericum 43; eschscholtziae 44; fergussoni 79; flavofuscescens 46; fraternum 76; fructigenum 30, 57; fulvum 58; fuscopurpureum 74; gedeum 77; gracile 47; griseoliniae 78; herbarum 39, 47, 58; humile 39, 47, 49\*; immutabile 76; javanicum 77; juncidum 75; karstenii 47, 49\*; lacteum 48; lanceolato-paraphysatum 48; larinicum 50; lasserri 75; lentrisporum 77; leucopus 76; limonicolor 50; limonium 51, 75; lividum 76; lutescens 43; lutisedum 79; maculosum 52, 53\*; magnificum 76; maritimum 52; mellum 78; metrosideri 78; microspermum 78; miniatum 74; montaniense 54; monticola 54; nigrescens 56; novae-zelandiae 60, 78; nyssicola 57; nyssogenum 57; obconicum 78; oenotherae 57; parile 48; pateriforme 48, 78; pezizoideum 74; phaeoconicum 58; phormium 79; prasinum 60, 78; procerum 76; propinquum 60; pseudociliatum 79; pullatum 61; quintiniae 77; quisquilarum 78; repandum 75; rhizicola 61, 62; robergei 76; robustius 62; rubens 62; rufocorneum 31, 62; scutellatum 64; scutula 47, 64, 65; scutula var. aesculicarpum 64; scutula var. menthae 64; scutula var. scutula 64; scutula var. suspectum 40; separabile 77; sepium 65; simulatum 66; solani 30; sordidum 74; spadicco-atrum 66; strumosum 68; subcarneum 68; subcinnabarinum 78; subconfluens 68; sublateritium 75; subserotinum 74; subsordidum 74; subtrabellinum 68, 69; tasmanicum 78; titubans 76; trabinellum 68, 69; tuba 30; vernal 78; vernum 78; vitigenum 46, 74; xeroplasticum 71\*, 72  
**Helvella** acicularis 29; dimidiata 145; fibuliformis 29; retiruga 144, 145  
**Henningsomyces** 118, 119, 128, 222, 288-290, 311, 318, 122; candidus 130, 119, 122, 130; poroides 148; **puberus** 117\*, 119, 122; puberus var. **americanus** 117\*, 119-121\*, 122; puberus var. puberus
- 115\*, 117\*, 119, 120  
**Heptasporium** 311  
**Hericiaceae** 269  
 Hericium 222, 247, 252, 269, 270, 273, 286, 309, 311, 314; alpestre 270; bresadolae 270; coraloides 270  
 Hericus 311  
 Herpethallon 298, 299, 311, 312  
 Herpethallonomycetes 311  
 Heterobasidion 281, 300  
 Heterobasidium 300, 311  
 Heterochaete 305  
 Heterochaetella 215  
 Heteromyces 311, 315, 374, 375, 381; fibrillosus 382; pauxillus 382  
 Heyderia 82, 84, 87, 89; abietis 87, 88\*, 89, 94  
 Hexagona 281  
 Hicoria 57  
 Himantia 311  
 Hirneola 311  
 Hirschioporus 177, 280, 281, 285  
 Hirsutella 302, 311  
 Hohenbuehelia 231  
 Holocoryne 311  
 Hologloea 281  
 Hormomitria 208, 252, 253, 311  
 Hyalinia 39, 61; chlorinella 38; incarnata 47  
 Hyaloscypha 52  
 Hydnellum 177, 222, 241, 247, 296, 301, 306, 311, 316; caeruleum 163; inquinatum 163; velutinum var. spongiosipes 163  
 Hydnochaete 273, 276, 306, 311  
 Hydnochaetella 311  
 Hydnodon 273, 296, 297, 311, 317  
 Hydnofomes 311  
 Hydnophysa 311  
 Hydnopolyporus 281  
 Hydnoporia 311  
 Hydnopsis 311  
 Hydnotrema 311  
 Hydnium 156-159, 161, 214, 215, 222, 242, 249, 254, 272, 273, 295, 297, 309, 311, 312, 320; sp. A. 169\*, 170; ambustum 155\*, 161; aitchisonii 183\*, 184; badium 164; basiasperatum 156, 171, 173\*, 174, 177; boveanum 156\*, 157; carbonarium 157; cirrhatum 188; crassum 158; crocidens 156, 158\*-161, 191; decurrens 191; duriusculum 178; elatum 160\*, 161, 162; ferreum 161; fragile 162, 177; gilvum 162; glabrescens 162, 171, 173\*, 174, 176; gleadowii 162; gleadowii 162; guaraniticum 176; helvolum 186, 187; henningsii 157, 162, 163, 187-189\*, 190, 191; imbricatum f. pumilum 170; kummerae 163; martioflavum 163, 164; meruliodes 164, 168, 187, 188, 189\*

- 190; modestum 164; mülleri 164, 171, 174, 175\*, 176; nigrescens 165\*, 166; polymorphum 167\*, 168, 191; pulcherimum 187; pygmaeum 170, 171; rawakense 171, 174-176; reniforme 171, 173\*, 174, 176, 177; repandum 156, 160, 161, 191, 237, 286; repandum var. repandum 160, 191; repandum var. rufescens 159-161; ridleyi 177; scabrum 177; schiedermieri var. kamerunensis 187; serpuloides 178, 187, 190, 191; sinclairii 178; sprucei 178, 179\*; stereoides 179, 180\*, 181; subfelleum 164; sub pallidum 181; tapeinum 182, 183\*, 184; thwaitesii 184, 185\*; uleanum 186, 187; versicolor 168, 187, 188, 189\*, 190; washingtonianum 191; wellingtonii 191
- Hydrobasidium* 374, 381; terrigenum 401
- Hygrophoropsis* 247, 248, 256;
- Hygrophorus* 245; § *Gliophorus* 355; *psittacinus* 355
- Hymenochaete* 222, 260, 274-277, 294, 312, 313
- Hymenochaetella* 312
- Hymenogloea* 294, 302, 312, 313
- Hymenogramme* 258, 259, 312, 313
- Hymenoscypha* 30, 31
- Hymenoscyphus* 29-31, 40, 43, 56, 61, 62, 68, 73; § *Ciboria* 30; § *Cupreum* 77; § *Cyathoidea* 30; § *Epiphyllum* 77; *Herbarum* 74, 77; § *Hymenoscyphus* 73; *Imberbis* 75; § *Prasinum* 77; § *Sclerotinia* 30; § *Scutula* 75; § *Trichoscypha* 30; *airae* 76; *albidus* 76; *albopunctus* 76; *atrosubiculatus* 74; *brevisporus* 75; *bysigenus* 74; *calyculus* 73; *camerunensis* 74; *caracasensis* 76; *carmichaeli* 73; *caudatus* 76; *cepii* 76; *ceratinus* 75; *cereus* 76; *chrysocomus* 30; *cortisepus* 75; *craginianus* 40; *crastophilus* 40, 41\*, 76; *crocatus* 76; *cupreus* 77; *cyathiformis* 41\*, 42, 75; *cyathoideus* 30; *dearnessii* 41\*, 75; *ellisi* 48, 49\*, 74; *emergens* 74; *epiphylloides* 77; *fagineus* 74; *fibulaeformis* 29; *flavo-fuscescens* 45\*, 46, 74; *fraternus* 76; *fructigenus* 30, 73; *fuscopurpureus* 74; *gracilis* 47; *gratus* 75; *herbarum* 77; *humuli* 77; *imberbis* 75, 42; *immutabilis* 76; *infarctiens* 74; *infundibuliformis* 30; *infundibulum* 30; *java-nicus* 77; *juncisedus* 75; *laburnum* 74; *lacteus* 48, 49\*; *laetus* 73; *lasiopodium* 74; *lasseri* 75; *leucopsis* 77; *leucopus* 76; *limonium* 51, 53\*, 75; *lividus* 76; *lutescens* 43, 75; *magnificus* 76; *mar-chantiae* 77; *metrosideri* 78; *micro-spermus* 78; *miniatius* 74; *montaniensis* 54, 55\*, 75; *musicola* 74; *parilis* 74; *phylogenitus* 76; *phyllophilus* 76; *pileatus* 75, 76; *prasinus* 78; *procerus* 76; *quintiniae* 77; *radiatus* 30; *rapaeformis* 29; *repandus* 75; *rhodoleucus* 76; *robustior* 75; *rufocor-neus* 62, 63\*, 74; *salicellus* 73; *sclero-genus* 74; *scutula* 73; *scutula* var. *fucatus* 75; *scutula* var. *menthae* 75; *scutula* var. *scutula* 75; *separabilis* 77; *serotinus* 73; *simulans* 65; *sordidus* 74; *spadiceo-ater* 66, 67\*, 78; *subcarneus* 43, 67\*, 68, 77; *subferrugineus* 73; *sublateritius* 75; *subserotinus* 74; *subsordidus* 74; *tenellus* 30; *titubans* 76, 77; *tubae-formis* 29; *vasaensis* 77; *velhaensis* 74; *vernus* 78; *vitigenus* 74
- Hyphoderma* 216, 222, 257-259, 273, 312, 314, 317, 373, 375, 398, 402; *definitum* 216; *polonense* 375, 400; *setigerum* 207
- Hyphodontia* 222, 232, 257-259, 273, 281, 312, 374
- Hypholoma* 355
- Hypochnella* 259, 312; *violacea* 312
- Hypochnicium* 259, 222, 312, 373; *bom-bycinum* 207
- Hypochnopsis* 259, 312
- Hypochnus* 295, 298, 312; *cucumeris* 374, 386, 390; *isabellinus* 373, 396; *filamentosus* 386, 387; *flavescens* 390, 391; *fusisporus* 374, 390, 391; *langloisii* 400; *sasakii* 384, 401; *solani* 228, 374, 386, 390
- Hypocrepa* 5; *bicolor* 3; *cubispora* 1, 2; *hirsuta* 2
- Hypocreopsis* 5; *rhododendri* 5; *riccioidea* 5
- Hypodrys* 312
- Hypolüssus* 249, 300, 302, 312; *montagnei* 306
- Hypomyces* 312
- Hyponeurus* 312
- Hypothele* 312
- Ilex* 36; *opaca* 35
- Inocybe* 231
- Inonotus* 240, 274, 276
- Irpea* 176, 273, 281, 285, 294, 312; *lacteus* 312; *merulioides* 187; *vellereus* 237
- Irpiciporus* 281
- Irpicochete* 273, 301, 312
- Ischnoderma* 280, 281
- Jaapia* 255, 259, 307, 312, 319, 398; *ochroleuca* 400
- Jambosa* 57
- Juglans* 152; *cinerea* 142; *regia* 108
- Juncus* 153
- Junghuhnia* 313
- Karstenia* 312, 317
- Kavinia* 239, 252, 268, 273, 312
- Kneiffia* 312, 314, 317; *polonensis* 401

- Kniffiella* 260, 296, 312, 319  
*Koleroga* 214, 228, 257, 258, 313, 315, 372,  
 382, 384, 386, 401; *noxia* 372, 382, 400  
*Kordyan* 222  
*Kordyanella* 302, 313  
*Kriegeria* 34; *alutipes* 34  
  
*Lachnella* 105, 106, 222, 290, 302, 313;  
 alboviolascens 106, 124; *campanula* 123;  
*cecropiae* 106; ciliata 104, 105; *populina*  
 62; *subfalcispora* 105, 106; *tiliae* 105,  
 106, 107\*; *villosa* 105, 106, 108  
*Lachnocladium* 206, 211, 230, 231, 252,  
 294, 302, 313, 319  
*Lachnum* 70  
*Lactarius* porninsis 348  
*Laeticorticium* 211, 216, 222, 258, 259, 294,  
 307, 313, 314, 373  
*Laetinacia* 35, 38; *carneopallida* 36, 37\*  
*Laetiportus* 236, 281  
*Langloisia* 300, 313  
*Laricifomes* 281  
*Larix* 50; *leptolepis* 36  
*Laschia* 248, 249, 301, 313  
*Laudatea* 299, 313  
*Laurilia* 263, 271, 294, 313  
*Laxitextum* 222, 269, 294, 313  
*Leia* 313  
*Lentaria* 252, 253, 268, 299, 313  
*Lentinellus* 232, 244-246, 313  
*Lentinus* 283; adhaerens 284; cyathiformis  
 284; variabilis 284  
*Lenzites* 222, 278, 279, 281, 283, 297  
*Lenzitopsis* 297, 313  
*Leotia* 72, 81, 86; *aquatica* 72; *lubrica* 72  
*Lepiotia* 348; *odorata* 331, 333, 342  
*Leptochaete* 313  
*Leptodon* 313  
*Leptoglossum* 89, 142, 144, 145, 147, 249,  
 290, 291, 302, 307, 310, 313, 314;  
 § *Xanthoglossum* 82; sp. 137\*, 146; bryophilum  
 147; *galeatum* 144; *laeve* 144;  
*lobatum* 146; *muscigenum* 146; *retirugum*  
 143\*, 144, 146, 147; *tremellosum* 94  
*Leptophoma* 21, 25; *acuta* 25; *urticace* 10  
*Leptotorpus* 279, 280  
*Leptosphaeria* *acuta* 25; *alliariae* 21;  
*cylindrospora* 21; *exitiosa* 22; *maculans*  
 17, 18, 20-22\*, 23\*, 24-26\*; *napi* 20, 21,  
 22; *virginica* 21  
*Leptotius* 142, 249, 290, 302, 313; *retirugus*  
 144  
*Leucosomes* 281  
*Leucoglyphana* 222, 255, 259, 282, 313  
*Leucoporus* 279, 281  
*Libellus* 302, 313  
*Libocedrus* *decurrens* 34  
*Licentia* 313  
*Lignosus* 265  
*Lindtneria* 281, 297, 313  
  
*Liquidambar* 70  
*Lloydella* 313  
*Lloydellopsis* 313  
*Lobaria* 241  
*Lomatia* 313  
*Lomatinia* 313  
*Lopharia* 222, 294, 313, 317, 319  
*Lycoperdon* 223  
*Lycopodium* clavatum 58  
*Lyomyces* 314  
*Lythrum* 57  
  
*Maireina* 108, 301, 314  
*Malacodermum* 301, 314  
*Malacodon* 273, 301, 314  
*Manina* 314  
*Manuripia* 294, 302, 314  
*Marsamius* 234, 276, 282, 290, 294, 303,  
 320; *cymatelloides* 315; *pulcher* 106  
*Martella* 314  
*Massecola* 252, 291, 292, 294, 314, 318  
*Matruchotia* 302, 314  
*Melanconium* 193, 194, 196, 197; *atrum*  
 193, 194-196\*, 197, pl. 3 fs. 1, 2; *arundinis*  
 194; *bicolor* 193, 194; *betulinum*  
 194; *conglomeratum* 194; *discolor* 194;  
*juglandinum* 194; *juglandis* 197  
*Melanconis* stilbostroma 197  
*Melanopus* 281  
*Membranicum* 314  
*Mensularia* 280  
*Meripilus* 281  
*Merisma* 314  
*Merismodes* 109, 110, 113, 114, 116, 290,  
 314, 315; *fasciculatus* 112\*-115\*, 116,  
 117; *fasciculatus* var. *fasciculatus* 117;  
**ochraceus** 116  
*Meruliodoria* 314  
*Merulopsis* 314  
*Meruliporia* 225, 259, 282, 314  
*Merulius* 150, 209, 222, 247, 248, 255, 256,  
 258, 259, 261, 262, 294, 306, 312, 314,  
 319; *corium* 262; *crispus* 150, 151;  
*fagineus* 151; *molluscus* 209; *retirugus*  
 144; *rufus* 209; *taxicola* 209, 262  
*Metabourdotia* 243, 375, 378-380; *tahitiensis*  
 380, 383\*  
*Microglossum* 81, 82-86, 88, 89, 93;  
 § *Melanoglossum* 89; § *Ochroglossum* 82;  
*atropurpureum* 89; *capitatum* 84, 94, 95;  
*fechtneri* 94; *minus* 94; *olivaceum* 82,  
 84, 93; *rufum* 82, 83\*; *shiraianum* 87;  
*tetrasporum* 84, 95; *viride* 82, 83\*, 84, 94  
*Microporus* 281  
*Mitrula* 81-89, 91, 93; § *Geomitrula* 85, 86;  
 § *Heyderia* 85-87; § *Microglossum* 85;  
 § *Mitrula* 86; § *Physomitrula* 85, 86;  
*abietis* 85-87; *bermudiana* 93; *brassicae*  
 86, 87; *cucullata* 86; *cucullata* var.  
*sphaerocephala* 95; *fusispora* 94; *gracilis*

- 86-88\*, 89, 95; *heyderi* 87; *lateritio-rosea* 94; *morcheilloides* 94; *multiformis* 86, 87; *omphalostoma* 87, 94; *paludosa* 84, 85\*, 86, 89; *paludosus* var. *sphaerocephala* 95; *rehmii* 95; *saccardoa* 95; *sclerotiorum* 86, 87; *sclerotipus* 86, 87; *sphaerocephala* 95  
*Mniopetalum* 147, 222, 290, 302, 314; *globosporum* 147  
*Mollisia* 35, 39, 43, 46, 57, 61; **dakotensis** 41\*, 42; *exigua* 46; *incarnata* 47; *oenotherae* 57; **propinquus** 59\*, 60; **pullata** 61, 63\*; *rubicunda* 73; *translucens* 69  
*Monarda* 43  
*Monodictys* 408  
*Muciporus* 300, 314  
*Mucronella* 208, 222, 239, 251, 252, 258, 270, 272, 314; *fascicularis* 270  
*Mucronaria* 314  
*Mucronoporus* 276  
*Musa* 144  
*Mycena* 203, 244, 282, 290, 294, 309  
*Mycenoporella* 244, 282  
*Mycoacia* 222, 258, 259, 273, 304, 314  
*Mycobonia* 281, 284, 294, 310, 311, 314; *disciformis* 289; *flava* 314  
*Mycocitrus* 6  
*Mycodendron* 301, 314  
*Mycoleptodon* 314; *rawakensis* 171; *reniformis* 171  
*Mycoleptodonoides* 184, 237, 273, 314; *aitchisonii* 184; *vassiljevae* 237  
*Mycorrhaphium* 273, 314; *pusillum* 238  
*Mycosphaerella* 18; *brassicaceola* 17, 19, 20, 26  
*Myricaria* *rosea* 56  
*Myrmeciella* 5  
*Myxomycidium* 208, 217, 218, 222, 224, 251-253, 314; *flavum* 218, 253, 314; *gianense* 217; *yakusimense* 217, 225, 314  
*Nectria* 6  
*Nectriella* 6  
*Nectriopsis* 6  
*Neokneiffia* 314  
*Neurophyllum* 267  
*Nevrophyllum* 249, 267, 268, 310, 315; *viride* 307  
*Nodularia* 315  
**Nothomitra** 82, 91; **cinnamomea** 92, 93\*, 95  
*Nyctalis* 249, 302, 315  
*Nyssa* 57; *multiflora* 56; *sylvatica* 57  
*Ocellaria* *aurantiaca* 65; *aurantiaca* var. *crataegi* 65  
*Ochroglossum* 82, 83; *capitatum* 94; *tetrasporum* 95  
*Octospora* **alutacea** 33\*, 34; *violacea* 73  
*Odontia* 222, 257-259, 273, 303, 309  
*Odontina* 315  
*Odontiochaete* 273, 301, 315  
*Oenothera* 57  
*Oidium* 380, 392, 394; *conspersum* 394; *curtisi* 394; *tomentosum* 394  
*Oliveonia* 214, 228, 258, 311, 315, 374, 375, 379-381; **atrata** 381, 399\*; *fibrillosa* 379, 381-383\*; *pauilla* 381-383\*  
*Ombrophila* *clavus* 72; *clavus* var. *grandis* 73; *verna* 78  
*Omphalina* 290  
**Oncopodiella** 409; **trigonella** 408\*, 409, 410\*; *tetraedrica* 408, 409  
*Onobrychis* *viciifolia* 10, 12  
*Onnia* 276  
*Orbilia* 30, 38, 42, 46, 47, 60, 61, 70; *auricolor* 69; *cruenta* 61; *cucurbitae* 40; *epipora* 70; *exigua* 46; *lutea-rubella* 47; *phyamatodes* 60; *pulviscula* 61  
*Orbiliopsis* 61  
*Ordonia* 302, 315  
*Osmoporus* 281  
*Oxydonta* 315  
*Oxyporus* 280, 281, 285  
*Pachydisca* 78; *bodenii* 36; *laeta* 73; *sepium* 65; *subturbinata* 78  
*Pachysterigma* 315  
*Palaeocephala* 294, 302, 315  
*Panellus* 244  
*Parapterulicum* 208, 230, 252, 258, 315; *subarbusculum* 208  
*Parrotia* *persica* 56  
*Patinellaria* *cubensis* 44  
*Paullicorticium* 214, 219, 228, 258, 315; *pearsonii* 400  
*Pelargonium* 57  
*Pellicularia* 224, 257, 258, 300, 315, 371, 372, 374, 375, 382, 386, 391, 392; *alba* 308; *angustispora* 395; *ansosa* 394, 398; *asperula* 398; *biapiculata* 396, 398; *chordulata* 398; *cystidiata* 398; *digitata* 398; *filamentosa* 374, 386-388, 390; *filamentosa* f. sp. *microsclerotia* 387, 400; *filamentosa* f. sp. *sasaki* 387, 401; *filamentosa* f. sp. *solani* 387, 390; *filamentosa* f. sp. *tmisii* 387; *flavescens* 374, 390, 391, 398; *fodinarum* 375, 398; *isabellina* 398; *koleroga* 371, 372, 374, 382, 384, 400; *langloisii* 394, 400; *lembospora* 395; *ochroleuca* 400; *otagensis* 400; *polonensis* 401; *praticola* 387, 388, 390; *pruinata* 395, 398; *rolfsii* 401; *salmonicolor* 401; *scabrida* 401; *subcoronata* 395; *vaga* 395, 396; *zealandica* 375, 402  
*Pellidiscus* 135, 139, 290, 302, 315, 316; *pallidus* 133\*, 135, 137\*-139; *subciculosus* 133\*, 136, 138, 139  
*Peniophora* 210, 219, 222, 230-232, 256-259, 294, 308, 310, 319; § *Coloratae* 210,

- 262, 315; § *Tubulifera* 320; *canadensis* 401; *heterobasidioides* 382; *lacta* 226; *ludoviciana* 212; *polonensis* 401; *quercina* 220, 221; *rimicola* 211  
*Peniophorella* 300, 315  
*Peniophorina* 302  
*Perenniporia* 266, 281  
*Perona* 290, 294, 302, 315  
*Peronia* 315  
*Persea palustris* 52  
*Persooniana* 315  
*Petasites* 98, 103  
*Pezizella* 65; *livida* 36; ***sepium*** 63\*, 65  
*Peziza* 30, 35; *aconiti* 32; *alutipes* 34; *aquifoliae* 35; *calyculus* 30; *campanula* 121\*, 123-125, 129\*; *carneopallida* 36; *carneorosea* 38; *caudata* 76; *chlorinella* 38, 46; *chrysocoma* 30; *clavus* 73; *coccinea* 39; *coronata* 30; *cortiseda* 75; *craginiana* 40; *croatica* 62; *cruenta* 61; *cucurbitae* 40; *cyathoidea* 30; *eschscholtziae* 44; *exarata* 44; *exidiella* 44, 46; *exigua* 45\*, 46; *faginea* 74; *fructigena* 30, 31; *grata* 75; *herbarum* 58, 77; *humuli* 77; *ianthina* 73; *imberbis* 75; *incarnata* 47; *infarciens* 74; *infundibulum* 30; *leucopsis* 77; *marchantiae* 77; *marmatica* 52; *micacea* 69, 70; *millothalma* 46; *nigrescens* 56; *nyssaegea* 56; *obstricta* 79; *ochracea* 114; *oenotherae* 57; *parilis* 74; *pastinacae* 58; *phymatodes* 60; *porioides* 148; *pulviscula* 61; *radiata* 30; *rapula* 29; *regalis* 61; *rhodoleuca* subsp. *robustior* 75; *salicella* 73; *sepium* 65; *simulata* 65; *spadiceo-atra* 66; *spiraceae* 66; *subcarnea* 68; *subferruginea* 73; *sublidioides* 51, 52; *tenella* 30; *tiliae* 106, 108; *translucens* 69; *tuba* 29; *vasaensis* 77; *vulgaris* 70; *vulgaris* var. *mycetica* 70, 71\*; *vulgaris* var. *sanguinella* 70, 71\*  
*Pezizella* 31, 32, 35, 38, 43, 46, 56, 60, 69, 70, 86; *aconiti* 31, 32; *albotincta* 58; *aquifoliae* 35; *aristospora* 35; *carneopallida* 36; *carneorosea* 37\*, 38; *chlorinella* 38, 41\*; *cucurbitae* 40; *dakotensis* 42; *eburnea* 80; *exidiella* 44, 45\*; *exigua* 46; *hungarica* 47, 49\*; *incarnata* 47; *lactea* 48; *lanceolato-paraphysata* 48; *micacea* 69; ***minutula*** 80\*; *oenotherae* 57; *pastinacae* 58; *phymatodes* 59\*, 60; *pulviscula* 61; *regalis* 61; *rehmii* 31, 32; *saxonica* 69; *spiraecae* 66; *translucens* 69; *tirolensis* 69; *tyrolensis* 69, 71\*; *vogelii* 70, 71\*; *vulgaris* 43, 69; *vulgaris* var. *mycetica* 70; *vulgaris* var. *sanguinella* 70; ***winteri*** 70, 71\*; *xeroplastica* 72  
*Phacorrhiza* 315  
*Phaeoaphelia* 251, 276, 294, 315  
*Phaeocarpus* 301, 315  
*Phaeociboria* ***agaricicola*** 32, 33\*
- Phaeoclavulina* 315  
*Phacocoriollellus* 281  
*Phaeocreopsis* 5; *hypoxylloides* 5; *peziziformis* 5  
*Phacocyphella* 301, 315; *muscicola* 146; *ochroleuca* 131  
*Phaeocyphellopsis* 109, 110, 113, 114, 116, 302, 315; *ochracea* 114, 116  
*Phacodaedalea* 281  
*Phaeodepas* 289, 291, 316  
*Phaeodon* 316; *thwaitesii* 184  
*Phacoglabrotricha* 134, 302, 316; *rubi* 131; *sessilis* 136  
*Phaeohelotium* 29, 43, 77, 78; *flavum* 54, 78; ***monticola*** 54, 55\*, 78  
*Phaeolus* 274, 276, 277; *schweinitzii* 277  
*Phaeophlebia* 287, 294, 305, 316  
*Phaeoporotheleum* 290 316  
*Phacopterula* 301, 316  
*Phaeoradulum* 316  
*Phaeoschizophyllum* 316  
*Phacosolenia* 244 290, 302, 316; *densa* 138  
*Phacospheria* *sowerbyi* 20  
*Phallus* *marcidus* 72, 73  
*Phanerochaete* 222, 259, 262, 308, 310, 314, 316, 318  
*Phellinus* 205, 240, 274-277  
*Phellodon* 170, 222, 246, 247, 272, 297, 316, 376; sp. 377\*; *alboniger* 170; *cokeri* 170; *confluens* 170; *delicatus* 171; *ellisianus* 171; *melaleucus* 171, 178; *niger* 170, 178; *putidus* 170; *sinclairii* 178; *tomentosus* 170  
*Phialea* 30, 31, 42, 51, 56, 60, 80; *alutipes* 34; *ampla* 35; *arenicola* 35; *cacaliae* 44; *craginiana* 40; *cyathiformis* 42; *cyathoidea* 30; *dearnessii* 43; *eschscholtziae* 44, 45\*; *exarata* 44; *gracilis* 47; *minutula* 80; *macrospora* 51; *myricariae* 56; ***nigrescens*** 55\*, 56; *phaeoconia* 58, 59\*; *porioides* 148; *simulata* 65; *subcarnea* 68; *tetraspora* 69, 71\*; *winteri* 69, 70  
*Phlebia* 150, 222, 257-259, 282, 287, 316, 318  
*Phiebiella* 316  
*Phlebophora* 302, 316  
*Phleogenia* 227  
*Phoma* 9, 12, 15, 17, 22-24; *acuta* 25; *brassicae* 20, 25; *cucurbitaceum* 42; *herbarum* 9, 10, 20, 27, pl. 1 fs. 1-3, 5-6, pl. 2 fs. 1-6; *herbarum* f. *galiorum* 13; *herbarum* f. *humuli* 13; *hibernica* 9, 10, 12-15; *incrassans* 20, 26; *lignicola* 9, 10, 12, 14, 15; *lingam* 13, 14, 17, 20-22, 25-27; *lingam* var. *napobrassicaceae* 20; *napobrassicaceae* 20, 21; *oleracea* 9, 10, 13, 14, 20, 21, 27; *oleracea* var. *helianthi-tuberosi* 10, 14; *oleracea* var. *scrophulariae* 10, 14; *oleracea* var. *urticae*. 10, 14; *pigmentivora* 10, 12, 14; *siliquastrum*

- 18, 20; urticae 9, 10, 12, 13; violacea 9-11, 14  
*Phomopsis* *incrassans* 20  
*Phragmites* 60  
*Phylacteria* 260, 295-297, 316  
*Phyllocarbon* 316  
*Phylloporia* 276  
*Phyllosticta* 17; sp. 26; *brassicae* 18-21, 26; *brassicaecola* 18, 26; *brassicola* 17-19; *brassicina* 18; *napi* 18, 19  
*Physalacria* 252, 253, 302, 305, 309; *inflata* 316  
*Physipsorus* *byssinus* 148  
*Phytolacca* 61  
*Picea* 341  
*Pinus* 149; *silvestris* 43, 47, 73, 347; *strobos* 152  
*Piptoporus* 280, 281  
*Piricaua* 407, 408; *paraguayensis* 408; *trigonella* 409  
*Pistillaria* 222, 250, 252, 307, 310, 316, 318  
*Pistillina* 252, 291, 308, 316  
*Pithomyces* 408  
*Placodes* 278  
*Platygloea* 243  
*Plenodomus* 14, 17, 21, 25; *lingam* 14, 16-22\*, 24\*-26\*, 27, pl. 1 f. 4; *rabenhorstii* 20, 21, 25, 26  
*Pleospora* *herbarum* var. *brassicae* 18; *maculans* 20; *napi* 20  
*Pleurobasidium* *telac* 401  
*Pleurodon* 286, 316  
*Pleurosordaria* *olerum* 17, 20  
*Pleurotellus* 147  
*Pleurotopsis* 302, 316  
*Pleurotus* 283, 284  
*Plicatura* 150, 249, 258, 259, 290, 316, 320; *alni* 150; *crispa* 151; *faginea* 151  
***Plicaturopsis*** 150, 222, 249, 288-291, 316, 320; ***crispa*** 143\*, 150  
*Pluteus* *cervinus* 231  
*Poculopsis* *oregnensis* 57  
*Podoscypha* 294, 316, 319; *undulata* 308  
*Podoserpula* 255, 316  
*Podostroma* 5  
*Podostrombium* 316  
*Pogonomyces* 281  
*Polydesmus* *exitiosus* 20  
*Polyozellus* 185, 241, 249, 296, 297, 316  
*Polyozus* 303, 316  
*Polyplius* 286  
*Polyporellus* 281  
*Polyporus* 186, 205, 206, 236, 241, 242, 278-281, 283-285; *brumalis* 283; *cinnabarinus* 355; *confluens* 286; *corticola* 314; *dichrous* 310; *fimbriatus* 148; *giganteus* 280; *maculatissimus* 284; *marginatus* 279; *ovinus* 241; *pezizoides* 148; *schweinitzii* 277; *squamulosus* 283, 284; *udus* 283; *varius* 283; *versicolor* 279  
*Polystictus* 162, 241, 276, 279; *funalis* 162; *gleadoni* 162; *leoninus* 162; *microcyclus* 174  
*Populus* 57, 126; *balsamifera* 126; *canadensis* 51; *nigra* 126; *tremula* 51, 125, 126; *tremuloides* 108, 124, 125; *trichocarpa* 124, 125  
*Poria* 120, 147, 148, 242, 279-281; *brevipora* 148; *byssina* 148; *fatiscens* 149; *fimbriata* 148; *medulla-panis* 266; *vulgaris* 280  
*Porodisculus* 281  
*Porogramme* 258, 259, 282, 317, 319  
*Porolaschia* 302, 317  
*Poromycena* 244, 282  
*Poronidulus* 281  
*Porostereum* 317  
*Porotheleum* 147, 148, 264, 287, 288, 290, 317; *fimbriatum* 148, 288; *lacerum* 148; *pezizoides* 148  
*Porothelium* 147, 148  
*Porphyrosoma* 5  
*Postia* 205, 281  
*Potentilla* 57  
*Prilleuxia* 317  
*Protocrea* 5  
*Prototremella* 317; *calospora* 374  
*Prunus* 57; *spinosa* 99  
*Psamma* *arenaria* 54  
*Psathyrella* 215  
*Pseudoasterodon* 301, 317  
*Pseudocraterellus* 236, 248, 249, 317  
*Pseudodasyscypha* 290, 301, 317  
*Pseudodiscinella* 78  
*Pseudofavolus* 281, 284, 294  
*Pseudofistulina* 264, 317  
*Pseudohelotium* *laricinum* 50; *pineti* 47; *strumosum* 68; *undulatum* 79  
*Pseudohydnum* 273, 302, 311, 317  
*Pseudombrophila* *decrata* 42  
*Pseudonectria* 6; ***aquifoliae*** 35, 37\*  
*Pseudopeziza* *carneopallida* 36  
*Pseudotomentella* 296, 317  
*Pseudotrametes* 281  
*Pseudotremelodendron* 215, 252, 294, 303, 317  
*Pseudotyphula* 252, 317  
*Pseudotulasnella* 378  
*Psilachnum* 70; ***lanceolato-paraphysatum*** 43, 48, 49\*; *micaceum* 70, 71\*  
*Pteridium* *aquilinum* 98, 103, 104  
*Pterula* 207, 208, 251, 252, 316, 317; *pennata* 179; *sprucei* 178  
*Pterulicum* 207, 236, 252, 258, 317  
***Pteruloidae*** 251  
*Ptychella* 303, 317  
*Punctularia* 287, 288, 290, 291, 294, 305, 316, 317; *tuberculosa* 287  
***Punctulariaceae*** 287  
*Pycnodon* 317  
*Pycnoporus* 281

- Pyrenopeziza 32, 66  
 Pyrenotrichum 306  
 Pyronema 355  
 Quercus 57, 104, 194; ilex 40; laurifolia 38  
 Radulochaete 273, 301, 317  
 Radulomyces 317  
 Radulum 273, 303, 317, 320; lactum 221, 226  
 Ramaria 208, 222, 236, 239, 252, 267, 268, 307, 308, 315, 317  
 Ramariicum 208, 239, 260, 268, 317  
 Ramariopsis 222, 252, 317  
 Repetobasidium 228, 257, 258, 317  
 Resupinatus 290, 302, 316  
 Rhizodium 317  
 Rhizopidonema 299, 317; crustaceum 317  
 Rhizopidonematomyces 317  
 Rhizoconchia 387, 388; microsclerotia 400; praticola 390; solani 372, 386, 390  
 Rhizomera 317  
 Rhodoarrhenia 290, 291, 317  
 Rhodocyphella 303, 318  
 Rhus 57  
 Ribes 57  
 Ricinophora 318  
 Rigidoporus 281  
 Rimbachia 208, 249, 290, 303, 318  
 Robinia pseudacacia 70  
 Rosa 57; canina 99, 102  
 Rubus 57, 64; caesius 64, 65; caesius var. asculicarpa 65; suberectus 138  
 Rumex 99, 103  
 Russula 233, 240, 247, 298, 299  
 Rutstroemia 77, 79; **belisense** 36, 37\*; calopus 54; **coracina** 39, 41\*; **maritima** 52, 53\*  
 Sabal blackburnianum 138  
 Salix 35, 57, 73, 117, 126, 138; sp. 195; alba 114  
 Sambucus 104  
 Sarawakus 2  
 Sarcodon 157, 158, 164, 177, 181, 185, 222, 247, 272, 295-297, 318; armeniacus 156, 163; atroviridis 157, 158, 185, 186; bubarinus 164; **carbonarius** 157, 158, 185, 186; fumosus 185; imbricatus 181; laevigatus 158, 181; **martioflavus** 164; pygmaeus 170; stereosarcinon 164; **thwaitesii** 157, 177, 185\*, 186  
 Sarcodontia 222, 257-259, 273, 315, 318; crocea 318; setosa 318  
 Sarcoleotia nigra 94  
 Sarcopodium 303, 318  
 Sarcoxylon 1  
 Sarothamnus scoparius 138; vulgaris 138  
 Scaphophorum 318  
 Scenidium 281  
 Schizonia 318  
 Schizophyllum 222, 288-291, 305, 312, 316-318  
 Schizopora 281  
 Sclerodon 318  
 Scleromitria 318  
 Scleromitrula 87  
 Sclerotinia nyssaegea 56; trifoliorum 87  
 Sclerotium deciduum 386; semen 17, 19; sphaeriaeforme 20, 21, 26; rufi-sii 401  
 Scopuloides 318  
 Scutiger 279, 286  
 Scyphophilus 318  
 Scytinopogon 247, 252, 296, 297, 318  
 Scytinostroma 210, 222, 239, 258, 259, 271, 272, 278, 294, 318, 373; portentosum 232; praestans 216  
 Sebacina 218, 379; bressadolae 207; fibrillosa 318, 382, 383\*; incrassata 207; prolifera 355  
**Septobasidiales** 243  
 Septobasidium 213, 243, 315  
 Septogloeum 197  
 Septoria sp. 25; brassicae 20, 21  
 Sequoia 35  
 Serpula 220, 222, 254, 255, 259, 282, 311, 313, 314, 318, 321; himantoides 200, 209; **mollusca** 209  
 Sesia 318  
 Sirobasidium 225  
 Sistotrema 212, 214, 218, 221, 222, 255, 257-259, 273, 282, 311, 318, 319, 373; confluens 258; hirschi 214; niveo-cremeum 221  
 Sistotremastrum 214, 221, 259, 318  
 Skeletocutis 281  
 Skepperia 249, 294, 301, 318  
 Skepperiella 249, 303, 318  
 Smilax 57  
 Solena 118, 288  
 Solenia 118, 119, 128, 130, 288, 290, 318; albissima 123; candida 118; confusa 110; eruciformis 123; fasciculata 128, 130; malbranchei 131; minima 130; ochracea 116, 118; polyporoidea 120; porioides 148; pubera 118, 119, 122; villosa 128  
 Soppitiella 318  
 Sorbus aucuparia 126  
 Sordaria 355  
 Sparassis 222, 252, 291, 292, 294, 314, 318; crispa 292; simplex 208, 293, 318  
 Sparaxis 291, 292  
 Spathularia 81  
 Sphaerella brassicacecola 17; brassicicola 17  
 Sphaeria 19; brassicace 17, 18, 19, 26; brassicacecola 17-19; brassicicola 17, 18; lingam 13, 20, 21, 25; maculans 20, 21; napi 20; olerum 19, 20  
 Sphaerostilbe 5, 6  
 Sphaerula 318

- Sphagnicola 29, 50, 78, 79; ciliifera 50, 78; **fergussonii** 78; iodocyanescens 79; **lari-**  
**cina** 50, 53\*, 79; marchantiae 79;  
**obstricta** 79; rivularis 79  
*Sphagnum* 92, 360, 361, 363  
*Spiraea filipendula* 50  
*Spongipellis* 281  
*Sporidesmium* 407; *trigonellum* 407-411  
*Spragueola* 85  
*Squamamanita* 331, 333; *schreieri* 331  
*Squamanita* 331-334, 336, 338, 340-342,  
348, 351-358; sp. 340; **odorata** 332-334,  
341, 342, 343\*, 345, 347, 351-353\*, 355,  
357; *odorata* f. *bispora* 343\*, 345; **para-**  
**doxa** 334, 348\*, 349\*, 350\*, 352, 353\*,  
355, 358; **pearsonii** 334, 345, 346\*-348,  
351-353\*, 355, 358; *schreieri* 331-334,  
336, 337\*, 338, 352, 353\*, 354; **scotica**  
(nomen provisorium) 334, 341, 346\*,  
351, 358; **tropica** (nomen provisorium)  
334, 338, 339\*, 340, 352, 353\*, 354, 356;  
**umbonata** 332, 334, 335\*, 336, 352, 354  
*Stecchericum* 269, 270, 273, 318  
*Steccherinum* 175, 176, 222, 273, 294, 309,  
313-315, 318; *adustum* 238; *morgani*  
164, 176; *ochraceum* 175; *rawakense*  
171, 172, 173\*-175\*, 176; *reniforme* 171  
*Steironema* 57; *ciliatum* 43  
*Stelligera* 319  
*Stemphylium* 20  
*Sterbeekia* 319  
*Sterellum* 319  
*Stereofomes* 301, 319  
*Stereoglocostidium* 319  
*Stereophyllum* 294, 319; *boreale* 144  
*Stereum* 222, 243, 257, 261, 271, 292-295,  
311, 319, 320; § *Phellina* 261; *acerinum*  
var. *nivosum* 367; *hirsutum* 208; *lepro-*  
*murraili* 308; *purpureum* 307;  
*seriatum* 367; *strumosum* 367; *sulcatum*  
313; *taxodii* 363, 313  
*Sticholoclavaria* 222, 251, 253, 299, 301, 319  
*Stigmatea brassicace* 18  
*Stigmatolemma* 290, 303, 318, 319  
*Stilbella* 6  
*Stilbocrea* 5, 6  
*Stilbospora* 197; *conglomerata* 194; *micro-*  
*sperma* 194; *sphaerosperma* 194  
*Stromatinia* 29; *rapulum* 29  
*Stromatocrea* 5  
*Stromatocyphella* 139, 140, 142, 290, 291,  
319; *aceris* 140; *conglobata* 137\*, 140;  
*lataensis* 121\*, 123-125, 140  
*Stromatoscypha* 147, 148, 264, 287, 288,  
290, 317, 319; *fimbriata* 148  
*Stypinella* 215  
*Suillosporium* 255, 259, 319, 398; *cysti-*  
*diatum* 398  
*Sulphurina* 319  
*Symporicarpos occidentalis* 43  
*Syzygospora* 319  
*Tapesia* 62  
*Tephrosia virginiana* 39  
*Terana* 319  
*Thanathophorus* 222, 224, 228, 258, 262,  
319, 374, 375, 379, 380, 384, 386-388,  
391, 392, 400, 401; *cucumeris* 214, 387-  
389\*, 390; *practicola* 376, 388, 389\*,  
390; **sterigmaticus** 388, 389\*, 390  
*Thelephora* 205, 206, 222, 241, 242, 252,  
260, 292, 243, 295-297, 299, 314, 316,  
318, 319; *acerina* 366; *candida* 366;  
*dryina* 366; *pallida* 260, 293; *terrestris*  
260, 297  
*Thelephorella* 301, 319  
*Thelepora* 319  
*Theleporus* 319  
*Thuemennella* 1, 2, 4, 5; **bicolor** 1, 3;  
**cubispora** 1, 2; **hexaspora** 1, 3, 4\*;  
**hirsuta** 1, 2; *javanica* 1, 2  
*Thuemenioides* 82, 89, 91, 94; *atropurpureum* 89, 90\*, 94  
*Thuja occidentalis* 51; *orientalis* 51  
*Thwaitesiella* 319  
*Thyronectria* 6  
*Tilia* 108  
*Tinctoporia* 319  
*Tomentella* 222, 247, 256, 260, 296, 297,  
312, 317, 319; § *Botrytes* 373; *granulata*  
396  
*Tomentellastrum* 296, 319  
*Tomentellina* 312, 319  
*Trabecularia* 319  
*Trametes* 222, 267, 279-281, 285; *ohiensis* 266  
*Trechispora* 221, 259, 318, 319, 373; *niveo-*  
*cremea* 221  
*Tremella* 217, 224, 376  
*Tremelloidendron* 207, 294; *candicans* 366  
*Tremelloidropsis* 243, 252, 294, 303,  
317, 319  
*Tremellobodon* 273, 302, 320  
*Trichaptum* 281  
*Trichocarpus* 320  
*Trichoderma* 5  
*Tricholoma* 316, 331, 381, 356, 357;  
§ *Coolia* 333; *caligatum* 340, 357; *focale*  
357; *odoratum* 332, 342, 345; *schreieri*  
332, 337; *sclerotoideum* 356  
*Trichopeziza* 32; *aconiti* 32; *tiliae* 106  
*Trimmatostroma* 193, 197  
*Troglia* 249, 303, 320; *crispa* 151  
*Trombetta* 320  
*Truncospora* 266, 281  
*Tuberularia* 6  
*Tubulinicrinis* 257, 259, 320  
*Tulasnella* 213, 214, 222, 224, 225, 227,  
241, 242, 256, 258, 261, 262, 310, 314,  
315, 317, 320, 376, 379; *anceps* 386;  
*metallica* 381

- Tumidapexus 252, 320  
 Turbinellus 320  
 Tylodon 320  
 Tylospurma 390  
 Tylospora 259, 320  
 Tympanis crataegi 65  
*Typha* 77; *latifolia* 134  
*Typhula* 222, 252, 315, 320; *betae* 17;  
 brassicaceae 17, 19; *idahoensis* 253  
*Tyrodon* 320  
*Tyromyces* 205, 279, 280, 281; *byssinus* 148  
*Ulex* sp. 138; *eupaeus* 99, 103  
*Ulmus* 36, 57, 99, 103, 108, 407, 410  
*Ungulina* 279; *ulmaria* 280  
*Urcocella spiraeae* 66  
*Urtica dioica* 10, 12, 13  
*Uthatobasidium* 224, 225, 228, 258, 262,  
 320, 374, 375, 379, 380, 390, 398;  
 § *Ypsilonidium* 390, 391; *citriforme* 391,  
 398; *fusisporum* 391, 393\*, 398; *ochraceum*  
 391  
*Vaccinium* 57  
*Vaginata umbonata* 332, 334, 336  
*Van-Romburgia* 294, 303, 320  
*Vararia* 208, 211, 230, 260, 271, 273-275,  
 277, 278, 305, 309, 313, 320, 374; *dura*  
 271  
*Veluticeps* 294, 320; *berkeleyi* 320  
*Verpatinia* 86, 87  
*Vibrissea* 30; *truncorum* 29  
*Viola odorata* 99, 102  
*Vitis* 57, 61  
*Volutella* 6  
*Volvariella* 352, 354  
*Vuilleminia* 211, 217, 218, 222, 241, 256,  
 259, 320, 373; *comedens* 216, 217, 226;  
*dryina* 217  
*Wainiocora* 320  
*Waitea* 258, 320, 373, 374, 380, 388, 391,  
 392; *circinata* 227, 378, 379, 391, 393\*  
*Whitfordia* 265, 285  
*Wiesnerina* 290, 291, 320  
*Woldmaria* 290, 320  
*Woronina* 310  
*Xanthochrous* 242, 274  
*Xanthoglossum* 82  
*Xanthoporia* 276  
*Xenasma* 211, 259, 320  
*Xenolachne* 223  
*Xenopus* 301, 320  
*Xenotype aterrima* 317  
*Xerocarpus* 320  
*Xerotinus* 281, 283  
*Xerotus* 281, 283, 285  
*Xylaria scruposa* 43  
*Xylobolus* 261, 294, 320  
*Xylodon* 301, 321  
*Xylomyzon* 321  
*Xylophagus* 254, 321  
*Zelkova* 98, 102  
*Zygodesmus* 301, 321