TAXONOMY OF OPERCULATE DISCOMYCETES

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Chairman, J. A. Nannfeldt, Uppsala

Contents

J. A. Nannfeldt (Sweden): Introductory remarks by the Chairman, 385.

J. van Brummelen (The Netherlands): Ascocarp ontogeny and a natural classification of the Ascobolaceae, 389.

J. W. Kimbrough (U.S.A.): Ascal structure, ascocarp ontogeny, and a natural classification of the Thelebolaceae, 395.

J. W. Paden (Canada): Imperfect states and the taxonomy of the Pezizales, 405.

A. Raitviir (Estonian S.S.R.): Statistical methods and specific delimitation in the genus *Otidea*, 415.

H. Dissing (Denmark): Specific and generic delimitation in the Helvellaceae, 425.

W. C. Denison (U.S.A.): Differentiation of tribes and genera in the family Sarcoscyphaceae, 433.

F.-E. Eckblad (Norway): The suboperculate ascus—a review, 439.

R. P. Korf (U.S.A.) (Convener): Taxonomy of Operculate Discomycetes: synthesis, 445.

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INTRODUCTORY REMARKS BY THE CHAIRMAN*

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A personal impression is given of the progress in the study of Discomycetes during the last half century. Boudier's fundamental ideas still form the main basis for a classification of the Discomycetes. Some of the recent trends in the taxonomy of the Operculates are considered.

I feel it a great honour to preside at this meeting and take the opportunity to say some introductory words.

It would have been natural to try to give a short historical sketch of the progress in "discomycetology" during the nigh 50—or more precisely 48—years I have been working in this branch. In recent times, however, Dr. Kimbrough in his excellent paper entitled "Current trends in the classification of Discomycetes" has already covered the historical background, so that I shall restrict myself to some personal impressions.

As we know, the French mycologist Boudier as early as 1879 had already suggested the high taxonomic value of the mode of dehiscence of the ascus, which opens either by means of a hinged operculum or a simple pore. Six years later he published a rather elaborate scheme of the classification of the Discomycetes, the main divisions of which were the Operculates and Inoperculates. In view of the optical equipment of his time it is surprising that he was able to see these subtle structures.

It would take a long time for Boudier's ideas to become generally known and accepted. Perhaps the time was not yet ripe, perhaps there was some other important reason.

Taxonomists, of course, are to a certain degree influenced by geographical boundaries, both natural and political, as most of their field work is necessarily restricted to a certain area or certain areas. Most publications, too, cover geographical areas of limited extent. While this is quite natural, it should nevertheless be borne in mind that the tendency of too many students to neglect more or less completely the investigations carried out in even closely neighbouring areas has slowed down progress considerably and become the source of a great deal of unnecessary confusion.

When I began studying Discos the standard works were first of all Rehm's magnificent volume in Rabenhorst's "Kryptogamenflora von Deutschland, Österreich und der Schweiz" but also Karsten's "Mycologia Fennica," Schroeter's Flora of

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Silesia, and Phillips' and Massee's Floras of Britain, all of the 19th century. Three of these had been published so late that their authors must have had ample time to seem to have been influenced, however, while Rehm only cursorily mentioned get acquainted with the ideas of the great French mycologist. The authors do not Boudier's work.

From the very beginning I had the privilege of having access to Boudier's "Icones Mycologicae". I studied this work carefully, admired the plates, read his other publications, compared Discos of various groups, and soon became convinced of the soundness of his ideas. Other contemporary students arrived at the same conclusion, and particularly after the publication in 1928 of Seaver's "North American cup-fungi (Operculates)" every serious student seems to have accepted the two main groups proposed by Boudier.

Up till now no new facts have been discovered to disturb the picture. It is true that there are still a number of Discos whose position is doubtful. Most annoying perhaps is the genus *Cyttaria*, which is most peculiar in almost every respect. After the recent studies by Dr. Kimbrough I am personally convinced that it is a true Operculate, the aberrant features of which may be explained by its ecology. To give one example, thick-walled cells and relative longevity of tissues form a combination of features which is known to have evolved independently in various groups of fungi. Suffice only to mention the lichenized fungi.

The Operculates constitute a much smaller group than the Inoperculates and one which is much more homogeneous and far less diversified. To my mind the Operculates form a natural monophyletic taxon, the origin of which dates far back in time. The group seems to have split up rather early into different evolutionary lines, of which at least the surviving members are not too numerous. The partial unveiling of these lines is perhaps the most important advance in our field during the last half-century. But here also Nature has not cared, of course, to mark the evolutionary lines with arrows indicating in which direction they run.

There are, in my opinion, clear indications that certain aberrant small groups or single species will eventually be found to constitute evolutionary lines of their own.

Fifty years ago developmental and cytological studies on the stages of ascocarp formation and related phenomena were very much in vogue. In most groups of plants and animals similar studies on early stages had given results of utmost phylogenetic interest, but in Ascomycetes almost every species studied showed a number of peculiar or even unique features, which made it impossible to discern a pattern of phylogenetic lines. Would it be possible to explain this phenomenon in the following way? The Ascomycetes, after having lost their normal sexuality, which entails the loss at least of the motility of ciliate male gametes, have tried to develop a substitute in various ways, and it is these ways which are still flexible and open to further experimentation.

Even if or, rather, perhaps because studies such as mentioned above have failed to elucidate the origin of the Ascomycetes and the main lines of their evolution, there is every reason to believe that similar investigations in smaller and well circum-

scribed groups will be very fruitful in tracing what I would like to call micro-evolution. Thus it is with great expectation that van Brummelen's paper is awaited.

There is another character, a cytological one of rather simple nature, which in recent times has proved to be very important taxonomically, viz. the number of nuclei in the mature spore. Four-nucleate spores were one of my motives in 1937 for emending the scope of the genus *Helvella*, and some 25 years later Berthet was able to demonstrate that the number of nuclei is of high value generally in characterizing the larger groups within the Operculates.

Further new approaches to a better understanding of the relationships are the studies on the apical apparatus of the ascus by Chadefaud and his collaborators, on the spore ornamentation by Mme Le Gal, on the carotinoids by Arpin, on various chemical reagents, on conidial stages, etc., etc.

It is always tempting to believe that a new approach promises to become the thread of Ariadne, with the help of which it should be possible infallibly to find the way out of the labyrinth, and so the significance of the results is sometimes grossly overemphasized.

A case in point is in my opinion the transference by Arpin of *Sepultaria*, *Tricharia*, *Mycolachnea*, and *Trichophaea* to the Otideaceae, because they were found devoid of carotinoids. Morphologically they deviate considerably from the typical members of this family, but show good agreement with *Scutellinia* and several other carotinoid-possessing genera, in the neighbourhood of which the genera under discussion have usually been placed. It may be remembered that albinistic mutants, e.g. in *Sarcoscypha coccinea*, are known to occur. Why would it not be possible for such a mutant to become genetically stable and give rise to a new species or a group of species? Moreover, can we be sure that the genera mentioned earlier are really devoid of carotinoids? Is it not possible to assume that these are present in the shape of colourless precursors or colourless derivatives? To my mind the situation is much the same as in the period of the first bold attempts at employing lichen-substances in lichen taxonomy.

Sound taxonomy should make use of all the characters available and weigh them against one another. Besides it should be kept in mind that in certain cases any character may fail to show up or appear in disguised form.

Our present knowledge of the classification of the Operculates has recently been excellently summarized, independently of each other, by Rifai and Eckblad. It is interesting to see how they arrived at similar conclusions in most respects. Their work also shows how numerous and big are the gaps in our knowledge. It is to be hoped that this meeting will contribute to at least some of the gaps being filled up, although on the other hand new gaps are likely to be uncovered. In this connection it should be pointed out that in almost all larger genera the species are badly in need of a careful and critical revision.

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ASCOCARP ONTOGENY AND A NATURAL CLASSIFICATION OF THE ASCOBOLACEAE*

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(With 1 diagram)

Ascocarp ontogeny has proved to be a very useful basis for the classification of the Ascobolaceae. A scheme of interrelationships between the sections of *Ascobolus* and *Saccobolus* is given. It is suggested that ascocarp ontogeny will play a prominent part in recognizing series of supra-specific taxa within other natural families of the Discomycetes, e.g. Thelebolaceae and Pyronemataceae.

Among the Pezizales the Ascobolaceae and their allies include many objects suitable for developmental studies. The coprophilous species in particular can often be easily isolated and grown on artificial media.

Since Yu's experiments (*1954*) on factors concerning the most favourable conditions for ascospore-germination in some coprophilous species of *Ascobolus*, several species have been studied that could not be cultured before. The development of Discomycetes that do not produce fruit-bodies in culture is usually incompletely known. Publications on the sexuality, compatibility and cytology of such species that have been cultured contain a great deal of information from which many data on ascocarp ontogeny can be deduced. The development of the sporophytic part of the ascocarp in particular has drawn the attention of investigators in these fields of research. Unfortunately identifications can only rarely be verified. Studies devoted to the ontogeny of both gametophytic and sporophytic parts of the ascocarp of Discomycetes are very rare.

Corner's classical publications (*1929a*, *1929b*, *1930a*, *1930b*, *1931*) laid a basis for a comparative morphology of Discomycetes with special emphasis on the dynamic aspects of ascocarp ontogeny. This, however, did not result in an increased interest in the problems and significance of ascocarp ontogeny of Discomycetes until the last decennium. Recently the Ascobolaceae and their allies have been the subject of ontogenetic studies by Gamundi & Ranalli (*1963*, *1964*, *1966*, *1969*), van Brummelen (*1967*), and Durand (*1971*).

METHODS

In developmental studies of Discomycetes the results of three methods should be combined to obtain a complete structural and functional image of ascocarp ontogeny.

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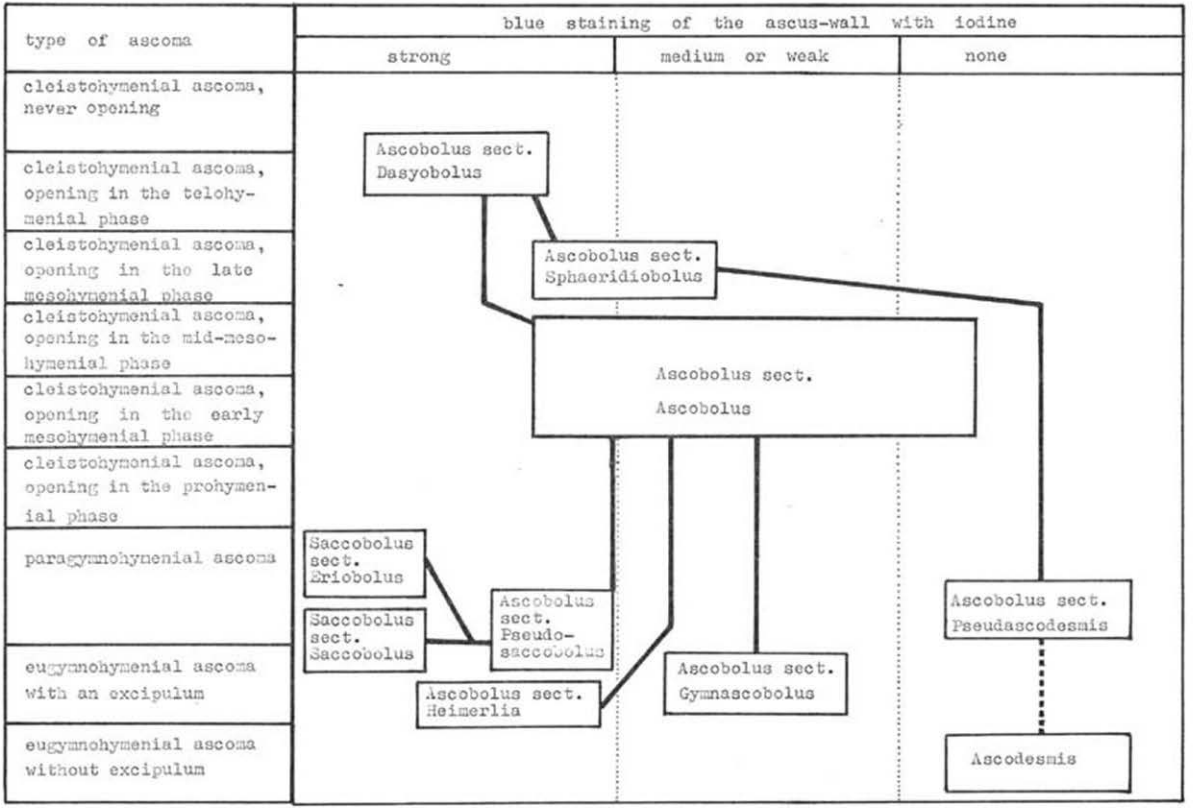
DIAGRAM I


type of ascoma
blue staining of the ascus-wall with iodine
strong
medium or weak
none
cleistohymenial ascoma, never opening
cleistohymenial ascoma, opening in the telohymenial phase
cleistohymenial ascoma, opening in the late mesohymenial phase
cleistohymenial ascoma, opening in the mid-mesohymenial phase
cleistohymenial ascoma, opening in the early mesohymenial phase
cleistohymenial ascoma, opening in the prohymenial phase
paragymnohymenial ascoma
eugymnohymenial ascoma with an excipulum
eugymnohymenial ascoma without excipulum
Ascobolus sect. Dasyobolus
Ascobolus sect. Sphaeridiobolus
Ascobolus sect. Ascobolus
Saccobolus sect. Eriobolus
Saccobolus sect. Saccobolus
Ascobolus sect. Pseudosaccobolus
Ascobolus sect. Heimerlia
Ascobolus sect. Gymnascobolus
Ascobolus sect. Pseudascodesmis
Ascodesmis

Besides a study of vital and stained microscopic preparations of whole mounts of the earliest stages (initiation) extensive investigations of series of microtome sections showing different stages are indispensable (topographic ontogeny). Omission of this method has led to erroneous interpretations and unacceptable generalizations. In several cases hyphae of various origin can be differentiated by staining. A third method (Corner's hyphal analyses) is an attempt to trace hyphae from their origin to their end or vice versa through their elaborate organization in the fruit-body. In hand-made sections or oriented fragments of tissue, elements are separated by gently pressing the cover-glass or pulling the hyphae with needles. Unfortunately, this method also does not help very much in unravelling the often perplexingly intricate structures of the early stages of the ascocarp.

Ascocarp ontogeny in Ascobolaceae

The first indication of ascocarp initiation is the development in the mycelial hyphae of weakly to strongly curved and swollen branches. Of these archicarps one or more terminal or subterminal cells differentiate into multinuclear ascogonia. Antheridia are also often found. In certain species parthenogenetic or apogamous processes have been reported.

From the base of the archicarp or from adjacent mycelial hyphae, and shortly before or after the differentiation of ascogonia, thin hyphae arise. These branch and form an incomplete or continuous sheath around the archicarp. This primary sheath is the beginning of the gametophytic part of the ascocarp. In open types of development, i.e. with gymnohymenial ascomata, the investing hyphae of the primary sheath have only a restricted growth in that they do not form an entire sheath over the hymenium during further development. In closed types of development, i.e. with cleistohymenial ascomata, the investing hyphae produce a continuous primary sheath. Thus small spherical bodies are formed. Usually there is a more or less centrally placed archicarp with a strongly swollen ascogonal apparatus in each of them, surrounded by intricate investing hyphae. Often the cells of the primary sheath undergo a change in becoming inflated and thick-walled, while their growing activity slows down.

Observations in species of *Ascobolus* with cleistohymenial ascomata have revealed that at a certain stage of development, when the primary sheath has reached a thickness of only a few layers of cells, a secondary sheath develops within it. The same has been observed in species of *Thelebolus*, while Durand (*1971*) described a similar development in a species of *Lasiobolus*. The hyphae of this sheath are relatively narrow and have dense cytoplasm. They arise near the base of the archicarp. Unfortunately it was not possible to establish with certainty from what cells they originate.

As a result of the active growth of hyphae of the secondary sheath within the primary sheath tangential forces are exerted on the peripheral layers. Depending on the structure and growth activity of the hyphae of the primary sheath different cortex-textures will result. Peripheral cells may become flattened, or break up into

small groups. During later development the process results in smooth and rough surfaces respectively. Both kinds are found in cleistohymenial ascomata of *Ascobolus*, *Thelebolus*, and *Lasiobolus*.

Peripheral gaps are also filled by interstitial growth of new elements from the inner layers. During further development hyphae of the secondary sheath form the medulla in the lower part and the palisade of paraphyses in the upper part of the young ascocarp.

There is a striking resemblance between the development of cleistohymenial ascomata in *Ascobolus* and its allies and the developmental scheme given by Doguet (*1955*) for perithecia in *Melanospora*.

From the ascogonia ascogenous hyphae grow upward. Their first cells are multinuclear. Soon branches are sent out whose cells are dikaryotic. On reaching the thin layer of small plasm-rich cells at the base of the paraphyses these branches spread centrifugally, with frequent sympodial ramification. Their cell-divisions are accompanied by conjugate nuclear divisions. The croziers, terminally formed on this sympodial system, grow up from between the bases of the paraphyses and give rise to the asci. The incipience, development, and ripening of the asci proceeds in a centrifugal direction; the oldest being in the centre of the hymenium.

Further development of the ascocarp is mainly brought about by intercalation of new elements and subsequent strong inflation of asci. Only in species of *Ascobolus* sect. *Gymnascobolus* is there a submarginal secondary growing zone (cf. Corner, *1929a*).

The types of development in Pezizales are distinguished by the developmental phase in which the hymenium becomes exposed. In an earlier study (van Brummelen, *1967*) two sets of descriptive terms were introduced.

During ascocarp ontogeny five phases were distinguished in respect to the ripening of the hymenium. These chronological phases were named (1) archihymenial phase: before the initials of the hymenium are present; (2) prohymenial phase: paraphyses are present but no croziers are as yet formed; (3) mesohymenial phase: the hymenium is in progress of ripening, but no asci have as yet ripened; (4) telohymenial phase: mature asci are present and normally ascospores are discharged; and (5) posthymenial phase: the hymenium becomes overripe or obsolate and decomposes.

With regard to the hymenial development two main types of ascomata were distinguished. (I) Cleistohymenial ascomata in which the hymenium is enclosed, at least during its early development. Ascomata of this type may be further subdivided according to the hymenial phase when they open to expose the hymenium. (II) Gymnohymenial ascomata: the hymenium is exposed from the first until the maturation of the asci.

Two subgroups of the latter were recognized: (a) paragymnohymenial ascomata in which the ascogonium is overarched by investing hyphae of limited growth that do not form a continuous sheath and (b) eugymnohymenial ascomata with a fully exposed ascogonium.

By the use of these unambiguous terms a more detailed differentiation in developmental types is possible than before. Of the seven types recognized (van Brummelen *1967*: *pl. 17*) no less than six occur within the genera *Ascobolus* and *Saccobolus*.

CLASSIFICATION

In my opinion the genera *Ascobolus* and *Saccobolus* form a very homogeneous and natural group of operculate Discomycetes, which can be given the rank of family (cf. Rifai, *1968*). Especially the existence of a violet episporial pigment of vacuolar origin is a unique character which unites these fungi. Between the Ascobolaceae and other coprophilous Pezizales with protruding asci the relations are more remote and less clear.

For a subdivision of the Ascobolaceae in taxa of lower rank the following structural characters proved to be of importance: the shape of ascocarps, asci and ascospores, the cortical texture, the ascospore-arrangement, and the reaction of the ascus-wall with iodine.

If the taxa of the Ascobolaceae are classified according to these structural criteria only, the resulting groups of species each show the same type of ascocarp ontogeny.

Exactly the same groups will be arrived at if the species are concatenated in series of over-all similarities (classification 'par enchaînement').

By classifying the Ascobolaceae according to the ontogeny of the ascocarp, supplemented with some of the structural criteria mentioned, a very useful classification is obtained which reflects empirical relations.

The genus *Ascobolus* is distinguished by the mutually free ascospores, which are not arranged in a regular package during any phase of maturation. In *Saccobolus* the ascospores are firmly or loosely united into a cluster according to a more or less regular pattern of arrangement.

In *Ascobolus* seven sections were recognized (van Brummelen, *1967*: 63): section *Dasyobolus* with cleistohymenial ascomata that do not open before the telohymenial phase; section *Sphaeridiobolus* with cleistohymenial ascomata opening in the late mesohymenial phase and globular ascospores with rounded warts; section *Ascobolus* with cleistohymenial ascomata opening in the early or mid-mesohymenial phase; section *Pseudascodesmis* with paragymnohymenial ascomata, the habit of *Ascodesmis*, and the ascus-wall not staining blue with iodine; section *Pseudosaccobolus* with para- or eu-gymnohymenial ascomata, the habit of *Saccobolus* and the ascus-wall staining deep blue with iodine; section *Heimerlia* with small eugymnohymenial ascomata and the cortex scarcely developed; and section *Gymnascobolus* with eugymnohymenial ascomata with an active submarginal growing zone.

Saccobolus was divided into two sections, section *Saccobolus* and section *Eriobolus*, both with paragymnohymenial or more rarely eugymnohymenial ascomata. These two sections, although slightly differing in ascocarp ontogeny, are distinguished on the basis of structural characters, such as pigmentation and ascospore-arrangement.

A tentative scheme of interrelationships between the sections of *Ascobolus* and

Saccobolus is given in the diagram on page 390. In this scheme the sections are arranged from the top downwards according to their ascocarp ontogeny from fully closed to fully open. In the same sequence there is a decreasing growth-activity of the hyphae of the primary sheath, especially in the archihymenial phase.

Conclusion

Ascocarp ontogeny has proved to be a very useful basis for the classification of the Ascobolaceae. It may also help in recognizing series of supra-specific taxa within other natural families of Discomycetes. The Thelebolaceae and the Pyronemataceae in particular are promising objects in this respect.

It would be of great importance to the taxonomy of Discomycetes to include in principle the stages of ontogenetic development in the comparative study of characters.

In the past extreme types of ontogenetic development (*Ascobolus immersus*, *Thelebolus stercoreus*, and *Ascodesmis*) have been the starting-point of far-reaching speculations on relationships within the Ascomycetes.

We must always be on guard, especially in ontogenetic and morphological studies, not to base generalizations on the study of a single or only a few taxa.

References

Brummelen, J. van (1967). A world-monograph of the genera *Ascobolus* and *Saccobolus* (Ascomycetes, Pezizales). *In* Persoonia (Suppl.) **1**: 1–260 *fs. 1–74. pls. 1–17.*

Corner, E. J. H. (1929a). Studies in the morphology of Discomycetes. I. The marginal growth of apothecia. *In* Trans. Br. mycol. Soc. **14**: 263–275 *fs. 1–4.*

—— (1929b). Studies in the morphology of Discomycetes. II. The structure and development of the ascocarp. *In* Trans. Br. mycol. Soc. **14**: 275–291 *fs. 1–7.*

—— (1930a). Studies in the morphology of Discomycetes. III. The Clavuleae. *In* Trans. Br. mycol. Soc. **14**: 107–120 *fs. 1–3.*

—— (1930b). Studies in the morphology of Discomycetes. IV. The evolution of the ascocarp. *In* Trans. Br. mycol. Soc. **15**: 121–134 *1 f.*

—— (1931). Studies in the morphology of Discomycetes. V. The evolution of the ascocarp. *In* Trans. Br. mycol. Soc. **15**: 332–350.

Doguet, G. (1955). Le genre «*Melanospora*»: biologie, morphologie, développement, systématique. Thèse, Bordeaux. [Also published *in* Botaniste **39**: 1–313. 1956 and *in* Bull. Inst. bot. Caen 1956, fasc. 8: 1–313.]

Durand, F. (1971) Sur le développement d'une Ascobolacée du genre *Lasiobolus*. *In* Bull. Soc. mycol. Fr. **86**: 725–740.

Gamundi, I. J. & Ranalli, M. E. (1963). Apothecial development in *Ascobolus stercorarius*. *In* Trans. Br. mycol. Soc. **46**: 393–400 *pls. 23–24 1 f.*

—— & —— Estudio sistemático y biológico de las Ascoboláceas de Argentina I. *In* Nova Hedwigia **7**: 517–533 *pls. 39–41.*

—— & —— (1966). Estudio sistemático biológico de las Ascoboláceas de Argentina II. *In* Nova Hedwigia **10**: 337–366 *pls. 106–112.*

—— & —— (1969). Estudios sistemático y biológico de las Ascoboláceas de Argentina III. *In* Nova Hedwigia **17**: 383–407. *pls. 97–102.*

Rifai, M. A. (1968). The Australasian Pezizales in the herbarium of the Royal Botanic Gardens Kew. *In* Verh. K. Ned. Akad. Wet. (Natuurk.) **57** (3): 1–295 *fs. 1–292.*

Yu, C. C. (1954). The culture and spore germination of *Ascobolus* with emphasis on *A. magnificus*. *In* Am. J. Bot. **41**: 21–30.

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ASCAL STRUCTURE, ASCOCARP ONTOGENY, AND A NATURAL CLASSIFICATION OF THE THELEBOLACEAE*

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(With Plates 16–19)

Many of the genera placed in the Pseudoascobolaceae by Boudier do not show true relationships and were based on the number of asci and ascospores, and other superficial features. Qualitative microscopic and microchemical characters of the asci and ascospores, combined with characters of ascocarp development, cultural features, and cytological aspects will provide a more natural classification of this group. The genera of the Thelebolaceae are discussed.

Thelebolus stercoreus Tode (*1790*) appears to be the first record of a hyaline-spored coprophilous discomycete. Strangely, however, *Thelebolus* Tode ex Fr., selected later as the type of the family Thelebolaceae, (Eckblad, *1968*) was considered by earlier mycologists to belong in the Gasteromycetes (Persoon, *1801*; Fries, *1822*). Essentially all of the coprophilous discomycetes were placed in the genus *Ascobolus*, Pers. ex Fr. by these authors, with a few remaining in *Peziza* Dill. ex St-Amans. Although the limits of *Ascobolus* were extended dramatically with the addition of many species by several authors, it was Fuckel (*1870*) who first considered *Thelebolus* an ascomycete, and eventually with the work of Heimerl (*1889*) it came to reside among the discomycetes.

Boudier's (*1869*) monumental work, "Mémoire sur les Ascobolés", laid the foundation for most of the subsequent studies of coprophilous discomycetes. He characterized the Ascobolei mainly by their relatively broad asci which protrude above the general level of the hymenium as they ripen. The spores commonly lie in two or three irregular rows in the ascus instead of in a single vertical row as in other discomycetes. He divided the Ascobolei into the "Ascobolei genuini" with pigmented ascospores and the "Ascobolei spurii" with hyaline ascospores. Boudier placed *Angelina* Fr., *Ascobolus*, and *Saccobolus* Boud. in the "Ascobolei genuini" and *Ascophanus* Boud., *Thecotheus* Boud., and *Ryparobius* Boud. in the "Ascobolei spurii." I will focus the remainder of this paper on a discussion of the latter group.

Until recent years the "Ascobolei spurii" of Boudier (*1869*) persisted more or less

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as a natural unit, although going under other names, i.e. Hyalosporae, Saccardo (*1884*); Hyalosporeae, Heimerl (*1889*); Groupe Pseudoascobolés, Boudier (*1885*); Thelebolcen, Brefeld (*1891*); Pseudoascoboleae, Rehm (*1895*); and Tribu Pseudoascobolés, Boudier (*1907*). Unaware of Boudier's work, Fuckel (*1870*) placed all of the Ascobolei known to him in the "Bulgariacei" and Karsten (*1871*) restricted *Ascobolus* to the pigmented forms while placing the hyaline-spored species either in *Peziza* (8-spored) or *Pezizula* Karst (multi-spored). As noted by Rifai (*1968*) and Kimbrough (*1970*), a number of workers continue to treat the Ascobolaceae in a broad sense to include both hyaline and pigmented spored taxa. I choose, however, to follow Eckblad (*1968*), and Rifai (*1968*) in recognizing the Thelebolaceae as a distinct family.

Boudier's (*1869*) "Ascobolei spurii" was divided first on spores per ascus, *Ascophanus* with 8 to 16, and *Ryparobius* and *Thecotheus* both multispored. *Thecotheus* was distinguished from *Ryparobius* by much larger thick-walled spores, more cylindric asci, more elongate paraphyses, and larger apothecia. A number of other genera subsequently have been proposed for hyaline-spored species (Table I). Renny (*1874*) proposed *Ascobolus* sect. *Ascozonus* for multispored species with asci that dehisce by a longitudinal apical split. Hansen (*1876*) elevated *Ascozonus* to generic rank. Saccardo (*1884*) proposed *Lasiobolus* for 8-spored species with setose apothecia;

TABLE I. GENERA OF HYALINE-SPORED COPROPHILOUS PEZIZALES

PERSOON, 1801	BOUDIER, 1907	SEAVER, 1928	ECKBLAD, 1968
Hymenothecii	Pseudoascobolei	Pezizaceae	Thelebolaceae
Ascobolus	*Boudierella*		*Ascozonus*
Peziza	*Cubonia*	Sphaerosporae	*Caccobius*
Gasteromycetes	*Thecotheus*	*Cubonia*	*Coprobolus*
Thelebolus	*Ascophanus*		*Coprotus*
	Lasiobolus	Humarieae	*Lasiobolus*
FRIES, 1822	*Ryparobius*	*Ascophanus*	*Thecotheus*
	Ascozonus	*Humarina*	*Thelebolus*
Elvellaceae	*Thelebolus*	*Streptotheca*	*Trichobolus*
Cupulati	*Aphanoascus*	*Ryparobius*	*Leporina*
Ascobolus	Pyronemacées	*Thecotheus*	
Peziza	*Zukalina*		Pyronemaceae
Gasteromycetes	Humariacées	Lachneae	*Cheilymenia*
Thelebolus	*Ciliaria*	*Lasiobolus*	*Coprobia*
BOUDIER, 1869	*Cheilymenia*	*Patella*	*Fimaria*
	Humaria		*Iodophanus*
Ascobolei spurii	*Coprobia*	Pezizeae	*Octospora*
Ascophanus		*Peziza*	
Ryparobius	Pezizacées		Pezizaceae
Thecotheus	*Aleuria*		*Peziza*

in *1889*, *Cubonia*, for hyaline, spherical-spored species; and in *1895*, *Boudierella*, for species with spherical, ornamented spores. Heimerl (*1889*) placed *Thelebolus* near *Ryparobius* and *Ascozonus* in the Hyalosporeae, and Boudier (*1907*) added *Aphanoascus* Zukal, but the recognition of this genus is currently in question (van Brummelen, *1967*; Eckblad, *1968*). Heim and Le Gal (*1936*) originally placed *Selenaspora* in the Pseudoascobolaceae, but later Le Gal (*1953*) had some doubt about its taxonomic position. The traditional arrangement of genera of the Pseudoascoboleae is similar to that in the following key.

A CLASSICAL KEY TO THE GENERA OF PSEUDOASCOBOLEAE

1. Apothecia setose . . . . . *Lasiobolus*
1. Apothecia without setae 2
2. Asci 8-spored. . . . . *Ascophanus*
2. Asci with more than 8 spores 3
3. Apothecium containing one large ascus . . . . . *Thelebolus*
3. Apothecium with several asci. 4
4. Asci opening by a vertical slit as far as an annular thickening . . . *Ascozonus*
4. Asci with a normal operculum. 5
5. Paraphyses abundant, asci elongate . . . . . *Thecotheus*
5. Paraphyses scanty, asci short . . . . . *Rhyparobius*

During a study of the structure and development of *Thelebolus zukalii* Heimerl (Kimbrough, *1966a*), it became apparent that this species differed significantly from the type, *T. stercoreus* Tode ex. Fr. In an attempt to determine the taxonomic position of *T. zukalii*, observations were made on a number of species of other genera of Pseudoascoboleae (Kimbrough, *1966b*). It was concluded that these genera did not show true relationships and that taxa previously ascribed to the Pseudoascoboleae should be founded on qualitative microscopic and microchemical characters, especially those of the asci and ascospores, rather than on quantitative and superficial features such as the number of asci and ascospores. Spore and ascal characteristics combined with those of ascocarp development, cultural features, and cytological aspects will provide, I feel, a more natural classification of this group.

The genus *Thelebolus*, for example, has a very distinct ascus. It is obvious, even when mounted in water, that the ascus of *T. stercoreus* has a peculiar structure. After screening a number of stains (Kimbrough, *1966b*) it was found that the ascal wall layers could be differentially stained, the outer wall with Congo red (Fig. 3), the inner wall with acid fuchsin in lactic acid (Fig. 1). The prominent ring in the *Thelebolus* ascus is part of the outer layer. The outer layer does extend beyond the ring, and at spore liberation the thin single layered apical portion splits irregularly. The ascus of *T. zukalii*, although superficially similar, has a quite different wall structure. The outer layer extends completely around the dome of the large ascus and there is a conspicuous absence of a ring. Both inner and outer wall layers become abruptly thinner near the ascus apex (Fig. 14). Although both develop angiocarpically, other differences between these species are obvious, *T. stercoreus* with small, thick-walled,

eguttulate spores, glabrous, more pigmented ascocarp, and more submerged growing habit; and *T. zukalii* with larger, thin-walled ascospores with deBary bubbles (Fig. 13), setose apothecia (Fig. 12), and less submerged growth habit. This prompted Kimbrough & Korf (*1967*) to transfer *T. zukalii* from *Thelebolus* to *Trichobolus*. Subsequently, species of *Trichobolus* with three or more asci were found, and recently species with 8-spored asci were discovered (Figs. 16–20).

In examining other Pseudoascoboleae, choosing initially the multispored genera, other interesting features of asci and apothecia were noted. Ascal structure in a majority of the species of *Rhyparobius* was basically like that of *T. stercoreus*, i.e. a Congo red-positive layer terminates with a ring around the dome of the ascus, and an inner layer of layers extends the complete length (Fig. 4). Although the species investigated thus far have a wide range of spores per ascus (Figs. 1, 2, 7) and asci per apothecium, (Figs. 2, 10) the basic structural features are identical to those of *T. stercoreus*. All are angiocarpic (Figs. 2, 6) and have asci that tear irregularly at spore liberation (Figs. 5, 11).

Several species previously assigned to *Rhyparobius* display a very obvious ring in the ascus, and consequently several mycologists considered them in *Ascozonus* (*Streptotheca* sensu Seaver, *1928*). A study of *Ascozonus* revealed another set of apothecial and ascal characteristics. The apothecia develop gymnocarpically, with a border of flexuous excipular cells (Fig. 33). A very prominent ring is evident in the ascus wall, and in Congo red this was shown again to be a part of the outer layer (Fig. 31). Unlike the *Thelebolus* ascus, the outer wall extends beyond the ring and almost to the tip (Fig. 32). A small papillate area at the tip is composed of only inner wall material (Fig. 31). Larger, naviculate spores characterize this genus (Fig. 33).

Thecotheus, the remaining multispored genus recognized by Boudier (*1869*), has a typical operculate ascus with a well formed wall indentation at the operculum (Figs. 43–45). The asci are diffusely amyloid, similar to a number of Ascobolaceae and Pezizaceae, the thickwalled spores have cyanophilous ornaments or perisporic sheath, (Fig. 44) and apothecia show a unique arrangement of excipular cells (Kimbrough, *1969*).

A large number of multispored species have operculate asci (Fig. 42), thin-walled spores with a conspicuous de Bary bubble (Fig. 42), and gymnocarpic apothecia which are white or scarcely pigmented (Fig. 37). Kimbrough & Korf (*1967*) placed these in *Coprotus* Korf & Kimbrough.

Peculiar ascal wall structures were also found in other multispored taxa. *Caccobius* Kimbrough & Korf (*1967*) has a very broad, essentially obclavate, thick-walled ascus (Fig. 34), which in youth has a conspicuous apical plug that stains in Waterman's blue-black ink (Fig. 35). The tip remains hyaline in Congo red (Fig. 36) and tears irregularly at spore liberation. Apothecia develop angiocarpically, with the paraphyses becoming highly branched and forming a pseudo-excipulum over the asci. *Coprobolus* Cain & Kimbrough (*1969*) has an ascus structure similar to *Caccobius* in that there is an apical thickening in youth and an irregular tear at spore liberation. The apothecial structure, however, is very dissimilar from that of *Caccobius* which is pigmented and bears marginal, agglulinated hairs.

TABLE II

MULTISPORED TENDENCY IN COPROPHILOUS DISCOMYCETES

	8-SPORED MULTIASCAL	MULTISPORED MULTIASCAL	MULTISPORED UNIASCAL
1.	*Thelebolus*	*Thelebolus*	*Thelebolus*
	Trichobolus	*Trichobolus*	*Trichobolus*
	Lasiobolus	*Lasiobolus*	*Lasiocolus*
	Coprotus	*Coprotus*	?
	Ascozonus	*Ascozonus*	?
	?	*Caccobius*	?
	?	*Coprobolus*	?
2.	*Thecotheus*	*Thecotheus*	
	Iodophanus		
	Peziza		
3.	*Coprobia*		
	Cheilymenia		
	Fimaria		
	Cubonia		

(1. Thelebolaceae; 2. Pezizaceae; 3. Humariaceae)

Boudier (*1907*) placed *Zukalina* Kuntze in the Pyronemacées but suggested a relationship of it to *Rhyparobius*. I have been unable to examine any material of this genus and can not make a taxonomic judgement at this time.

In searching for possible relationships in the 8-spored Pseudoascoboleae (Kimbrough, *1966b*), a number of very significant observations were made. Most European and American mycologists have followed Boudier (*1869*) or Saccardo (*1889*) in placing essentially all of the hyaline, 8-spored species either in *Ascophanus* or *Lasiobolus*. Boudier (*1907*), however, recognized that *A. granulata* differed in a number of features and transferred it to *Coprobia* Boud. of the Humariacées. Our studies support this transfer, and a number of current workers (Eckblad, *1968*; Rifai, *1968*; Dennis, *1968*; Kimbrough, *1970*), recognize this genus. Very few workers have recognized Chenantais' (*1918*) transfer of *A. cinereus* to the genus *Thecotheus*, but Kimbrough (*1969*) pointed out that a number of species previously assigned to *Ascophanus* actually belong in *Thecotheus*. The morphological and cytochemical features of the asci (Figs. 43–45) ascospores, and excipulum are the same as those of the type, *T. pelletieri* (Cr. & Cr.) Boud.

Van Brummelen (*1962*) showed that a number of taxa transferred by various

authors to *Ascophanus* resemble it only superficially. He transferred some of these to *Fimaria* Vel., which differed greatly from *Ascophanus* in ascal and excipular characters. Observations of numerous other collections of *Ascophanus* or *Ascophanus*-like organisms revealed other taxonomically different groups (Kimbrough, *1966b*). A number of species with brownish, initially cleistocarpous apothecia, possessed asci with the same microscopic and microchemical features as *Thelebolus stercoreus* Tode ex Fr. Although the asci were very numerous, paraphyses much more inflated and sometimes pigmented, and the apothecia expanded much earlier, the basic structure of spores, asci and excipular elements were the same as *Thelebolus* (Figs. 7–11). The lectotype of *Ascophanus, A. subfuscus* (Cr. & Cr.) Boud. (chosen by Seaver, *1928*) falls into this complex.

Ascophanus carneus and other species were characterized by the presence of callosepectic marked spores, diffuse amyloidy of asci, carotenoid pigments in the paraphyses and excipular cells, and an *Oedocephalum* imperfect state in some. These were transferred to *Iodophanus* Korf in the Pezizaceae (Kimbrough & Korf, *1967*). A small number of species of *Peziza* are also coprophilous.

One of the largest segregates of *Ascophanus* is *Coprotus*, with 18 species found thus far in North America. As was mentioned earlier with the multispored forms, the asci are operculate (Fig. 38) with uniform wall thickness, spores contain de Bary bubbles (Fig. 40) and apothecia are nonpigmented and gymnocarpic (Fig. 37). The spores per ascus may range from 4 to 256 and asci per apothecium vary from 5 or 6 to several hundred.

In recent examinations of 8-spored, setose species believed to be *Lasiobolus*, a number of features appeared in some which were atypical for that genus. Apothecial hairs were uniformly tapered, with a number of septa (Fig. 17) as opposed to those of *Lasiobolus* which are typically barrel-shaped at the base and nonseptate (Figs. 25–29). The two-layered ascus wall becomes considerably thinner at the apex, (Fig. 18) stains uniformly with Congo red, and dehisces by an irregular tear at spore liberation, (Fig. 19). This is evidently a species of *Trichobolus* with numerous 8-spored asci. Its spores with de Bary bubbles are similar to those of *Coprotus*, *Lasiobolus*, and other species of *Trichobolus*.

Lasiobolus was emended by Kimbrough and Korf (*1967*) to include not only 8-spored species but also the multispored *L. cainii* (Fig. 26). Recently, however, a beautiful uniascal species of *Lasiobolus* was discovered near Gainesville, Florida. Its superficial appearance is similar to that of *T. zukalii* (Fig. 21), but the asci were definitely operculate (Fig. 22) with a chemically differentiated area of dehiscence (Fig. 23) and the hairs are of the bulbous, nonseptate type (Fig. 25). Thus, this makes a total of three genera, *Thelebolus*, *Trichobolus*, and *Lasiobolus*, with species that range from those with uniascal apothecia and multispored asci, to those with numerous 8-spored asci.

If one examines closely a large number of coprophilous taxa distributed among the discomycetes, pyrenomycetes, and loculoascomycetes, he is impressed with the variety of ways these fungi have adapted to this peculiar environment. One of the most striking features is a tendency toward an increased spore number per ascus

accompanied by a decrease in asci per ascocarp. However, in the Sporomiaceae, instead of increased spores per ascus, there is an increase in the number of cells in each of the eight ascospores. The tendency toward increased spores and reduced number of asci is evident to some degree in all genera of the Thelebolaceae. Table II compares these tendencies in the Thelebolaceae and coprophilous genera of Pezizaceae and Humariaceae. All of the Thelebolaceae, with the possible exception of *Thelebolus* spp., have been found only on dung. Those species of *Thelebolus* collected elsewhere were likely on stercoroid soil. Also, *Thecotheus pelletieri* is the only non-Thelebolaceae found thus far with multispored asci. The recent discovery of wood inhabiting species of *Thecotheus* (Pfister, *1971*) enables us now to say that all genera of Pezizaceae with coprophilous species also have lignicolous species. The coprophilous genera of Humariaceae (= Aleuriaceae Arpin, *1969*) very likely have soil inhabiting species as well.

Within the Thelebolaceae we see a number of modifications in the apothecium which have accompanied the reduced ascus number. *Thelebolus*, *Trichobolus*, and *Lasiobolus* are all angiocarpic, or according to van Brummelen (*1967*), cleistohymenial. Apothecia in the uniascal species of these genera remain closed until spore liberation. Those with few asci open in the telohymenial phase, while those with numerous 8-spored asci open during the prohymenial phase. Species of *Coprotus* examined thus far are gymnocarpic, or eugymnohymenial with an excipulum (terminology of van Brummelen, *1967*). In multispored species the excipular growth exceeds that of the hymenium, making the development appear pseudo-angiocarpic. Although not studied in culture, *Caccobius* and *Coprobolus* appear to be cleistohymenial while *Ascozonus* appears gymnohymenial. With few exceptions an increase in spores per ascus is accompanied by a decrease in spore size. Although paraphyses are somewhat variable in 8-spored species of these genera, with a reduction in asci per apothecium the paraphyses are more highly branched and filamentous. It appears that the earlier the apothecium expands the more inflated the paraphyses become. The best example of this is found in *Thelebolus* where in uniascal *T. stercoreus* there is a thin layer of highly branched, filamentous paraphyses, in multiascal *T. crustaceus* slightly inflated paraphyses, and in *T. subfuscus*, greatly inflated and sometimes pigmented paraphyses. In *Coprotus*, however, the 8-spored species have highly variable paraphyses and thus this correlation does not hold.

Preliminary results indicate that the cytological aspects of a number of the Thelebolaceae may enable us to better understand relationships within this family and to other confused taxa. Contrary to Berthet (*1964*) and Eckblad (*1968*), who state that the mycelia of the Pezizales are coenocytic, we have found in research currently underway in my laboratory that the mycelium and vegetative cells in species of *Thelebolus*, *Trichobolus*, *Lasiobolus*, and *Coprotus* are consistently uninucleate. A very reduced ascogenous system has already been reported for *Thelebolus* (Ramlow, *1906*) and *Trichobolus* (Kimbrough, *1966a*). A similar system is present in the uniascal *Lasiobolus* mentioned earlier. We also have some evidence that there is a modified crozier system present in the 8-spored, multiascal genera. For example, in *Coprotus*

lacteus (Ck. & Phil.) Kimbrough the crozier system is of the "aporhynque type", even though the ascal base would lead one to suspect the typical crozier system was at work. We anticipate that a great amount of taxonomically useful information will come from similar cytological and developmental studies.

References

ARPIN, N. (1968). Les caroténoïdes des Discomycètes: essai chimiotaxinomique. Thèse No. 527, Univ. Lyon, 169 pp. (& *in* Bull. mens. Soc. linn. Lyon **38** (Suppl.): 169 pp. 1969).

BERTHET, P. (1964). Essai biotaxinomique sur les Discomycètes. Thèse No. 340, Univ. Lyon, 158 pp.

BOUDIER, J. L. E. (1869). Mémoire sur les Ascobolées. *In* Annls. Sci. nat. (Bot.) V **10**: 191–268.

—— (1885). Nouvelle classification naturelle des Discomycètes charnus connus généralement sous le nom de Pézizés. *In* Bull. Soc. mycol. Fr. **1**: 91–120.

—— (1907). Histoire et classification des Discomycètes d.Europe. vii & 223 pp., Paris.

BREFELD, O. (1891). Untersuchungen aus dem Gesammtgebiete der Mykologie **9**: viii & 156 pp.

BRUMMELEN, J. VAN (1962). Studies on Discomycetes—II. On four species of Fimaria. *In* Persoonia **2**: 321–330.

—— (1967). A world monograph of the genera *Ascobolus* and *Saccobolus* (Ascomycetes, Pezizales). *In* Persoonia (Suppl.) **1**: 260 pp.

CAIN, R. F. & J. W. KIMBROUGH (1969). *Coprobolus*, a new genus of the tribe Thelebolaeae (Pezizeae). *In* Can. J. Bot. **47**: 1911–1914.

CHENANTAIS, J. (1918). Trois Discomycètes. *In* Bull. Soc. mycol. Fr. **34**: 34–40.

DENNIS, R. W. G. (1968). British Ascomycetes. Lehre, xxxii & 455 pp.

ECKBLAD, F.-E. (1968). The genera of the operculate Discomycetes. A re-evaluation of their taxonomy, phylogeny, and nomenclature. *In* Nytt Mag. Bot. **15**: 1–191.

FRIES, E. M. (1822). Systema mycologicum **2** (1). Lundae.

FUCKEL, K. W. G. L. (1870). Symbolae mycologicae: Beiträge zur Kenntniss der rheinischen Pilze. *In* Jb. nassauischen Ver. Naturk. **23–24**: 1–459.

HANSEN, E. C. (1877). De danske Gjødningssvampe. (Fungi fimicoli danici). *In* Vid. Meddr dansk naturh. Foren. **1876**: 89–354.

HEIM, R. & M. LE GAL (1936). Un genre nouveau nécrlandais d'Ascobolacés. *In* Revue Mycol. **1**: 307–313.

HEIMERL, A. (1889). Die niederösterreichischen Ascoboleen. *In* Jber. K. K. Oberrealschule Bezirke Sechshaus Wien 15: 1–32.

KARSTEN, P. A. (1871). Mycologia fennica. Pars prima. Discomycetes. *In* Bidr. Känn. Finl. Nat. Folk **19**: (i) & viii & 264 pp.

KIMBROUGH, J. W. (1966a). The structure and development of *Trichobolus zukalii*. *In* Mycologia **58**: 289–306.

—— (1966b). Studies in the Pseudoascoboleae. *In* Can. J. Bot. **44**: 685–704.

—— (1969). North American species of *Thecotheus* (Pezizeae, Pezizaceae). *In* Mycologia **61**: 99–114.

—— (1970). Current trends in the classification of Discomycetes. *In* Bot. Rev. **36**: 91–161.

KIMBROUGH, J. W. & R. P. KORF (1967). A synopsis of the genera and species of the tribe Thelebolaeae (= Pseudoascoboleae). *In* Am. J. Bot. **54**: 9–23.

LE GAL, M. (1953). Les Discomycètes de Madagascar. 465 pp. Paris (Prodr. Fl. mycol. Madag. **4**).

PERSOON, C. H. (1801). Synopsis methodica Fungorum. xxx & 706 pp. Gottingae.

PFISTER, D. H. (1971). A monograph of the psilopezioid fungi. Thesis, Cornell Univ., Ithaca, N.Y.

RAMLOW, G. (1906). Zur Entwicklungsgeschichte von *Thelebolus stercoreus* Tode. In Bot. Ztg. **64**: 85–97.
REHM, H. (1895). Ascomyceten: Hysteriaceen und Discomyceten. *In* Rab. Krypt.-Fl., Pilze, **3**: 1041–1168.
RENNY, J. (1874). New species of the genus *Ascobolus*. *In* J. Bot., Lond. **12**: 353–357.
RIFAI, M. A. (1968). The Australasian Pezizales in the Herbarium of the Royal botanic Gardens Kew. *In* Verh. K. Ned. Akad. Wet., Afd. Natuurk. II **57**: 295 pp.
SACCARDO, P. A. (1884). Conspectus generum Discomycetum hucusque cognitorum. *In* Bot. Cbl. **18**: 213–220, 247–256.
—— (1889). Sylloge fungorum omnium hucusque cognitorum **8**: xvi & 1143 pp.
—— (1895). Sylloge fungorum omnium hucusque cognitorum **11**: vii & 718 pp.
SEAVER, F. J. (1928). North American cup-fungi (Operculates). 284 pp. New York.
TODE, H. J. (1970). Fungi mecklenburgenses selecti. Fasciculus I. Nova fungorum genera complectens. 50 pp. Luneburgi.

EXPLANATION TO PLATES 16–19

PLATE 16

Figs. 1–8. Species of *Thelebolus*. — 1. An ascus of *T. stercoreus* stained in acid fuchsin with the outer wall and ring at apex (arrow) remaining hyaline. × 300. — 2. Young cleistohymenial ascocarp of *T. polysporus*. × 300. — 3. An ascus of *T. stercoreus* in Congo red showing unstained apex and small bacilloid spores within. × 300. — 4. An ascus of *T. crustaceus* with hyaline apex in Congo red. × 500. — 5. An empty ascus of *Thelebolus obscura* showing irregular tear after spore liberation. × 500. — 6. A young cleistohymenial ascocarp of *T. crustaceus* showing young asci and filamentous paraphyses. × 250. — 7. An ascus of *T. microsporus* showing faint apical ring in Congo red. × 1000. — 8. A typical clavate paraphysis of *T. microsporus*. × 1000. (Figs. 1, 3, 4, 5 after Kimbrough, *1966b*).

PLATE 17

Figs. 9–11. *Thelebolus microsporus*. — 9. Mature apothecia on dung. × 50. — 10. An apothecial section with pigmented excipulum, encrusted paraphyses and numerous asci. X 400. — 11. A partially empty ascus with apical tear. × 800.

Figs. 12–20. Species of *Trichobolus*. — 12. A mature apothecium of *T. zukalii*. × 25. — 13. Mature ascospores of *T. zukalii* with conspicuous de Bary bubbles. × 1000. — 14. An almost empty ascus of *T. zukalii* showing manner of dehiscence at spore liberation. × 250. — 15. Septate, thick-walled base of hair of *T. zukalii*. × 1000. — 16. Ectal excipulum of an 8-spored species of *Trichobolus*. × 1200. — 17. Sharp. septate hair of an 8-spored *Trichobolus*. × 600. — 18. Ascus of 8-spored *Trichobolus* showing thinner apical region (arrows). × 1200. — 19. Apex of ascus of 8-spored *Trichobolus* showing manner of dehiscence at spore liberation. × 1200. — 20. Paraphyses of 8-spored *Trichobolus*. × 1200. (Figs. 12–15 after Kimbrough, *1966a*).

PLATE 18

Figs. 21–30. Species of *Lasiobolus*. — 21. Setose, uniascal ascocarp of *Lasiobolus monascus*. × 100. — 22. Empty ascus of *L. monascus* showing operculum and filamentous paraphyses. × 160. — 23. Apical portion of ascus showing chemically differentiated area of dehiscence. × 1200. — 24. Ascal wall of *L. monascus* in Congo red showing thinner area of outer wall (arrows). × 1200. — 25. Pointed, nonseptate, barrel-shaped hair of *L. monascus*. × 1200. — 26. An ascus of *L. cainii* with thinner areas for dehiscence (arrows). × 440. — 27. An apothecium of *L. lasioboloides*. × 120. — 28. Ascus apices of *L. lasioboloides* in Congo red showing operculum in one and hyaline area of dehiscence in others (arrows). × 1000. — 29. Barrel-shaped nonseptate base of hair of *L. ciliatus*. × 1000. — 30. The epidermoideae excipulum in *L. ciliatus*. × 1000. (Fig. 26 after Kimbrough & Korf, *1967*).

PLATE 19

Figs. 31–45. Species of *Ascozonus*, *Caccobius*, *Coprotus* and *Thecotheus*. — 31. An ascus of *Ascozonus cunicularius* in Congo red, showing prominent ring in outer wall and unstained nippled tip (arrow). × 1200. — 32. An ascus of *A. cunicularius* in acid fuchsin showing thicker inner wall. × 1200. — 33. A mature ascus of *A. cunicularius* with naviculate spores within and surrounded with flexuous excipular cells. × 1000. — 34. Young ascus of *Caccobius miniusculus* with extremely thick walls. × 750. — 35. Young ascus of *C. miniusculus* showing apical plug in blue-black ink (arrow). × 1000. — 36. Mature ascus of *C. miniusculus* with small eguttulate spores and hyaline apical plug in Congo red. × 1000. — 37. Apothecia of *Coprotus lacteus* on dung. × 5. — 38. Operculate ascus of *C. lacteus*. × 1000. — 39. An apothecial section showing excipulum and asci. × 500. — 40. An ascus of *C. lacteus* with 8 spores containing de Bary bubbles. × 1000 — 41. An ascus of *C. sexdecimsporus*. × 1000. — 42. An ascus apex of *C. winteri* showing oblique operculum with thinner wall areas (arrows). × 1000. — 43. An ascus apex of *Thecotheus pelletieri* showing indentations in ascus wall (arrows). × 1000. — 44. Young ascus of *T. cinereus* showing thick inner wall with indentation. × 1000. — 45. Mature ascus of *T. cinereus* with well delimited operculum. × 1000. (Figs. 31–33 after Kimbrough, *1966b*; Figs. 34–36 after Kimbrough & Korf, *1967*; Figs. 37–42 after Kimbrough, Luck-Allen, & Cain, in press; Figs. 43–45 after Kimbrough, 1969).

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IMPERFECT STATES AND THE TAXONOMY OF THE PEZIZALES*

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(With Plates 20–22)

Certainly only a relatively few species of the Pezizales have been studied in culture. I hope that this paper will stimulate more efforts in this direction. A few patterns are emerging from those species that have been cultured and have produced conidia but more information is needed. Botryoblastospores (*Oedocephalum* and *Ostracoderma*) are frequently found in cultures of *Peziza* and *Iodophanus* (Pezizaceae). Aleurospores are known in *Peziza* but also in other genera. *Botrytis*-like imperfect states are known in *Trichophaea* (Otidiaceae). Sympodulosporous imperfect states are known in several families (Sarcoscyphaceae, Sarcosomataceae, Aleuriaceae, Morchellaceae) embracing both suborders. *Conoplea* is definitely tied in with *Urnula* and *Plectania*, *Nodulosporium* with *Geopyxis*, and *Costantinella* with *Morchella*. Certain types of conidia are not presently known in the Pezizales. Phialospores, porospores, annellospores, blastospores and a few other types have not been reported. The absence of phialospores is of special interest since these are common in the Helotiales. The absence of conidia in certain groups, e. g. Helvellaceae and Theleboleaceae may also be of significance, and would aid in delimiting these taxa. At the species level critical comparison of imperfect states may help clarify taxonomic problems and supplement other data in distinguishing between closely related species. *Peziza*, *Plectania* and perhaps *Sarcoscypha* are examples of genera where such studies might prove valuable.

One large group of the Pezizales in desparate need of study in culture are the tropical species. Very few of these appear to have been cultured. Undoubtedly some surprises are in store for mycologists who culture tropical forms. Species of *Rhizoctonia* may also yield pezizaceous apothecia, as the study of Whitney & Parmeter (*1964*) has shown. Such cultural studies are laborous but must be undertaken if we are to ever approach complete understanding of this group of fungi.

Introduction

Imperfect states have been known in the Pezizales for over one hundred years, the first report being that of the Tulsane's (*1853*, *1865*) of the *Oedocephalum* state of *Peziza vesiculosa*. Brefeld (*1891*) described and illustrated this imperfect state and the

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Oedocephalum states of *P. repanda*, *P. cerea*, and *P. ampliata*. Molliard (*1904a*, *1904b*) found *Costantinella* conidial states in *Morchella*. Since these early papers, there have been only a few reports of conidial states in the Pezizales until recent years. Commencing with Gremmen's (*1949*) report of the *Verticicladium* imperfect state of *Desmazierella acicola*, more and more reports of conidial states have appeared in the literature, and it is becoming evident that the Pezizales may be rich in undiscovered imperfect forms. Further, as will be discussed in detail below, some excellent correlations between perfect states and imperfect states are becoming evident.

In the remainder of the paper I will discuss the taxonomic implications of pezizaceous conidial states. The system of classification I will follow will be essentially that of Kimbrough (*1970*) except that Korf's (*1970*) division of the Sarcoscyphineae into two families will be adhered to. For the imperfect states I will follow Hughes' (*1953*) system as modified by Barron (*1968*).

METHODS

Spore germination.

Ascospores have been harvested by suspending apothecia or fragments of apothecia over agar and allowing the spores to be discharged. The ascospores of many species of Pezizales germinate readily, however the spores of some species are extremly refringent and germination is difficult or impossible to obtain. Heat shock plus furfural induced a low percentage of germination in *Peziza brunneoatra* ascospores (Paden, *1967*). In *P. saniosa* Fr., germination has been obtained by shooting the ascospores onto 2 % Difco nobel agar, then dropping 50 % aqueous dimethylsulfoxide containing 20 PPM furfural onto the spores and incubating at 13° C. This results in about 1 % germination. The ascospores of *Caloscypha fulgens* (Pers.) Boud. have been induced to germinate only by shooting them onto 2 % Difco nobel agar containing 10^{-4} M n-nonyl alcohol and incubating at 21 to 23° C. About 50 % germination is attained by this technique. The nonyl alcohol method also induces germination in *Aleuria aurantia* (Fr.) Fckl. and *Melastiza chateri* (Sm.) Boud. but less than 1 % of the ascospores germinate.

Potato-carrot agar (PCA) prepared according to the C.M.I. formula (Dade, *1960*) has been routinely employed for pure culture studies. PCA has proven to be by far the best culture medium for most species of Pezizales. A few species of the Sarcosomataceae will grow or sporulate only on a conifer litter decoction (*Paden & Tylutki*, *1968*, *1969*). Cultures have been incubated at 21 to 23° C and given diurnal incandescent illumination. 2.5 PPM aureomycin and 250 PPM streptomycin are incorporated into all media to surpress bacteria.

Imperfect states presently known in the Pezizales and their taxonomic implications

Suborder Sarcoscyphineae

Family Sarcoscyphaceae (sensu Korf, 1970).

There are few reports of conidial states in this family. Boedijn (*1929*, *1932*) described small, globose conidia borne on short conidiophores arising from ascospores in *Cookeina sulcipes* and *C. tricholoma*. Close examination of Boedijn's illustrations indicates that the conidia are probably sympodulospores. Boedijn (*1932*) reports that these conidia germinate readily when placed in water. This latter observation is of considerable interest as I have never been able to germinate the conidia of any species of the Sarcoscyphineae.

Production of conidia in a manner similar to *Cookeina* was reported by Alexopolous & Butler (*1949*) for *Sarcosypha coccinea* (as *Plectania coccinea*). Rosinski (*1953*) also observed this phenomonon in material he considered to be *S. coccinea* var. *jurana*. Rosinski (*1953*) observed only germination by germ tube in *S. coccinea* var. *coccinea*. The drawings of Alexopolous & Butler (*1949*) and the drawings and photomicrographs of Rosinski (*1953*) strongly suggest a sympodulosporous manner of conidium formation in *S. coccinea* var. *jurana*.

I have cultured only what I beleive is *S. coccinea* var. *coccinea* (Paden 571 from British Columbia; Paden 766 from Quebec[1]. Ascospores from both of these collections germinated by germ tube. Colonies on PCA are white, appressed to slightly floccose, and cover a plate in about two weeks. A conidial state develops in two to three weeks (Fig. 1). The conidia are sympodulospores. This conidial state cannot be accomodated in a presently known genus (Hughes, personal communication). Rosinski (*1953*) noted that the apothecial colour and ascospore shape he observed were opposite to that reported by Boudier (*1906–1907*) and that Le Gal (*1941*) had also observed considerable variation and intergradation in ascospores size and shape between the two varieties of *S. coccinea*. The presence of two distict conidial forms and two types of ascospore germination in the species *S. coccinea* is a further basis for distinguishing between the two varieties.

In Korf's (*1970*) scheme *Cookeina* is placed in the Boedijnopezizeae and *Sarcoscypha* in the Sarcoscypheae. If the conidia of *Cookeina* are in fact sympodulospores, then this similar means of conidium formation could be taken as evidence of a close relationship. Hopefully, additional species will be cultured in the future and *Cookeina* reinvestigated. I have cultured *Pithya vulgaris* Fckl. (Sarcoscypheae) but it did not form conidia.

Family Sarcosomataceae (sensu Korf, 1970).

Gremmen (*1949*) first connected *Verticicladium* with *Desmazierella acicola* Lib. in pure culture studies. Hughes (*1951*) determined the imperfect state to be *Verticicla-*

[1] Specimens cited are deposited in the University of Victoria herbarium or in the University of Idaho herbarium (ID).

dium trifidum Preuss. Davidson (*1950*) suggested that *Urnula craterium* (Schw.) Fr. was the perfect state of *Strumella* canker but was unable to obtain conidia in culture. This has been accomplished by Hughes (personal communication). Wolf (*1958a*) obtained conidia of *U. craterium* by innoculating sterile oak branches. The correct name of the imperfect state of *U. craterium* is *Conoplea globosa* (Schw.) Hughes (Hughes, *1960*). It should be noted at this point that both *Conoplea* and *Verticicladium* are sympodulosporous genera.

Recently I have obtained the imperfect states of *Plectania nannfeldtii* Korf and two possibly undescribed species of *Plectania* in culture. The imperfect state of *P. nannfeldtii* is close to or conspecific with *Conoplea juniperi* var. *robusta* (Hughes, personal communication). "Plectanic Taxonomic species II" from California and Oregon is a close relative of *P. nannfeldtii* and also has an imperfect state in the *C. juniperi* group (Hughes, personal communication). "Plectanic Taxonomic species I" from Vancouver Island, British Columbia has an imperfect state in the *C. fusca* group (Hughes, personal communication). The conidia of all *Plectania* species thus far studied possess a germ pore while the conidia of *U. craterium* possess a germ slit. *Plectania* and *Urnula* are without question closely related. Nannfeldt (*1949*) separated them on anatomical grounds. The basic difference in the conidia of the two genera is perhaps evidence for keeping them separate. (The conidia of *Desmazierella acicola* also possess a germ slit.)

Sarcosoma globosa was cultured by Berthet (*1964a*), who did not observe an imperfect state. McCallam (*1919*) germinated the ascospores of *S. globosa* (as *Bulgaria platydiscus*) but was unable to obtain cultures because of contaminants. His figures show germination by one or two germ tubes and no evidence of conidia. Paden & Tylutki (*1969*) cultured *S. mexicana* and did not obtain an imperfect state. The grounds for separating *Sarcosoma* and *Plectania* are tenuous. A case in point is *S. latahensis* Paden & Tylutki (*1969*). This is a borderline species only reluctantly placed in *Sarcosoma*. According to Hughes (personal communication) the conidial state is in the *Conoplea geniculata* group and is not a *Verticicladium*. The presence of a *Conoplea* imperfect state (with a germ pore) is, in my opinion, evidence for including *S. latahensis* in *Plectania*. (The new combination to be made in a separate paper.)

Pseudoplectania is closely related to *Plectania* and should, perhaps, be merged with the latter genus. Imperfect states are not known in *Pseudoplectania* (Korf, personal communication; Paden, unpublished data). Ascospores of *Pseudoplectania* posess a gelatinous sheath, as do the ascospores of some species of *Plectania*. At present, in *Plectania*, there is no relationship between the presence or absence of an ascospore sheath and the presence or absence of an imperfect state.

Imperfect states are unknown in the tribe Galielleae Korf. *Neournula nordmanensis* has never formed conidia (Paden & Tylutki, *1968*) nor has *Galiella rufa* (Schw.) Nannf. & Korf (Paden, unpublished data). There are no records of anyone having cultured *Wolfina*, the third genus included by Korf (*1970*) in this tribe.

Suborder P e z i z i n e a e

Family Pezizaceae (sensu Rifai, 1968).

As treated by Rifai, this family includes those genera of Pezizales with J+ asci (excepting some species of the Ascobolaceae). *Oedocephalum* imperfect states are known in *Peziza* (numerous reports) and *Iodophanus* (Korf, *1958*; Gamundi & Ranalli, *1964*). Schneider (*1954*) published the new ellipsoid-spored species *Plicaria fulva* with a description of its conidial state which is an *Ostracoderma*. Korf (*1960*) transferred this species to *Peziza* (as *P. ostracoderma* Korf). An *Ostracoderma* imperfect state (as *Rhinotrichum*) was described by Wolf (*1958b*) for *Peziza trachycarpa* Curr. (as *Lamprospora*). As pointed out by Korf (*1960*) the presence of *Ostracoderma* imperfect states in J+ species with both globose and ellipsoid ascospores is a strong argument for classifying all such species under the older name *Peziza* St.-Amans.

Recently I have obtained *Ostracoderma* conidial states in cultures of *Peziza leiocarpa* Curr. (Fig. 5) and *P. anthracina* Cke., both species with globosa ascospores. This leaves *P. ostracoderma* as the only ellipsoid spored species with a known *Ostracoderma* imperfect state. However relatively few species in the large genus *Peziza* have as yet been cultured and is it very likely that *Ostracoderma* states will be found in additional species with ellipsoid ascospores. The conidial states of *P. leiocarpa*, *P. trachycarpa*, and *P. ostracoderma* are very similar. The conidial state of *P. anthracina* is more compact with shorter conidiophores and broader ampullae. *Peziza anthracina* has been treated as var. *muricata* Grelet of *P. trachycarpa*. However as pointed out by Maas Geesteranus (*1967*), the var. *muricata* was not validly published, and the correct name is *P. anthracina*. The difference in morphology of the conidial states of these species is additional evidence that they should be kept separate.

Paden (*1967*) described an aleurospore-like conidial state in *Peziza brunneoatra* Desm. Recently I have noted both aleurspoores and an *Oedocephalum* conidial state in *P. petersii* Berk. & Curt. (Fig. 2, 4) and aleurospores in *P. saniosa* Fr. (Fig. 6). Possibly aleurospores are common in *Peziza*. I have also seen aleurospore-like structures in cultures of *P. ostracoderma*. Since the *Oedocephalum* and *Ostracoderma* states now known in *Peziza* vary strikingly in morphology, they should be of considerable taxonomic value as more species are cultured and accurate descriptions of conidial states published.

Thecotheus is closely related to *Iodophanus* (Kimbrough & Korf, *1967*), but there are no reports of associated imperfect states. I have been able to culture *T. cinereus* from ascocarp tissue and obtained a few aleurospores on PCA but no other imperfect state.

Imperfect states have not been reported in *Pachyella* or *Sarcosphaera*. I have not been able to germinate ascospores in either of these genera or obtain cultures from tissue explants.

Family Pyronemateceae.

Used in the sense of Rifai (*1968*) and Arpin (*1968*) this family includes the single genus *Pyronema* Carus. Two species, *P. domesticum* and *P. omphalodes* were treated by

Moore & Korf (*1963*). As these authors point out, conidia are unknown in *Pyronema* and earlier reports of conidial states are in error. Berthet (*1964b*) described "oidia" in *P. omphalodes*.

Family Otideaceae Eckblad emend. Arpin.

The limits of this family are in some doubt. As originally defined by Eckblad (*1968*) *Otidea*, *Pustulina* (*Pustularia*), *Sowerbyella*, *Geopyxis*, and *Ascosparassis* were included. Arpin (*1968*) removed *Geopyxis* and *Sowerbyella* to the Aleuriaceae and included *Sepultaria*, *Tricharia*, *Trichophaea*, *Mycolachnea*, and *Pseudombrophila*. Kimbrough (*1970*) suggests that *Jafnea*, *Nothojafnea*, *Jafneadelphus*, *Sphaerosporella*, and possibly *Marcelleina* also belong in the Otidiaceae.

Only a few imperfect states have been reported for species in the Otidiaceae. It has been known for some years the *Trichophaea abundans* (Karst.) Boud. and probably other *Trichophaea* species have *Botrytis*-like imperfect states (Dodge, *1922*; Gwynne-Vaughn & Williamson, *1927*; Kervorkian, *1932*; Webster, & *al.*, *1964*). Whitney & Parmeter (*1964*) note that *Rhizoctonia*-like mycelium may be common among discomycetes and my own studies would definitly confirm this observation. Berthet (*1966*) described aleuro-spore-like conidia in cultures of *T. confusa* (Che.) Berthet. Cain & Hastings (*1956*) published the new species *Sphaerospora minuta* with a *Botrytis*-like imperfect state. The conidia in this species are borne on very broad denticles. However they are botryoblastospores and thus basically like conidia in other "*Botrytis*" species. Since *Sphaerospora* is illegitimate (Eckblad, *1968*) *S. minuta* should perhaps be included in *Trichophaea*.

There are no reports of imperfect states in the related genus *Tricharia*. I have cultured a *Tricharia* sp. (Paden 623) but it did not produce conidia. I have not been able to germinate ascospores of *Otidea* or *Pustulina*. I have cultured *P. catinus* (Fr.) Eckblad (Paden 525) from tissue explants. Cultures are slow-growing and creamy white. There is no conidial state on PCA or malt extraxt.

Family Aleuriaceae Arpin.

Arpin (*1968*) divided the Aleuriaceae into three groups based on carotenoid ratios. Group a includes *Coprobia*, *Cheilymenia*, *Scutellinia*, and *Geopyxis*; group b, *Aleuria*, *Melastiza*, and *Octospora*; group c, *Pulvinula*, *Anthracobia*, *Caloscypha*, and *Sowerbyella*. Kimbrough (*1970*) suggests that *Fimaria*, *Leucoscypha*, *Lamprospora*, *Inermesia*, *Genosperma* and *Rhizoblepharis* belong in the Aleuriaceae.

In group a I have discovered a *Nodulosporium* conidial state in *Geopyxis majalis* Fr. (Fig. 7). This conidial state is formed abundantly on PCA. Cultures of *G. carbonaria* and *G. vulcanalis have remained sterile. Nodulosporium* is sympodulosporous and is related to *Costantinella*, the imperfect genus tied in with *Morchella. Coprobia granulata* was studied in culture by Gwynne-Vaughn and Williamson (*1930*). They do not mention a conidial state. Both Dr. W. C. Denison and myself have cultured *Scutellinia* species and have not seen conidia.

Species in group b lack known conidial states. I have cultured *Melastiza chateri* (Sm.) Boud. and *Aleuria aurantia* (Fr.) Fckl. from germinated ascospores and have

not observed conidia. Berthet (*1964a*) likewise did not observe conidia in cultures of *A. aurantia* or *Octospora euchroa* (Karst.) Boud.

In group c Gwynne-Vaughn (*1937*) and Rosinski (*1956*) studied ascocarp development in *Anthracobia melaloma* (Fr.) Boud. in culture and did not observe conidia. I have cultured *A. macrocystis* (Che.) Boud. (Paden 146, ID) and *Pulvinula archeri* (Berk.) Rifai (Paden 371, ID) and have not seen conidia. *Caloscypha fulgens* (Pers.) Boud. develops an imperfect state on PCA. Colonies are slow-growing, floccose, and a blue-green colouration appears in the agar beneath the colony but does not diffuse further. Conidial formation is sympodulosporous (Fig. 3) and the *C. fulgens* imperfect state is congeneric with the *Sarcoscypha coccinea var. coccinea* imperfect state (Hughes, personal communication). I have discussed the *C. fulgens* problen at some length with Dr. W. C. Denison and we are both of the opinion that the ascus of this species is not suboperculate and that it should not be placed in the Sarcoscyphaceae. The texture and colouration of *C. fulgens* do, however, suggest a sarcoscyphaceous species (Denison, personal communication). Possibly *C. fulgens* is a primitive species of the Aleuriaceae not too far removed from a sarcoscyphaceous ancestry.

Family Morchellaceae.

Molliard (*1904a*, *1904b*) described *Costantinella* imperfect states for species of *Morchella*. I have obtained the *Costantinella* state of *M. elata* Fr. in culture (Fig. 8). *Costantinella* thus seems definitely tied in with *Morchella*. Barron (*1968*) has pointed out the close relationship of *Costantinella* and *Nodulosporium*. Since a *Nodulosporium* state is now known for *Geopyxix majalis* (Aleuriaceae), a possible connection between the two families may be indicated. There are no reports of conidial states in the other genera of the Morchellaceae: *Verpa*, *Ptychoverpa*, and *Disciotis*. Berthet (*1964a*) cultured *D. venosa* (Pers.) Boud. and *P. bohemica* (Krombh.) Boud. but did not observe conidia.

Family Helvellaceae.

At the present state of our knowledge a broad concept of this family such as that of Berthet (*1964a*) should perhaps be adhered to. Conidial states are at this time unknown in species of the Helvellaceae and the ascospores of many have proven impossible to germinate. I have not been able to germinate the ascospores of species of *Helvella*, *Wynella*, or *Discina*. In contrast, the ascospores of *Gyromitra esculenta* Fr. and *G. infula* (Fr.) Quél. germinate readily. Colonies of Gyromitra on PCA are fast-growing, thin, nearly colourless, and do not form conidia. I have obtained a culture of *Rhizina undulata* Fr. from Dr. A. Funk of the Canada Department of Forestry and Rural Development, Victoria, B. C., that had been made by Dr. J. Ginns. Dr. Ginns had told me that he germinated the ascospores by heat shock. *Rhizina undulata* grows rapidly on PCA and forms colourless, somewhat floccose colonies. There is no conidial state.

Family Ascobolaceae.

Oidia are known in a few speciew of *Ascobolus* (Dodge, *1912*; Green, *1931*). These

can act either as vegetative propagules or male cells. A *Papulaspora* state was reported by Dodge (*1920*) for *A. magnificus*, but Lohwag (*1927*) points out that this may represent aborted ascocarps. Some of Hotson's (*1917*) illustrations of *Papulaspora* species are very suggestive of ascogonial initials. Conidia have not been reported in *Saccobolus*. Obrist (*1961*) did not observe conidia in cultures of *Ascodesmis*. The oidia in *Ascobolus* are of little taxonomic significance, except that their presence or absence may help to delimit a given species.

Family Thelebolaceae Rifai.

Kimbrough & Korf (*1967*) have presented a synopsis of this family (as tribe Theleboleae). Kimbrough (*1966*) has summarized all information regarding cultural characters. Imperfect states are not known in the Thelebolaceae at the present time. Since several species have been cultured, it seems likely that the family can be characterized by a lack of imperfect states.

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Note added in proof.

Since this paper was submitted a *Nodulosporium* imperfect state has been found in *Geopyxis carbonaria* (Alb. & Schw. ex Fr.) Sacc. An imperfect state congeneric with the imperfect states of *Sarcoscypha coccinea* var. *coccinea* and *Caloscypha fulgens* has been found in *Pithya cupressina* (Fr.) Fckl.

REFERENCES

ALEXOPOULOS, C. J. & E. E. BUTLER (1949). Conidia-like structures in *Plectania coccinea*. *In* Mycologia **41**: 180–182.

ARPIN, N. (1968). Les caroténoïdes des Discomycètes: essai chimiotaxonomique. Thèse No. 527, Univ. Lyon, 169 pp. (& *in* Bull. mens. Soc. linn. Lyon **38** (Suppl.): 169 pp. 1969).

BARRON, G. (1968). The genera of hyphomycetes from soil. Baltimore, 365 pp.

BERTHET, P. (1964a). Essai biotaxinomique sur les Discomycètes. Thèse No. 340, Univ. Lyon, 160 pp.

—— (1964b). Formes conidiennes de divers Discomycètes. *In* Bull. Soc. mycol. Fr. **80**: 125–149.

—— (1966). L'appareil conidien de *Trichophaea confusa* (Cooke) Berthet, nov. comb. *In* Bull. Soc. mycol. Fr. **82**: 473–474.

BOEDIJN, K. B. (1929). Beitrag zur Kenntnis der Pilzflora von Sumatra. *In* Recl Trav. bot. néerl. **26**: 346–439.

—— (1932). The genera *Phillipsia* and *Cookeina* in Netherlands India. *In* Bull. Jard. bot. Buitenz. III **13**: 57–76.

BOUDIER, J. L. E. (1906–1907). Icones mycologicae 2: *pls. 322–323.*
BREFELD, O. (1891). Untersuchungen aus dem Gesammtgebiete der Mykologie **9**: viii & 156 pp.
CAIN, R. F. & N. A. HASTINGS (1946). Studies of soil fungi. II. A new species of *Sphaerospora* with a *Botrytis*-like stage. *In* Can. J. Bot. **34**: 360–367.
DADE, H. A. (1960). Laboratory methods in use in the culture collection, C.M.I. *In* Herb. I.M.I. Handbook 40–69. Commonwealth Mycological Institute, Kew.
DAVIDSON, R. W. (1950). *Urnula craterium* is possibly the perfect stage of *Strumella coryneoideae*. *In* Mycologia **42**: 735–742.
DODGE, B. O. (1912). Methods of culture and the morphology of the archicarp in certain species of the Ascobolaceae. *In* Bull. Torrey bot. Club **39**: 139–197.
—— (1920). The life history of *Ascobolus magnificus*. Origin. of the ascocarp from two strains. *In* Mycologia **12**: 115–134.
—— (1922). A *Lachnea* with a botryose conidial state. *In* Bull. Torrey bot. Club **49**: 301–305.
ECKBLAD, F.-E. (1968). The genera of the operculate Discomycetes. *In* Nytt Mag. Bot. **15**: 1–191.
GAMUNDI, I. J. & M. E. RANALLI (1964). Estudio sistemático y biológico de las Ascoboláceas de Argentina. I. *In* Nova Hedwigia **7**: 517–533.
GREEN, E. (1931). Observations on certain Ascobolaceae. *In* Trans. Br. mycol. Soc. **15**: 321–332.
GREMMEN, J. (1949). De imperfecte vorm van *Desmazierella acicola* Lib. *In* Fungus **19**: 32–35.
GWYNNE-VAUGHAN, H. C. I. (1937). Contribution to the study of *Lachnea melaloma*. *In* Ann. Bot. II **1**: 189–205.
GWYNNE-VAUGHAN, H. C. I. & H. S. WILLIAMSON (1927). Germination in *Lachnea cretea*. *In* Ann. Bot. **41**: 489–495.
—— & —— (1930). Contribution to the study of *Humaria granulata* Quél. *In* Ann. Bot. **44**: 127–145.
HOTSON, J. W. (1917). Notes on bulbiferous fungi with a key to described species. *In* Bot. Gaz. **64**: 265–284.
HUGHES, S. J. (1951). Studies on microfungi. IX. *Calcarisporium*, *Verticicladium*, and *Handsfordia* (gen. nov.). *In* Mycol. Pap. 43: 25 pp.
—— (1953). Conidiophores, conidia, and classification. *In* Can. J. Bot. **31**: 577–659.
—— (1960). Microfungi. V. *Conoplea* Pers. and *Exosporium* Link. *In* Can. J. Bot. **38**: 659–696.
KERVORKIAN, A. G. (1932). Prominence of a conidial stage in *Patella abundans*. *In* Mycologia **24**: 233–239.
KIMBROUGH, J. W. (1966). Studies in the Pseudoascoboleae. *In* Can. J. Bot. **44**: 685–704.
—— (1970). Current trends in the classification of Discomycetes. *In* Bot. Rev. **36**: 91–161.
KIMBROUGH, J. W. & R. P. KORF (1967). A synopsis of the genera and species of the tribe Theleboleae (= Pseudoascoboleae). *In* Am. J. Bot. **56**: 1187–1202.
KORF, R. P. (1958). Japanese discomycete notes. I-VIII. *In* Sci. Rep. Yokohama natn. Univ. II **7**: 7–35.
—— (1960). Nomenclatural notes. IV. The generic name *Plicaria*. *In* Mycologia **52**: 648–651.
—— (1970). Nomenclatural notes. VII. Family and tribe names in the Sarcoscyphineae (Discomycetes) and a new taxonomic disposition of the genera. *In* Taxon **19**: 782–786.
LE GAL, M. (1941). Observations sur *Sarcoscypha coccinea* var. *Jurana* Boud. et sur *Saccobolus citrinus* Boud. et Torr. *In* Bull. Soc. mycol. Fr. **57**: 50–55.
LOHWAG, H. (1927). Das Oogon als Wesensbestandteil der Geschlechtsorgane im Pilzreich. *In* Biol. gen. **3**: 699–722.
MAAS GEESTERANUS, R. A. (1967). Studies in cup-fungi—I. *In* Persoonia **4**: 417–425.
MCCALLAM, A. W. (1918). The occurrence of *Bulgaria platydiscus* in Canada. *In* Mycologia **11**: 239–295.

MOLLIARD, M. (1904a). Mycelium et forme conidienne de la morille. *In* C.r. hebd. Séanc. Acad. Sci., Paris **138**: 516–517.
—— (1904b). Forme conidienne et sclérotes de *Morchella esculenta* Pers. *In* Rev. gén. Bot. **16**: 209–218.
MOORE, E. J. & R. P. KORF (1963). The genus *Pyronema*. *In* Bull. Torrey bot. Club **90**: 33–42.
NANNFELDT, J. A. (1949). Contributions to the mycoflora of Sweden. 7. A new winter discomycete, *Urnula hiemalis* Nannf., n. sp., and a short account of the Swedish species of Sarcoscyphaceae. *In* Svensk bot. Tidskr. **43**: 468–484.
OBRIST, W. (1961). The genus *Ascodesmis*. *In* Can. J. Bot. **39**: 943–953.
PADEN, J. W. (1967). The conidial state of *Peziza brunneoatra*. *In* Mycologia **59**: 932–934.
PADEN, J. W. & E. E. TYLUTKI (1968). Idaho discomycetes. I. A new genus of the Sarcocyphaceae. *In* Mycologia **60**: 1160–1168.
—— & —— (1969). Idaho discomycetes. II. *In* Mycologia **61**: 683–693.
RIFAI, M. A. (1968). The australasian pezizales in the herbarium of the Royal botanic Gardens Kew. *In* Verh. K. Ned. Akad. Wet., Afd. Natuurk. II **57**: 295 pp.
ROSINSKI, M. A. (1953). Two types of spore germination in *Sarcoscypha coccinea*. *In* Mycologia **45**: 302–306.
—— (1956). Development of the ascocarp in *Anthracobia melaloma*. *In* Mycologia **48**: 506–533.
SCHNEIDER, R. (1954). *Plicaria fulva* n. sp., ein bisher nicht bekannter Gewachshausbewohner. *In* Zentbl. Bakt. (II. Abt.) **108**: 147–153.
TULASNE, E. L. R. (1853). Nouvelles recherches sur l'appareil reproducteur des champignons. *In* Annls Sci. nat. (Bot.) III **20**: 129–182.
TULASNE, E. L. R. & C. TULASNE (1865). Selecta Fungorum carpologia **3**: *pl. 14 figs. 19–20*.
WEBSTER, J. & al. (1964). Culture observations on some discomycetes from burnt ground. *In* Trans. Br. mycol. Soc. **47**: 445–454.
WHITNEY, H. S. & J. R. PARMETER (1964). The perfect stage of *Rhizoctonia hiemalis*. *In* Mycologia **56**: 114–118.
WOLF, F. A. (1958a). Mechanism of apothecial opening and ascospore expulsion by the cupfungus *Urnula craterium*. *In* Mycologia **50**: 837–843.
—— (1958b). The conidial state of *Lamprospora trachycarpa* (Currey) Seaver. *In* J. Elisha Mitchell scient. Soc. **74**: 163–166.

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STATISTICAL METHODS AND SPECIES DELIMITATION IN THE GENUS OTIDEA

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(With three Tables, five Text-figures)

The aim of this study is to show how some simple statistical techniques introduced into routine taxonomical work renders it possible for the species to be delimited with greater exactness and to be identified with more reliability. The study was based on the genus *Otidea*.

For several years I paid attention to the genus *Otidea* and made extensive collections. The number of species in this genus is neither too large nor too small for a preliminary study with the help of statistical methods. Several different patterns of variation can be found in the genus and, although Nannfeldt (*1966*) calls *Otidea* a much neglected genus, his own study and papers by other authors (Kanouse, *1949*; Maas Geesteranus, *1967*) have thrown enough light on this group to try to produce an inductive classification.

This study is based in its essential part on the collections of the Mycological Herbarium of the Institute of Zoology and Botany of the Academy of Sciences of the Estonian SSR (TAA). Several specimens sent to the author for identification or lent from other herbaria were investigated, too. The range of geographical distribution of the material studied covers all the U.S.S.R. Also several Indian collections and some older collections from western Europe were studied. Unfortunately there was no time to borrow American material for biometric study and only Kanouse's type specimens were consulted.

Sections of fruitbodies made by hand were soaked in a drop of 5 % KOH solution, then covered with coverslip and studied under a MBI-6 light microscope. All measurements of microscopic characters were made using a 40x apochromate objective a 7x compensation ocular at the magnification 700x with ocular micrometer scale. 20 spore lengths and 10 spore widths were measured of each fruitbody studied to calculate individual mean values.

The necessary computations were carried out in the Tartu State University Computing Center on an Ural-4 computer and in the ETKVL Computing Center on a Minsk-22 computer. At first nine characters were considered: height of fruitbody, diameter of fruitbody, spore length, spore width, ascus length, ascus width, width of the paraphyses, width of their tip, and width of the hyphae of the medullary excip-

* Paper read at the Symposium "Taxonomy of operculate Discomycetes" held at the First International Mycological Congress, Exeter, 1971.

ulum. The ectal excipular details were found to be strongly correlated with fruitbody colour and rataer difficult to code. Eventually the study was restricted to spore dimensions because the other characters added comparatively little to the distinction of the species.

Since the study was planned as inductive, all specimens were studied and measured first, then grouped into species. For this step no computer aid was required, since experience showed that the species are sufficiently clear-cut to be distinguished graphically from scatter diagrams, using so-called indicator characters. For the species of *Otidea* the indicator characters are spore length and spore width. In addition a third indicator character was used: the material was divided into dark excipled species (like *O. bufonia*) and light excipled ones (including medium brown species like *O. leporina*). Species with regular cup-shaped apothecia were not included in this study. The advantage of the scatter diagram method lies also in the fact that possible errors of measurement can readily be detected. The results of the clustering technique are shown in Figs. 3 and 4.

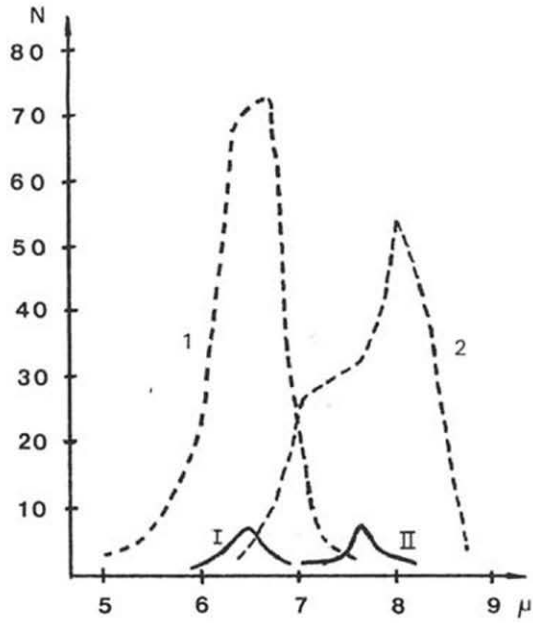

FIG. 1. Spore width distribution curves of *O. onotica* (1, I) and *O. leporina* (2, II). 1 and 2 are compound distributions based on measurements of all spores from all individuals studied. I and II are distributions of individual mean values. The far higher discrimination power of the latter distributions is evident.

The analysis of spore dimensions and other microscopic meristic characters was based on the following principles. Spore dimensions are one of the basic characters of the fungus species. They are usually presented in descriptions by their total range of variability. The total range of variability of single spore dimensions has, however, some unfortunate properties which do not permit its effective use for distinction between species whose spore dimensions are comparatively close together. There is a better way to show the difference between species on the basis of spore dimensions, as can be seen from the following considerations.

Each species has a statistical entity as a set of individuals which are imagined as points in multidimensional space according to the number of characters involved. It is important to emphasize that the distribution of a character, not the character itself, describes the species. The points for single characters, e.g. fruitbody diameter, are determined by a single measurement. Each measurement always has an error but it is usually so insignificant that it may be ignored in the following analysis. Spore and ascus dimensions and other microscopic meristic characters are multiple characters: they can be measured practically in very large numbers in each individual. The distribution of such characters within an individual is more or less normal and characterized by two parameters—mean value and standard deviation.

The mean value of a multiple character j in an individual i determines the point x_{ij} for this individual. The confidence limits of a mean value can be considered analogous to the error of measurement of single character. Practically the mean value is approximated by the arithmetical mean $\bar{x}$ with an error $\varphi \pm \frac{s}{\sqrt{n}}$. It is important for the exactness of the following analysis to reduce the confidence limits of the arithmetical mean to the measurements error ε with an ocular micrometer scale,

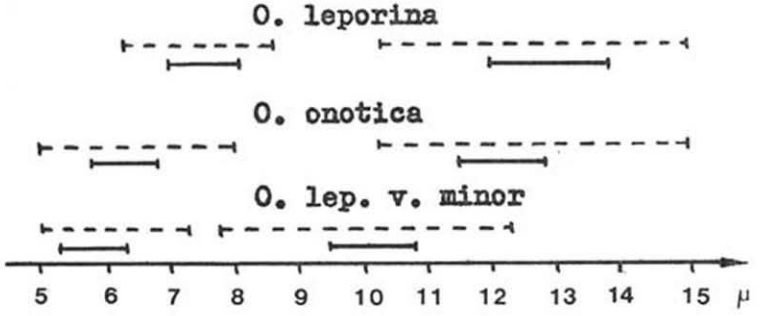

FIG. 2. Comparison of total ranges of variability (dotted line) and ranges of variability of individual mean values of spore width (left) and spore length (right) in three species of *Otidea*. Species indistinguishable in the basis of total ranges of variability can be separated by the ranges of variability of individual mean values.

i.e. to find a sufficient number of single measurements of a character from the equation $n = \frac{(t.s)^2}{\varepsilon}$ where t can be found from the Student's t-table, ε is the wanted minimum value for the error, and standard deviations s has to be found by probe analysis. In the *Otidea* species and in the majority of Discomycetes n varies between 20 and 30 for spore length and does not exceed 10 for the spore width.

Thus spore length and other meristic multiple characters can be presented by two different distributions: (1) the distribution of single spore lengths, and (2) the distribution of individual mean values. The former distribution is based on the spores, the elements of the individual, and can be used for the description of the individual. The species is characterized by the second distribution, which is based on the individuals, the elements of species. The commonly used total range of variability is in fact based on compound distribution summed up from several unequal individual distributions and so is a rather inexact way to describe a species, since it involves a jump over a level of organization, introducing considerable background noise. The correct way to present the multiple character data even in routine taxonomic work should be via specimen mean values. The main advantage of this method—good discrimination between species—can be seen in Figs. 1 and 2. The distribution of specimen mean values can be described in practical taxonomic work by its range of variability or, more correctly, by its tolerance limits, which can be found from the corresponding tables (Owen, *1962*).

The total range of variability, the specimen mean values range of variability, and the tolerance limits for the latter are given for some species of *Otidea* in Table 1. The tolerance limits are given with $P = 90$ which means that at least 90 % of the individual mean values of the given species fall in a given range, ant with $\gamma = 90$ which means that this statement is correct with 90 % probability since the limits are calculated from statistical data.

Turning to the analysis of spore dimension data, graphically presented in Figs. 3 and 4, let us consider first the light-excipled species in Fig. 3. This group is, in fact, distinctly heterogeneous as regards the colour of the apothecia, and should be divided into five subgroups: (1) species with rust-brown or reddish brown apothecia—*O. leporina* (Fr.) Fuck., *O. caligata* (Nyl.) Sacc., and a species for which I have no better name than *O. leporina var. minor* (Rhem) Sacc. sensu Kanouse; (2) species with very light cream-coloured apothecia—*O. alutacea* (Pers.) Massee, *O. rainierensis* Kanouse, and *O. kauffmanii* Kanouse. *Otidea rainierensis* is excluded from this study, since the material available was insufficient, but it may be noted that *O. alutacea var. microspora* Kanouse is identical, while its spore dimensions evidently overlap those of *O. concinna*; (3) light ochraceous to yellowish brown species represented in this study by *O. felina* (Pers.) Bres.; (4) bright ochraceous species with rosy hymenium like *O. onotica* (Fr.) Fuck., which seems to be unique in this group; (5) externally bright lemon-yellow species such as *O. concinna* (Fr.) Sacc., which seems to be unique too. The colour differences between some species are very notable in fresh apothecia but the exact colour is often difficult or even impossible to determine

TABLE 1. — Spore dimension data of some *Otidea* species

	Spore length in microns			Spore width in microns		
	Total range of variability	Range of variability of individual mean values	Tolerance limits for individual maen values $P = 90$, $\gamma = 90$	Total range of variability	Range of variability of individual mean values	Tolerance limits for individual mean values $P = 90$, γ 90
1. *O. leporina* v. *minor*	7.8–12.3	9.5–10.8	9.3–11.0	5.0– 7.3	5.3– 6.6	5.1– 6.9
2. *O. onotica*	10.3–15.0	11.5–12.8	11.5–13.0	5.0– 8.0	5.8– 6.8	6.0– 6.9
3. *O. leporina*	10.3–15.0	12.0–13.8	12.0–13.8	6.3– 8.6	7.0– 8.1	7.0– 8.3
4. *O. caligata*	16.6–21.8	17.8–20.4	17.2–21.4	8.3–12.0	9.5–12.0	9.0–11.8
5. *O. alutacea*	14.1–19.1	15.5–16.8	14.6–17.6	6.6– 8.3	7.5– 8.0	7.5– 8.5
6. *O. felina*	12.0–17.0	13.3–15.8	13.6–16.0	6.0– 7.6	6.3– 7.1	6.3– 7.3
7. *O. kauffmanii*	10.8–13.6	11.5–13.1	10.7–13.4	4.5– 6.0	4.8– 5.3	4.6– 5.5
8. *O. concinna*	9.6–12.3	10.5–11.3	10.1–11.5	5.0– 6.3	5.1– 5.6	5.0– 6.0
9. *O. smithii*	11.5–16.0	13.0–14.4	11.6–15.5	5.5– 7.5	5.8– 6.8	5.3– 7.3
10. *O. bufonia*	12.3–17.3	14.6–16.3	13.8–16.4	5.6– 8.0	6.1– 7.0	6.0– 7.3

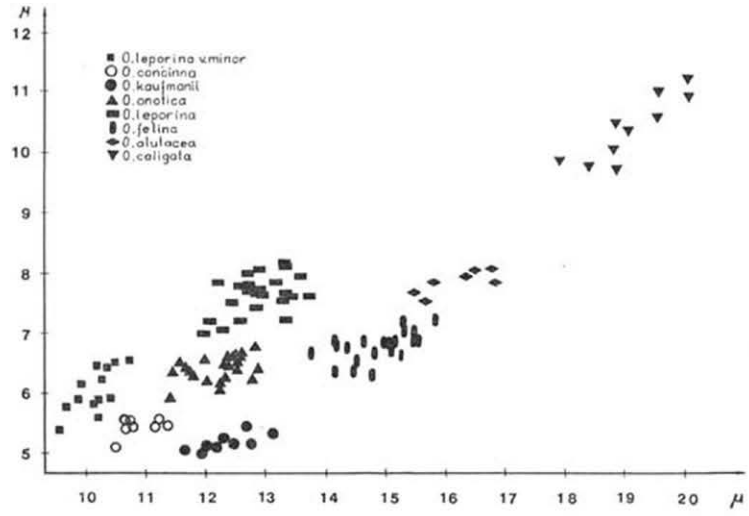

FIG. 3. Spore dimension scatter diagram of light-coloured species of *Otidea*.

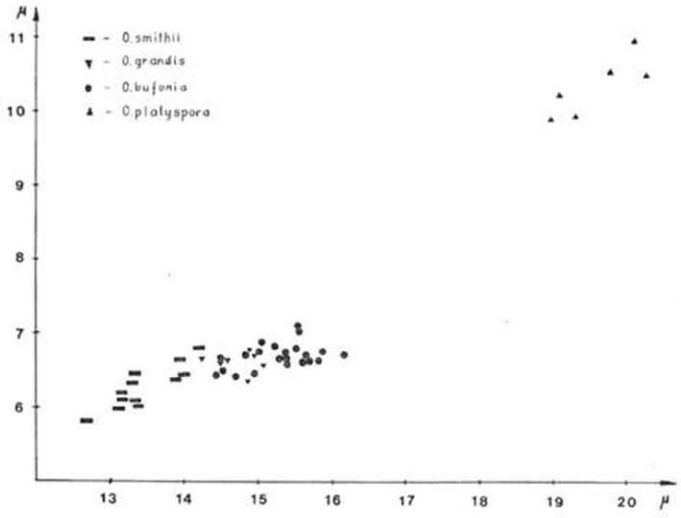

FIG. 4. Spore dimension scatter diagram of dark-coloured species of *Otidea*.

TABLE 2. — D^2 values based on spore length and spore width among 10 species of *Otidea*

	D^2									
	1									
1. *O. caligata*	XXX									
		2								
2. *O. felina*	143	XXX								
			3							
3. *O. alutacea*	67	14	XXX							
				4						
4. *O. kauffmanii*	319	36	93	XXX						
					5					
5. *O. concinna*	342	53	105	16	XXX					
						6				
6. *O. leporina*	147	44	42	93	51	XXX				
							7			
7. *O. onotica*	218	25	52	27	10	17	XXX			
								8		
8. *O. bufonia*	152	1	17	34	60	58	33	XXX		
									9	
9. *O. smithii*	195	59	34	16	24	38	10	8	XXX	
										10
10. *O. lep.* v. *minor*	188	51	45	26	7	14	10	61	34	XXX

TABLE 3. — F values among 10 species of *Otidea* calculated from D^2 values in Table 2.

	N	F								
		1								
1. *O. caligata*	10	XXX								
		459	2							
2. *O. felina*	22		XXX							
		120	32	3						
3. *O. alutacea*	7			XXX						
		713	116	167	4					
4. *O. kauffmanii*	10				XXX					
		670	145	168	31	5				
5. *O. concinna*	8					XXX				
		565	251	108	283	147	6			
6. *O. leporina*	26						XXX			
		701	131	128	87	27	97	7		
7. *O. onotica*	22							XXX		
		503	5.48	43	113	168	347	181	8	
8. *O. bufonia*	24								XXX	
		552	26	75	45	58	179	43	37	9
9. *O. smithii*	16									XXX
		517	214	97	72	17	63	42	267	123	10
10. *O. lep.* v. *minor*	15									XXX

in dried material, which justifies the inclusion of all these species in one group.

The difference between species based on spore dimensions which is evident in scatter diagram can be proved using Mahalanobis' D^2 technique (Rao, *1952*) connected with Hotelling's T^2 and test of significance (Reyment, *1969*). D^2 values between 10 species of *Otidea* are given in Table 2, and variance ratio F values, calculated from D^2 by means of the following formula

$$F = D^2 \frac{N_1 N_2}{(N_1 + N_2)} \frac{(N_1 + N_2 - p - 1)}{[p (N_1 + N_2 - 2)]}$$

where p is the number of variables, are given in Table 3. The majority of F values are far above the significance level and even in the case of considerable overlapping of spore dimensions (*O. felina* and *O. bufonia*) the difference between two species is significant. For the 2 and 44 degrees of freedom the critical value at the 99 % level is $F = 5.12$ whereas the computed $D^2 = 1.054$ converts into $F = 5.48$, which proves significant difference between the two groups.

For the dark-coloured species (Fig. 3) the picture is essentially the same as for the light-coloured species with the exception of considerable overlapping of *O. bufonia* and *O. grandis* sensu Boud. These species have, however, completely different hymenial colours when fresh, so they cannot be confused.

It becomes evident that closely related species, well distinguished by qualitative characters (colour, gross morphology of fruitbody) usually have very similar spores, the differences between which can be shown only by statistical methods; on the

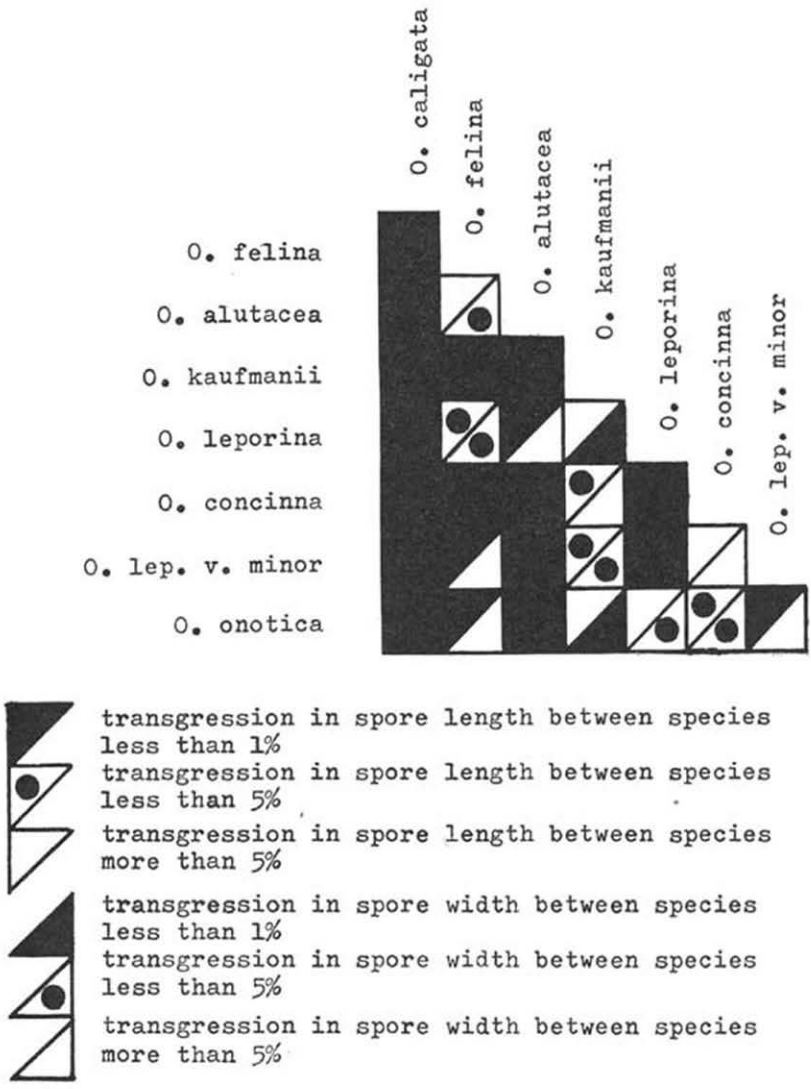

FIG. 5. Evaluation of spore length and spore width as key characters in light-coloured species of *Otidea*.

other hand, species very similar in qualitative characters are completely different in spore dimensions. This phenomenon also proved to occur in the genus *Discina* (*Neogyromitra*), where three species had distinctly different spore width (Raitviir, *1970*).

The next step in this study was the construction of a key to the species of *Otidea* based predominantly on spore dimensions. For this purpose, spore length and spore width were evaluated as key characters by means of Lubishchev's (*1959*) discrimination coefficient $K = \frac{(\bar{x}_1 \quad \bar{x}_2)^2}{S_1^2 + S_2^2}$, which is in fact Student's t squared. The critical values K = 18, K = 11, and K = 5.8 correspond to total absence of linear transgression, 1 % transgression and 1 % probability of error, and 5 % transgression and 5 % probability of error. The results of this analysis are shown in Fig. 5. It may be seen that spore dimensions fail to distinguish between species only in a single instance: between *O. leporina var. minor* and *O. concinna*, but in this case the spore length-width ratio can be used as a key character. This key and data on the geographical distribution of the species studied will be published elsewhere.

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REFERENCES

KANOUSE, B. B. (1950). Studies in the genus *Otidea*. *In* Mycologia **41**: 660–677.

LUBISHCHEV, A. A. (1959). O primenenii biometrii v sistematike. *In* Vestn. Leningr. Univ. (Ser. Biol.) **9**: 128–136.

MAAS GEESTERANUS, R. A. (1967). De fungi van Nederland 2a Pezizales deel 1. *In* Wet. Meded. K. Ned. natuurh. Ver. **69**: 72 pp.

NANNFELDT, J. A. (1966). On *Otidea caligata*, *O. indivisa* and *O. platyspora* (Discomycetes Operculatae). *In* Annls bot. fenn. **3**: 309–318.

OWEN, D. B. (1962). Handbook of statistical tables. Reading, Mass.

RAITVIIR, A. (1970). Once more on *Neogyromitra caroliniana*. *In* Trans. Tartu St. Univ. **268**: 364–373.

RAO, C. R. (1952). Advanced statistical methods in biometrical research. New York.

REYMENT, R. A. (1969). Biometrical techniques in systematics. *In* Systematic Biology, Washington, D.C. 542–587.

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SPECIFIC AND GENERIC DELIMITATION IN THE HELVELLACEAE*

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(With Plate 23)

A revised Latin and English diagnosis is given for the family Helvellaceae as emended by Berthet and Dissing. The delimitation of the genera and some species in the family is discussed. Some comments are given on a new tool: the scanning electron microscope (SEM).

The studies by Le Gal on spore morphology (*1947*) and especially the cytological studies by Berthet (*1964*) yielded important information that made it possible to give a more reliable classification of the composing elements of the family Helvellaceae and of the operculate discomycetes in general. All members of the family are devoid of carotinoid pigments, a conclusion also reached by Arpin's chemical studies (*1970*).

It would be very interesting to know the chemical composition of the pigments in the Helvellaceae, while the guttules of the spores might also be worth a study.

The Helvellaceae as discussed below is taken in the sense of Berthet (*1964*) and as emended by Dissing (*1966*). It includes the following taxa: tribus Helvelleae Diss., with *Underwoodia* Peck (not considered by Berthet, l.c.), *Helvella* L. ex St-Amans emend. Nannf., and *Wynella* Boud.; tribus Gyromitreae Diss., with *Gyromitra* Fr., including *Pseudorhizina* Jačevskij (= *Helvellella* Imai; not considered by Berthet); and tribus Discineae Diss., with *Neogyromitra* Imai, *Discina* (Fr.) Fr., *Rhizina* Fr. ex Pers.

This concept of the family was accepted by Dennis (*1968*; European genera only), Rifai (*1968*), and Kimbrough (*1970*), while Maas Geesteranus (*1967*) and Eckblad (*1968*) found reasons not to do so.

Maas Geesteranus recognized three families in the group: Helvellaceae, including *Helvella*, *Gyromitra*, and *Pustulina* (*Wynella* was not considered), while his Discinaceae and Rhizinaceae correspond to these families as conceived by Benedix (*1961*).

Eckblad (l.c.) restricted the Helvellaceae to the genera included in the tribus Helvelleae Diss.; he excluded the Rhizinaceae corresponding to Dissing's tribes Gyromitreae and Discineae. Characters of the excipulum motivated Eckblad to make this separation.

Since the Helvellaceae have been radically emended since the inception new descriptions are given below.

* Paper read at the Symposium "Taxonomy of operculate Discomycetes" held at the First International Mycological Congress, Exeter, 1971.

HELVELLACEAE Fr. emend.

Carposoma sessile vel stipitatum, cupulatum, ephippioides, auriforme, gyromitroides vel clavatum (raro pulvinatum). Stipes, si praesens, teres, compressus vel lacunosus. Hymenium planum vel convolutum, albidum, cinerascens, fuscescens vel nigrum. Superficies exterior glabra vel pubescens.

Excipulum omnino textura intricata vel medullare excipulum texture intricata ab excipulo exteriore textura globosa vel angulata insigni bene discretum.

Asci operculati, 8-spori, cylindrici, J–, non ex hymenio eminentes. Paraphyses plerumque rectae, septatae, apice paulum incrassatae, pigmentis carotenoidibus nullis. Sporae hyalinae, quadrinucleatae, 1–4nas guttulas sat magnas continentes, aut globulares vel anguste ellipticae laeves, interdum involucro perisporiali indutae, aut late ovales vel ellipticae vel fusiformes, pustulis rotundatis vel reticulo cyanophilo ornatae.

Nulli status imperfecti in familia observati.

Terrestris vel ligno carioso arborum coniferarum connexa.

GENUS TYPIFICUM:—*Helvella* L. ex St-Amans emend. Nannf.

Fruitbody sessile or stipitate, cup-shaped, saddle-shaped, ear-shaped, gyromitroid, or clavate (rarely pulvinate). Stipe when present, terete, compressed, or lacunose. Hymenium even or convoluted, whitish, greyish, brownish or black. Outer surface glabrous or pubescent.

Excipulum of textura intricata throughout, or medullary excipulum of textura intricata and well distinct from the outer excipulum of textura globosa to textura angulata.

Asci operculate, 8-spored, cylindric, J–, not protruding beyond the hymenium. Paraphyses normally straight, septate, slightly enlarged above, without carotinoid pigments. Spores hyaline, tetranucleate, with 1—4 large guttules, globose or narrow elliptic, smooth, sometimes with a perisporial sheath, or broadly ovale, or elliptic to fusiform, with blunt pustules or a reticulate cyanophilous ornamentation.

No imperfect stages known in the family.

Terrestrial, or connected with decaying wood of coniferous trees.

TYPE GENUS:—*Helvella* L. ex St-Amans emend. Nannf.

SURVEY OF THE GENERA

HELVELLA L. ex St-Amans emend. Nannf.

Generic delimitation in accordance with Nannfeldt (*1932*, *1937*), who worked out Quélet's ideas (*1886*). Dissing (*1966*: 12–14) gave a brief historic review of the genus.

Maas Geesteranus (*1967*), Eckblad (*1968*), Rifai (*1968*), Kempton & Wells (*1970*), Kimbrough (*1970*), Nothnagel (*1971*) accepted Nannfeldt's generic delimitation and Dissing's species concept, although some authors intimated that the number of species recognized (26) was rather low. Dennis (*1968*) still found reasons to keep the genera *Paxina*, *Cyathipodia*, and *Leptopodia* apart in addition to *Helvella* sensu stricto.

Svrček & Moravec (*1968*) added *Helvella branzeziana* to the list of European species. In 1967 Dr. A. Raitviir, Estonia found a *Helvella* in Asia which is considered to be identical with *Acetabula aestivalis* Heim & Remy. This will be published as *Helvella aestivalis* (Dissing & Raitviir, *1973*) in a joint paper.

Thus the number of species now recognized is 28.

There can be no doubt that serious studies of the North American flora will increase this number. A study of a rather rich material from India (carefully collected by Drs. R. A. Maas Geesteranus and C. Bas, The Netherlands, and at present in the author's possession) will probably further increase the number of species.

Until now distinctive characters on the species level are: type of fruitbody, colour, glabrous or pubescent outer surface. With the exception of *H. macropus* the spores are of minor diagnostic value.

Keys to the European species (except *H. branzeziana*) were given by Dissing (*1966*; in English). A German translation was given by Nothnagel (*1971*). Maas Geesteranus (*1967*) gave a key to the species known from The Netherlands (in Dutch).

Wynella Boud.

Only one species: *W. silvicola* (Beck apud Sacc.) Nannf. Nannfeldt (*1967*) discussed its delimitation, nomenclature and distribution.

I agree with Nannfeldt in all points but one: viz. that *Wynella* (as represented by *W. silvicola*) should be placed in a tribe of its own. Surely it differs from the other genera of the family because of its ear-shaped apothecia but due to characters of the spores and the excipulum I regard it closely allied to *Helvella* and continue to believe that it has to be placed in the same tribus (cf. Helvelleae Diss., *1966*).

The reddish brown colours found in *W. silvicola* seem (i.e. without a chemical analysis) to correspond to those found in *Helvella aestivalis* (see Dissing & Raitviir, *1973*). One might therefore be tempted to claim that the only difference between the two genera is that *Wynella* has ear-shaped apothecia. However, I agree with Nannfeldt (l.c.) that the 'horny consistency' of the dried fruitbodies is a character of importance. At present it is difficult to evaluate this character. When describing the excipulum of *Wynella* one has to use the same terms as when describing for instance *Helvella lacunosa*. It is true that there are quantitative but no qualitative differences, although it might be necessary to examine the content of the cells in the excipulum to find a sound explanation for the difference in the consistence.

Underwoodia Peck

The distribution of the species of this genus is remarkable, with one species in each of the following continents: North America (*U. columnaris* Peck), South America (*U. fuegiana* (Speg.) Gamundi), Australia (*U. beatonii* Rifai).

Gamundi (*1957*), who did not circumscribe the Helvellaceae, considered *Underwoodia* a true member of that family. Dissing (*1966*) found the characters of the excipulum and of the spores very similar to those of some species of *Helvella* and he included *Underwoodia* as a member of the tribus Helvelleae.

It has never been shown that the spores in any *Underwoodia* species actually possess four nuclei.

Eckblad (*1968*), who stresses anatomical characters, included the species of *Underwoodia* in *Helvella*, because it "does not differ in any other character than form".

Although this might be correct, it seems that the form is so deviating from any known fruitbody type in *Helvella* that it cannot possibly be included in that genus.

A key to the known species of *Underwoodia* is given by Rifai (*1968*).

GYROMITRA Fr.

"The genera in the tribus Gyromitreae have a habit much like the highest developed species in the genus *Helvella* (considered to be the species in the sections *Lacunosae* and *Elasticae*), but can be separated well on characters of the spores and on anatomy. The spores are narrow elliptical with two small guttulae, or sphaerical with one guttula. In the genera *Gyromitra* and *Helvellula* it is not possible to distinguish clearly an outer excipulum and a medullary excipulum. . . . Mutually the genera *Gyromitra* and *Helvellulla* are mainly separated on characters of the spores, but I am not at all sure these characters can separate the genera if examined in detail." (Dissing, *1966*: 28).

Harmaja (*1969b*) included *Pseudorhizina* (*Helvellulla*) *sphaerospora* in *Gyromitra*. I can accept this, whereas I disagree in including *Discina* and *Neogyromitra* in *Gyromitra* as well (see below). At present the following species can be referred with certainty to *Gyromitra*: *G. esculenta* (Pers. ex Fr.) Fr., the type species, *G. infula* (Schaeff. ex Fr.) Quél., *G. ambigua* (Karst.) Harmaja, *G. californica* (Phill.) Raitv., *G. tasmanica* Cooke, and *G. sphaerospora* (Peck) Sacc. Raitviir (*1965*) described *G. infula* var. *apiculatispora*, with "apiculate" perisporium, Harmaja (*1969b*) found this taxon identical with *G. ambigua*. He further evaluated in a promising way the character of the perisporium. However, I find that the presence of a perisporium in some species of *Gyromitra* cannot justify the merging of *Gyromitra*, *Discina*, and *Neogyromitra*.

Hitherto only one species (*G. tasmanica*) has been described from the Southern hemisphaere (New Zealand), but material from South America may increase the number of species by two (Gamundi, personal information). A critical study of the whole genus is highly needed.

A key to the species is not known to me.

DISCINA (Fr.) Fr.

Fruitbodies sessile or short stipitate, cup-shaped or expanded. Eckblad (*1966*) included *Neogyromitra* in *Discina* because" . . . . *Neogyromitra* actually does not differ from *Discina perlata* in any other character than a slight difference in form: pileate apothecia in *Neogyromitra* versus stipitate, cupulate to convex apothecia with folded hymenium in *Discina*".

I feel much attracted by Eckblad's ideas, which might well prove to be correct. I hesitate however to follow him until details of the ornamentation of the spores have been studied in both genera (see Appendix p. 429).

Harmaja (*1969a*) combined the genera *Gyromitra*, *Discina*, and *Neogyromitra*. At a first glance his illustration (l.c., fig. 1) looks very fascinating. Still it is not proved (as far as I know) that the perisporial sheath is homologous with the appendages

found on the spores in *Discina* and *Neogyromitra*. According to Harmaja it is the periplasma which stains in spores of *Gyromitra*, while it is the ornamentation that is taking stain in *Discina* and *Neogyromitra*. Further the fruitbodies do not reflect the same beautiful line (of "evolution") expressed in Harmaja's figure.

McKnight (*1969*) made a critical study of the North American species of *Discina*; European species were also considered. He gave a key to the six species recognized by him.

Paradiscina Benedix (*1969*) is considered to be superfluous.

Neogyromitra Imai

Fruitbodies stipitate, gyromitroid. Closely allied to species of *Discina*. Fruitbodies varying much in size, shape, and colour. A greater number of 'species' have been described (formerly as species of *Gyromitra*; see Nannfeldt, *1932*), but modern authors have reduced the number of species to two: *N. gigas* (Krombh.) Imai and *N. caroliniana* (Bosc ex Fr.) Imai (see Maas Geesteranus, *1965*). The two species are separated by characters of the spores (Maas Geesteranus, l.c., figs. 2–4).

Fastigiella Benedix (1969) is considered to be superfluous.

Rhizina Fr. ex Pers.

Only one species, *Rhizina undulata* Fr. ex Fr., which is unique in the Helvellaceae for three reasons: the brown, non septate setae in the hymenium (originating from the medullary excipulum), the numerous root-like structures from the underside of the fruitbody, and the parasitic habit, on young, planted coniferous trees. *Rhizina undulata* grows mostly on burnt areas (see Hagner, *1962*; Petersen, *1970*).

Some authors prefer to place this species in a family of its own (Benedix, *1961*; Maas Geesteranus, *1967*).

Appendix

In Plate 23 some spores are shown photographed in the scanning electron microscope (SEM). The opportunity is used to show spores from non-helvellaceous discomycetes as well, because I wish to demonstrate that the SEM technique might prove to be a valuable tool in future work in the group. I do not, of course, expect that the use of the SEM in general will make revolutionary alterations in the classification of operculate discomycetes. Because the characters of the spores are so important in this group it is believed that in many cases use of SEM techniques will give more reliable, and better reproduceable results than drawings. This is in no way meant as slighting the very painstaking and skillful illustrators in discomycetology such as Le Gal, Rifai, Maas Geesteranus, and van Brummelen. It goes without saying that the much higher resolving power of the SEM makes it possible also to realize details which cannot be seen in the light microscope. Some examples are shown in Plate 23. It shows that in *Rhizina undulata* (Figs. f, i) the ornamentation does not cover the ends of the spores (arrow in Fig. f) while in *Neogyromitra* the whole

spore is covered by ornamentation. I believe it will be valuable to have the spores of all species of *Rhizina*, *Discina* and *Neogyromitra* illustrated in a similar manner.

It is also interesting that *Pustulina ochraceus* and *Peziza fimeti* are not "smooth-spored" as described in literature. In *Helvella acetabulum* the spores are completely smooth. The wart in the middle of the meshes in spores of *Aleuria aurantia* (Fig. g) can also be seen in light microscope provided the spores are stained in cotton blue. This has never been mentioned in previous descriptions.

Material and methods.

All collections photographed in Plate 23 are deposited in the Botanical Museum, Copenhagen (C). *Neogyromitra gigas* is illustrated from Swedish material and *Saccobolus versicolor* was growing on horse dung sent from Greenland. All other collections are from Denmark.

Preparation of the spores for study in the scanning electron microscope was very simple. The spores in Figs. c, d (in culture), e, f, h, i, j, k, n were all from fresh fruitbodies which were allowed to puff the spores on the metal stub. Because the fruitbodies are so tiny fresh material of *Peziza fimeti* and *Saccobolus versicolor* was placed in a drop of water on the stub, thus allowing the spores to be shot off in the water. After shooting had ceased the stub with water and spores was freeze-dried.

The specimens of *Neogyromitra gigas* and *Aleuria aurantia* (Figs. a, b, g) had been dried, but with spores deposited on the hymenium. A fragment of the hymenium was placed in a drop of 70 % alcohol on the stub. The spores then loosened from the hymenium; after this the alcohol was substituted by water, and the stub finally freeze-dried.

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REFERENCES

ARPIN, N. (1968). Les caroténoïdes des Discomycètes: essai chimiotaxinomique. Thèse, Univ. Lyon (& *in* Bull. mens. Soc. linn. Lyon **38** (Suppl.): 169 pp. 1969).

BENEDIX, E. H. (1961). Zur polyphyletischen Herkunft der Helvellaceen. *In* Z. Pilzkunde **27**: 93–102.

—— (1969). Art- und Gattungsgrenzen bei höheren Discomyceten. 3. *In* Kulturpflanze **17**: 253–284.

BERTHET, P. (1964). Essai biotaxinomique sur les Discomycètes. Thèse, Univ. Lyon.

DENNIS, R. W. G. (1968). British Ascomycetes. Lehre.

Dissing, H. (1966). The genus *Helvella* in Europe, with special emphasis on the species found in Norden. *In* Dansk bot. Ark. **25** (1)172 pp.
Dissing, H. & A. Raitviir (1973). Discomycetes of Middle Asia. X. *In* Eesti NSV Tead. Akad. Toim. (In press).
Eckblad, F.-E. (1968). The genera of the operculate Discomycetes. A re-evaluation of their taxonomy, phylogeny and nomenclature. *In* Nytt Mag. Bot. **15**: 191 pp.
Gamundi, I. J. (1957). Sobre la identidad de *Geomorium* Spegazzini con *Underwoodia* Peck ("Discomycetes"). *In* Darwiniana **11**: 418–422.
Hagner, M. (1962). Några faktorer av betydelse för rotmurklans skadegörelse. *In* Norrlands Skogsv. Förb. Tidskr. **9**: 245–270.
Harmaja, H. (1969a). A wider and more natural concept of the genus *Gyromitra* Fr. *In* Karstenia **9**: 9–12.
—— (1969b). A neglected species, *Gyromitra ambigua* (Karst.) Harmaja, n. comb., and *G. infula* s. str. in Fennoscandia. *In* Karstenia **9**: 13–19.
Kempton, P. E. & V. L. Wells (1970). Studies on the fleshy fungi of Alaska. 4. A preliminary account of the genus *Helvella*. *In* Mycologia **62**: 940–959.
Kimbrough, J. W. (1970). Current trends in the classification of Discomycetes. *In* Bot. Rev. **36**: 91–161.
Le Gal, M. (1947). Recherches sur les ornamentations sporales des Discomycètes operculés. *In* Annls Sci. nat. (Bot.) XI **8**: 73–297.
Maas Geesteranus, R. A. (1965). Einiges über *Neogyromitra caroliniana*. *In* Proc. K. Ned. Akad. Wet. (C.) **68**: 128–134.
—— (1967). De fungi van Nederland. 2a Pezizales – deel 1. *In* Wet. Meded. K. Ned. natuurh. Ver. **69**: 72 pp.
McKnight, K. H. (1969). A note on *Discina*. *In* Mycologia **61**: 614–630.
Nannfeldt, J. A. (1932). Bleka Stenmurklan, *Gyromitra gigas* (Krombh.) Cke. *In* Friesia **1**: 34–45.
—— (1937). Contributions to the mycoflora of Sweden. 4. On some species of *Helvella* together with a discussion of the natural affinities within Helvellaceae and Pezizaceae trib. Acetabulae. *In* Svensk bot. Tidskr. **31**: 47–66.
—— (1966). On *Otidea caligata*, *O. indivisa* and *O. platyspora* (Discomycetes Operculatae). *In* Annls. bot. fenn. **3**: 309–318.
Nothnagel, P. (1971). Die *Helvella*-Monographie von Dissing. *In* Mykol. Mitteil Bl., Halle **15**: 8–25.
Petersen, P. M. (1970). Danish fireplace fungi, an ecological investigation on fungi on burns. *In* Dansk bot. Ark. **27**: 97 pp.
Quélet, L. (1886). Enchiridion Fungorum in Europa media, et praesertim in Gallia vigentium. Lutetiae.
Raitviir, A. (1965). Taxonomical notes on the genus *Gyromitra*. *In* Eesti NSV Tead. Akad. Toim. (Biol. Seeria) **3**: 320–323.
Rifai, M. A. (1968). The Australasian Pezizales in the Herbarium of the Royal Botanic Gardens Kew. *In* Verh. K. Ned. Akad. Wet., Afd. Natuurk. II **57** (3): 295 pp.
Svrček, M. & J. Moravec (1968). *Helvella* (*Leptopodia*) *branzeziana* sp. nov., eine neue Spezies aus Böhmen. *In* Česká Mykol. **22**: 87–89.

Explanation of Plate 23

Scanning micrographs. Spores. — a, b, *Neogyromitra gigas*, Lundell & Nannf. exs.

No. 1353, a, ×1,625, b, ×2,880. — c, *Peziza echinospora*, H.D. 71.23, ×3,120. — d, *Ascobolus crenulatus*, H.D. 71.14, ×5,225. — e, h, *Pustulina ochraceus*, H.D. 71.24, e, ×2,652, h, ×5,250. — f, i, *Rhizina undulata*, H.D. 71.42, f, × 1.195, i, × 5.320. — g, *Aleuria aurantia*, H.D. 64.236, ×2,625. — j, *Peziza micheli*, H.D. 71.102, ×2,800. — k, *Peziza praetervisa*, H.D. 71.31, ×2,780. — l. *Peziza fimeti*, H.D. 71.12, × 2,150. — m, *Saccobolus versicolor*, H.D. 71.06, × 900. — n, *Helvella acetabulum*, H.D. 71.37, × 1,550.

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DIFFERENTIATION OF TRIBES AND GENERA IN THE FAMILY* SARCOSCYPHACEAE

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(With Plates 24—25)

Taxonomic criteria used in differentiating genera are described and illustrated. The genera are assigned to three tribes, the two existing tribes: Sarcoscypheae and Boedijnopezizeae, and a new tribe Pithyeae.

One product of the intensive study of operculate discomycetes in the past decade has been recognition of new families with clearly defined boundaries (Eckblad, *1968*, Kimbrough, *1970*). This paper discusses the internal structure of one of these new families, the Sarcoscyphaceae sensu Korf (*1971*). It describes criteria, common to all genera, which delimit the family, then proceeds to those which occur in some genera and not in others, and which are, therefore, useful in delimiting genera. Finally it discusses the division of the family into three tribes, including a new one, the Pithyeae.

As presently circumscribed, the family Sarcoscyphaceae no longer includes those genera with dark-colored apothecia formerly placed in the tribe Urnuleae. They have been transferred to a separate family, the Sarcosomataceae (Korf, *1971*).

The family Sarcoscyphaceae is characterized by two groups of taxonomic characters. One consists of characters shared by all members of the family. Some of these also occur in the Sarcosomataceae. The other group is equally characteristic, but is made up of characters which occur in some genera and not in others. The first group is described at this point: the second will be included among the criteria for delimiting genera.

The suboperculate ascus (Le Gal, *1946*) occurs in all members of the suborder Sarcoscyphineae. A characteristic organelle, the subapical pad, can be seen as a thickened addition to the inner side of the apex of the ascus wall (Plate 23, Figs. B, C).

In the families Sarcoscyphaceae and Sarcosomataceae the tissues of the medullary excipulum are filamentous, *textura intricata*, as seen either in vertical section or in crush mounts. As a consequence the texture of the apothecia in these families is tough, leathery to rubbery.

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In the families Sarcoscyphaceae and Sarcosomataceae the ascospores are single-celled, but they contain numerous nuclei, 16 or 32 in most genera (Berthet, *1964*).

In the family Sarcoscyphaceae the cells of the paraphyses are multinucleate, whereas in the family Sarcosomataceae the cells of the paraphyses are uninucleate (Berthet, *1964*).

In the family Sarcoscyphaceae the hymenial pigments are bright colored (red, orange, yellow) caroteinoids (Arpin, *1968*), and the exterior of the apothecium is light colored. In rare instances hymenial pigments are absent and the hymenium is white.

In the family Sarcoscyphaceae, apothecia occur on wood or on foliage in early stages of decomposition. In a few genera they are found on soil, although they probably arise from buried wood or roots. They seldom, if ever, occur on very well-rotted wood, on dung or compost, or on charcoal.

The family Sarcoscyphaceae consists of sixteen genera arranged in three tribes: Sarcoscypheae, Boedijnopezizeae, and Pithyeae.

DESCRIPTION OF GENERIC CHARACTERS

The following characters are useful in delimiting genera within the family. Table 1 lists the genera and summarizes the distribution of these characters among the genera.

APOTHECIAL SIZE.—There is a wide range of apothecial size within the family. Most members of the tribe Sarcoscypheae have medium-sized to large apothecia, ranging from 1–5 cm or more in diameter. In the tribe Pithyeae, however, apothecia are seldom more than a few millimeters across.

APOTHECIAL SHAPE.—Most genera in the family have shallow, cupshaped to discoid apothecia with short stipes. Two groups of genera depart from this pattern. In *Boedijnopeziza*, *Cookeina*, *Microstoma*, *Geodina*, and sometimes in *Sarcoscypha*, the apothecium is deeply cup-shaped or funnel-shaped with a long stipe. In *Wynnea* and *Aurophora*, on the other hand, the apothecium is strongly unequal-sided (fan-shaped or ear-shaped) with a lateral stipe.

SYNCHRONOUS ASCUS DEVELOPMENT.—In the genera *Microstoma*, *Boedijnopeziza*, and *Cookeina*, ascus development is synchronous, so that all of the asci in an apothecium are at the same stage of development (Plate 22 Fig. B). Specimens of these genera must be collected at full maturity in order to find any mature spores. In the remaining genera the asci mature a few at a time, so that a section of the hymenium shows all stages of development from young asci to mature or discharged ones.

LATERAL OPERCULUM.—In nine genera the operculum is strongly eccentric and the opening is to one side of the apex of the ascus. In undischarged asci, the subapical pad may be seen in this position (Plate 23 Fig. C.). The remaining genera have terminal, or nearly terminal operculi and subapical pads (Plate 23 Fig. B.).

FOUR-SPORED ASCI.—In the monotypic genus *Thindia* (Korf & Waraitch, *1971*); in two of the three species of *Nanoscypha* (Denison, *1971*); and in some species of

Table 1.
Generic Characters of the family Sarcoscyphaceae

	Desmazierella	Thindia	Pseudopithyella	Pithya	Nanoscypha	Phillipsia	Rickiella	Aurophora	Sarcoscypha	Wynnea	Acervus	Pindara	Geodina	Cookeina	Boedijnopeziza	Microstoma
apothecia																
1-9 mm	+	+	+	+	+				+		?	+			+	+
10-90 mm						+	+	+	+	+	+		+	+	+	
ear-shaped						+		+		+						
funnel-shaped									+				+	+	+	+
discoid or cup-shaped	+	+	+	+	+	+	+		+		+	+		+		
asci																
synchronous			-													
lateral operculum					+	+	?	+		+			+		+	+
terminal operculum	+	+	+	+					+		?	+				
4-spored					+	+										
ascospores																
spherical				+												
ellipsoidal	+	+	+		+	+	+		+		+		+	+	+	+
asymmetrical					+	+		+		+					+	
sculptured					+	+		+		+			+	+		
hairs																
flexuous				+		+		+	+	+	+	?			+	+
bristles	+	+														
scales															+	
fasciculate													+	+		
ectal excipulum																
Pithya-type	?	+	?	+	+					?		?				
Cookeina-type											?		+	+	+	+
Phillipsia-type						+	+	+								
Sarcoscypha-type									+							
pigment																
phillipsia-xanthine	?	?	?		?	+	?	?		?	?	?	?	+	?	?
plectania-xanthine	?	?	?	+	?	+	?	?	+	?	?	?	?		?	?
habitat																
tropical					+		+	+	?	?	+	?	+	+	+	?
temperate	+	+	+	+					+	+	+	+				+
on wood							+	+	+	+	+	+		+	+	+
on foliage, etc.	+	+	+		+											
on soil											+	+	+			+

Phillipsia, the asci are regularly four-spored and the ascospores are larger than in related eight-spored species. Species which are normally eight-spored produce a few four-spored asci, but in these one usually finds the remains of four aborted spores.

ASCOSPORE SHAPE.—The species of *Pithya* have spherical ascospores. In ten other genera the ascospores are symmetrical and ellipsoidal (Plate 23 Fig. B.). In the remaining five genera most ascospores are asymmetrical. They are slightly unequal-sided to curved (Plate 23, Fig. C.). Although in *Phillipsia* and *Nanoscypha* a majority of species have unequalsided ascospores, there is in each genus at least one species with symmetrical ascospores.

CYANOPHOBIC SCULPTURING.—Five genera of the family have cyanophobic sculpturing on the surface of their ascospores. This consists of longitudinal ridges or folds which do not stain in aniline or cotton blue dye (Plate 23 Fig. C.). In *Geodina* and sometimes in *Cookeina* the longitudinal ridges are connected by cross ridges (Denison, *1965*). The remaining genera have smooth ascospores.

PARAPHYSES.—In the tribe Boedijnopezizeae the paraphyses branch freely and the branches anastomose laterally to form a network enclosing each ascus. In the other tribes the paraphyses are less frequently branched and form no such network. In two species, *Desmazierella acicola* and *Cookeina sulcipes*, some of the paraphyses have thick-walled, bristle-like appendages which project above the hymenium. The adaptive significance of these elements, if any, is unknown.

HAIRS.—Many genera have species with excipular hairs which may take several distinctive forms. The most common is a flexuous, hypha-like, hyaline hair (Plate 22 Fig. A.). *Cookeina* and *Geodina* have compound hairs composed of bundles of parallel, unbranched, thick-walled hyphae (Plate 23 Fig. A.). *Boedijnopeziza* has scales composed of excipular hairs adhering side by side. In *Thindia* and *Desmazierella* the hairs are simple and bristle-like, with thickened, dark brown walls.

ECTAL EXCIPULUM.—In the tribe Boedijnopezizeae, and in the genus *Geodina*, the ectal excipulum is sharply differentiated from the medullary excipulum and consists of rows of cells, *textura globulosa* to *textura prismatica*, with the rows perpendicular to the exterior of the apothecium (Plate 22 Fig. B.). In the tribe Pithyeae, and in the genus *Nanoscypha*, the ectal excipulum is also sharply delimited from the medullary excipulum, but the cells are smaller, *textura angularis* to *textura epidermoidea*, and not arranged in rows (Plate 22 Fig. D.). In *Sarcoscypha* the ectal excipulum is easily identified, but there is a broad zone of transition to the medullary excipulum. The ectal excipulum is *textura porrecta* with the long axes of the cells parallel to the exterior of the apothecium (Plate 22 Fig. A.). In *Phillipsia*, *Rickiella*, and *Aurophora* the ectal excipulum is poorly differentiated from the medullary excipulum and of *textura intricata* to *textura epidermoidea* (Plate 22 Fig. C.).

PIGMENTS.—The family Sarcoscyphaceae has apothecia in which the hymenium is brightly colored. The pigmentation, localized in the paraphyses, consists, according to Arpin (*1968*) of caroteinoids including: beta-carotene, lycopene, torulene, torula-rhodine, phillipsiaxanthine, and plectaniaxanthine. The latter two are of

particular interest because of their uneven distribution within the family. Plectaniaxanthine occurs in *Pithya*, *Sarcoscypha*, and *Phillipsia*, whereas phillipsiaxanthine occurs in *Phillipsia* and *Cookeina*.

Substrate.—All species of the tribe Pithyeae occur on the foliage and twigs of conifers. *Nanoscypha* occurs on the foliage and twigs of angiosperms. *Acervus*, *Geodina*, *Pindara*, and *Wynnea* are found on soil. The remaining genera occur on wood, usually on wood in early stages of decay.

Distribution.—The family is sharply divided between temperate and tropical genera. When temperate genera, such as *Pithya*, are found at low latitudes, they occur at high elevations where the temperatures resemble those of the temperate zone. The temperate genera are: *Desmazierella*, *Thindia*, *Pithya*, *Sarcoscypha*, *Pindara*, *Acervus*, *Wynnea*, and *Microstoma*. The remaining genera are tropical.

Grouping into Tribes

There is a suprageneric structure to the family Sarcoscyphaceae. There is a group of core genera, the tribe Sarcoscypheae sensu Korf (*1971*), in which *Phillipsia* occupies a central position surrounded by smaller, mostly specialized genera. There are two other small, closely related groups of genera. The tribe Boedijnopezizeae Korf (*1971*) consists of three genera in which the asci mature synchronously, in which the apothecia are deeply cupulate, and the paraphyses form a reticulum. The remaining group I choose to recognize as a new tribe, Pithyeae, consisting of four genera: *Pithya*, *Pseudopithyella*, *Thindia*, and *Desmazierella*, in which the apothecia are small, resembling those of inoperculate discomycetes. All occur on foliage of conifers; all have similar excipular tissues; and all are temperate in distribution.

Pithyeae Denison, *trib. nov.*

Asci suboperculati, in apothecio singulo deinceps maturescentes; *ascospori unicellulares, hyalini, laeves*; *apothecia clare colorata, minuta, ad folia gymnospermi, clima temperati vigentes.*

Type genus: *Pithya* Fuckel.

Other included genera: *Pseudopithyella* Seaver; *Thindia* Korf & Waraitch; and *Desmazierella* Libert.

References

Arpin, N. (1968). Les caroténoïdes des Discomycètes: essai chimio-taxinomique. Thèse, Univ. Lyon, 169 pp. (& *in* Bull. Soc. linn. Lyon **38** (Suppl.): 169 pp. 1969).

Berthet, P. (1964). Essai biotaxinomique sur les Discomycètes. Thèse, Univ. Lyon, 160 pp.

Denison, W. C. (1965). Central American Pezizales. I. A new genus of the Sarcoscyphaceae. *In* Mycologia **57**: 649–656.

—— (1971). Central American Pezizales. IV. The genera *Sarcoscypha*, *Pithya*, and *Nanoscypha*. *In* Mycologia **64**: 609–623.

Eckblad, F.-E. (1968). The genera of the operculate Discomycetes. A re-evaluation of their taxonomy, phylogeny and nomenclature. *In* Nytt Mag. Bot. **15**: 1–191.

KIMBROUGH, J. W. (1970). Current trends in the classification of Discomycetes. *In* Bot. Rev. **36**: 91–161.
KORF, R. P. (1971). Some new discomycete names. *In* Phytologia **21**: 201–207.
KORF, R. P. & K. S. WARAITCH (1971). *Thindia*, a new genus of the Sarcoscyphineae. *In* Mycologia **63**: 98–103.
LE GAL, M. (1946). Les Discomycètes suboperculés. *In* Bull. Soc. mycol. Fr. **62**: 218–240.

EXPLANATION OF PLATES 24, 25

PLATE 24

FIGS. A-D. — A. *Sarcoscypha coccinea*. Vertical section through the ectal excipulum and part of the medullary excipulum. Note the hypha-like excipular hairs. × 200. — B. *Cookeina sulcipes*. Vertical section showing appendaged paraphysis (upper right), synchronous asci, and excipular tissues. × 200. — C. *Phillipsia domingensis*. Vertical section through the ectal excipulum and part of the medullary excipulum. × 200. — D. *Pithya cupressina*. Vertical section through the ectal excipulum and part of the medullary excipulum. × 400.

PLATE 25

FIGS. A-C. — A. *Cookeina tricholoma*. Longitudinal section of a fasciculate hair. × 200. — B. *Sarcoscypha coccinea*. Apex of an ascus stained with Congo red. Note the nearly terminal position of the subapical pad. × 3000. — C. *Phillipsia domingensis*. Apex of an ascus stained with Congo red. Note the lateral position of the subapical pad. × 3000.

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THE SUBOPERCULATE ASCUS—A REVIEW*

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The suboperculate nature of the asci of the Sarcoscyphaceae is discussed, and it is concluded that it does not exist in its original sense, and further that the Sarcoscyphaceae is not closely related to the Sclerotiniaceae.

The question of the precise nature of the ascus in the Sarcoscyphaceae is important in connection with the treatment of the taxonomy of the Discomycetes. The family Sarcoscyphaceae has been established as a highranking taxon, the Suboperculati, by Le Gal (*1946b*, *1953*), on the basis of its asci being suboperculate. Furthermore, the Suboperculati has been regarded as intermediate between the rest of the Operculati, The Pezizales, and the Inoperculati, especially the order Helotiales, and its family Sclerotiniaceae (Le Gal, *1953*). Recent views on the taxonomic position of the Sarcoscyphaceae are given by Rifai (*1968*), Eckblad (*1968*), Arpin (*1968*), Kimbrough (*1970*) and Korf (*1971*).

The Suboperculati were regarded by Le Gal (*1946a*, *b*) as intermediates because they had both the operculum of the Operculati, and in addition, beneath it, something of the pore structure of the Inoperculati. In the Suboperculati the pore structure is said to take the form of an apical chamber with an internal, often incomplete ring-like structure within it. Note that in this case the spores on discharge have to travers a double hindrance, the internal ring and the circular opening, and that the diameters of these obstacles are both smaller than the smallest diameter of the spores. Therefore, the spores have to be forced through a double hindrance; this seems rather improbable.

There may be other reasons for accepting the Sarcoscyphaceae as a high ranking taxon, but what I am going to maintain here is that the suboperculate nature of their asci, as first described, is not a good reason, since, in my opinion, few if any of its members have asci that are suboperculate in the way described by Le Gal. Furthermore, I am going to suggest that if this suboperculate nature of their asci is denied, in fact very little remains to place the Sarcoscyphaceae in close phylogenetic relationship to the Sclerotiniaceae.

The term 'suboperculate ascus' was introduced by Le Gal (*1946a*). Later the same year, Le Gal (*1946b*) stated that the term 'paraoperculate ascus' introduced by Chadefaud (*1946*) covered the same thing. The term 'suboperculate' has been accepted by everbody. (Nannfeldt, *1949*, Korf, *1957*, Denison, *1965*, Rifai, *1968*,

* Paper read at the Symposium "Taxonomy of operculate Discomycetes" held at the First International Mycological Congress, Exeter, 1971.

Eckblad, *1968*). Le Gal (*1946a*) first described the phenomenon in *Cookeina sulcipes* while Chadefaud (*1946*) described the same phenomenon, as the paraoperculate ascus, in *Sarcoscypha coccinea*. In *Cookeina sulcipes* the suboperculate ascus was described by Le Gal (*1946*) as having a three layered ascus wall. Within an enlargement of the middle layer the apical chamber is formed.

In a later paper, Le Gal (*1946b*) gave more detailed descriptions and drawings of the suboperculate ascus of a number of species, all belonging to the family Sarcoscyphaceae. In this paper the suboperculate ascus is stated to have two wall layers, and she appears now to regard the *Cookeina* ascus as two-layered too. The ascus wall has been demonstrated to be two-layered also in several operculate genera not belonging to the Sarcoscyphaceae, viz. *Ascobolus* and *Saccobolus* (van Brummelen, *1967*), Thelebolus (Kobayasi *et al.*, *1967*). I have also seen the double wall on electronmicrographs in *Gyromitra esculenta* (unpublished).

According to Le Gal (*1946b*) there are three different types of suboperculate asci in the Sarcoscyphaceae.

The first type is found in a number of species now belonging to the genera *Pseudoplectania*, *Pithya*, *Urnula*, *Plectania*, *Wynnea* and *Sarcoscypha*.

In all these genera the inner wall layer is said to become thicker at the top of the ascus, and the apical chamber to be formed within this thickening. Within this chamber again is formed an internal ringlike structure which is considered to correspond—according to Le Gal—to the internal pore canal of the ascus apex of many inoperculate Discomycetes.

In the second group, consisting of the tropical genera *Phillipsia*, *Cookeina* and *Boedijnopeziza* the apical chamber is said to develop, not within the inner layer, but between the two layers. In the case of *Phillipsia* at least it appears from her drawings that the ring-like structure is reduced to a thickening on the inside of the circular opening left by the operculum. The third group, represented only by *Urnula geaster*, or more correctly, *Chorioactis geaster*, differs only slightly from the latter type.

In her paper on the Discomycetes of Madagascar Le Gal (*1953*) also described the suboperculate apical apparatus of some genera closely associated with the Sarcoscyphaceae, viz. *Phaedropezia* Le Gal, and *Midotiopsis* Henn., and of *Rutstroemia nummiformis* (Pat.) Le Gal of the Sclerotiniaceae.

The hypothesis that the Sarcoscyphaceae form a taxon intermediate between the Inoperculati and the Operculati, or more especially between the Sclerotiniaceae and the Pezizales was in the main based on these findings.

I hasten to assure that the thickened inside of the opening of the ascus of *Phillipsia* I have also seen. In fact this thickening or apical pad was clearly described and illustrated by Boedijn (*1953*). The lid itself is also thickened on the inside.

If this type of apical 'apparatus' is what is generally understood by a suboperculate ascus, I do not deny its existence. But it should be remembered that in this case the apical chamber has disappeared, and also the internal ring like structure within it. With its disappearance the double hindrance of the spore discharge vanished too. What is left is a thickening of the operculum and the opening itself.

Table I. Characters of Sarcoscyphaceae and Sclerotiniaceae compared

	Sarcoscyphaceae	Sclerotiniaceae
mode of nutrition	saprobic	parasitic
substrate	epixylous	not epixylous, except *Rutstroemia, Martinia*
mycelium	plurinucleate	plurinucleate
sclerotia or stroma	not, except in *Wynnea*	common
apothecia	hairy	glabrous
colour	Yellow, orange, red, black	yellowish-brown
paraphyses	mostly plurinucleate except "*Sarcosoma*", *Urnula, Pseudoplectania*	uninucleate, except *Sclerotinia tuberosa*
asci	long	short
asci	cylindrical	clavate
asci	nonamyloid	amyloid
asci	aporhynque	aporhynque or pleurorhynque
ascospores	large	small
ascospores	one-celled	mostly one-celled
ascospores	hyaline	mostly hyaline
ascospores	globose, ellipsoid often inaequilateral	ellipsoid, sometimes slightly inaequilateral
ascospores	plurinucleate	uninucleate, except *Sclerotinia tuberosa* 2–6 *Ciboria batschiana* 1–2
conidial states	mostly none except *Verticicladium Conoplea*	common *Botrytis, Monilia* etc.

Furthermore, this type of opening is definetly known only from the genera *Phillipsia, Cookeina*, and *Boedijnopeziza*, but may occur also in the monotypic genera *Geodina* and *Aurophora*, which both are closely related to *Phillipsia*. It may occur in a few other genera too.

Of the existence of the suboperculate ascus in the original sense, I have so far seen no corroboration in the literature in the form of a description, drawing or photograph based on personal studies. True, there are several records of suboperculate asci in new species and genera, *Galiella* (Korf, *1957*), *Geodina* (Denison, *1965*), *Aurophora* (Rifai, *1968*), *Neournula* (Paden & Tylutki, *1969*), *Korfiella* (Pant & Tewari, *1970*) and *Thindia* (Korf & Waraitch, *1971*). In none of these cases, however, is there any drawing or photograph of the apical apparatus. What features of the ascus are referred to by the term suboperculate, has not been described.

I have studied in detail only few species of the Sarcoscyphaceae. But I have studied two of them, *Pseudoplectania nigrella* and *Sarcoscypha coccinea*, and especially the former in detail. The asci of *Pseudoplectania* I have studied for three years without finding

the slightest indication either of an apical chamber or of an internal ring. Judging from Le Gal's drawing (*1946b*, Fig. 2, 2) the internal ring of *Pseudoplectania nigrella* would be approximately 8 microns wide and 3 microns thick, i.e. clearly visible even in a light microscope. In *Sarcoscypha coccinea* the structure is described as much smaller, although not at all of a submicroscopical nature. The asci have been studied fresh in water mounts or in various media, or stained. The result is the same.

In these two genera the suboperculate apparatus of the ascus is nonexistent. On the basis of these negative results in two central genera, I feel that fresh evidence for the existence of this structure is now necessary. The most satisfactory evidence would be longitudinal sections of the ascus studied in light and electron microscope. This sort of evidence has not yet been produced, probably because of the technical difficulties in obtaining such sections.

It is necessary to keep in mind that I distinguish between two types of asci in the Sarcoscyphaceae.

I. The *Phillipsia—Cookeina* type, in which the operculum itself and the rim of the opening of the ascus is thickened. There is no apical chamber and there is a single hindrance to the spores. This type I accept. In my opinion this type of ascus should not be termed suboperculate, since this would amount to a virtual redefinition of the term considering the sence it was originally given by Le Gal (*1946a*).

II. The *Pseudoplectania* type, where there should be both the operculate opening, and beneath it a second hindrance, the internal ring. I do not believe that this type exists.

On the other hand I will, of course, not deny that the ascus of the Sarcoscyphaceae possesses a series of peculiar characters. Few of these characters are found in the asci of all species, however.

The asci are often thick-walled and often very long and with a flexuous narrowing base, which is aporhynque, according to Berthet (*1949*) i.e. without croziers. In some genera the operculum and opening is oblique and thickened on the inside. In a few genera all asci ripen simultaneously. The spores are often inaequilateral and often with longitudinal or traverse ridges or striations which are not stained by cotton blue or similar dyes, and are mostly plurinucleate (Berthet, *1964*).

These characters together with the characters of the excipulum (see Nannfeldt, *1949*, Le Gal, *1953*, Rifai, *1968*, Eckblad, *1968*) the epixylous habitat and the tropical distribution of several genera certainly gives the family or families (Korf, *1971*) a somewhat exotic image.

I am, however, quite unable to see that these characters point to a relationship with the Sclerotiniaceae or for that matter, with any other group of the Inoperculati. In Table 1, I have confronted a number of characters of the Sarcoscyphaceae and of the Sclerotiniaceae. Very few of the characters are the same, mostly they are different.

My conclusion is then—in the absence of positive evidence—that the Suboperculati as a whole do not possess a suboperculate apical apparatus as originally defined, and that lacking this—there is no reason to seak a phylogenetic relationship between the Suboperculati and the Inoperculati.

REFERENCES

ARPIN, N. (1968). Les caroténoïdes des Discomycètes: essai chimiotaxinomique. Thèse, Univ. Lyon (& *in* Bull. mens. Soc. linn. Lyon **38** (Suppl.)).

BERTHET, P. (1964). Essai biotaxinomique sur les Discomycètes. Thèse, Univ. Lyon.

BOEDIJN, K. B. (1933). The genera *Phillipsia* and *Cookeina* in Netherlands India. *In* Bull. Jard. bot. Buitenz. III **13**: 57–76.

BRUMMELEN, J. VAN (1967). A world monograph of the genera *Ascobolus* and *Saccobolus* (Ascomycetes, Pezizales). *In* Persoonia (Suppl.) **1**.

CHADEFAUD, M. (1946). Les asques para-operculés et la position systématique de la Pézize *Sarcoscypha coccinea* Fries ex Jacquin. *In* C.r. hebd. Séanc. Acad. Sci., Paris **222**: 753–755.

DENISON, W. C. (1965). Central American Pezizales. I. A new genus of the Sarcoscyphaceae. *In* Mycologia **57**: 649–656.

ECKBLAD, F.-E. (1968). The genera of the operculate Discomycetes. A re-evaluation of their taxonomy, phylogeny and nomenclature. *In* Nytt Mag. Bot. **15**: 1–191.

KIMBROUGH, J. W. (1970). Current trends in the classification of Discomycetes. *In* Bot. Rev. **36**: 91–161.

KOBAYASI, Y., N. HIRATSUKA, R. P. KORF, K. TUBAKI, K. AOSHIMA, M. SONEDA, &. J. SUGIYAMA. (1967). Mycological studies on the Alaskan Arctic. *In* A. Rep. Inst. Ferment. Osaka **3**: 1–138.

KORF, R. P. (1957). Two bulgarioid genera: *Galiella* and *Plectania*. *In* Mycologia **49**: 107–111.

—— (1971). Nomenclatural notes. VII. Family and tribe names in the Sarcoscyphineae (Discomycetes) and a new taxonomic disposition of the genera. *In* Taxon **19**: 782–786.

KORF, R. P. & K. S. WARAITCH (1971). *Thindia*, a new genus of the Sarcoscyphineae. *In* Mycologia **63**: 98–103.

LE GAL, M. (1946a). Mode de déhiscence des asques chez les *Cookeina* et les *Leotia*, et ses conséquences du point de vue phylogénétique. *In* C.r. hebd. Séanc. Acad. Sci., Paris **222**: 755–757.

—— (1946b). Les Discomycètes suboperculés. *In* Bull. Soc. mycol. Fr. **62**: 218–240.

—— (1953). Les Discomycètes de Madagascar. Paris.

PADEN, J. E. & E. E. TYLUTKI (1969). Idaho Discomycetes. I. A new genus of the Sarcoscyphaceae. *In* Mycologia **60**: 1160–1168.

PANT, D. C. & V. P. TEWARI (1971). *Korfiella*, a new genus of Sarcoscyphaceae. *In* Trans. Br. mycol. Soc. **54**: 492–495.

RIFAI, M. A. (1968). The Australasian Pezizales in the Herbarium of the Royal Botanic Gardens, Kew. *In* Verh. K. Ned. Akad. Wet., Afd. Natuurk. II **58** (3): 1–295 pp.

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TAXONOMY OF OPERCULATE DISCOMYCETES: SYNTHESIS*

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A general consideration is given on various aspects of the taxonomy of Operculate Discomycetes. The thesis is advanced that the genus, rather than the species, may represent the basic evolutionary unit. More detailed considerations are devoted to a few topics, for instance to the systematic position of the genera *Cyttaria* and *Medeolaria*.

It is no accident that here at this First International Mycological Congress a special session on Taxonomy of Operculate Discomycetes should be convened, for the time was ripe. As you have already heard today, there are a large number of active workers seriously applying themselves to the problems of taxonomy in this most intriguing group of fungi.

Nevertheless, the great strides forward in taxonomy of Operculate Discomycetes can be traced back, in nearly all instances, to the brilliant analyses of the cup fungi by three mycologists publishing a century ago: the great French master, Émile Boudier, the brilliant Swiss mycologist Leopold Fuckel, and the Scandinavian giant, P. A. Karsten. All three possessed not only the ability to discern species, a quality of all great mycologists, but had in addition that rare gift of rearranging the pieces of the puzzle to provide a classification giving an insight into relationships. That some of the genera that they proposed have fallen by the wayside, or have proven to be polyphyletic in the ensuing century, should in no way diminish our admiration for their ability to recognize affinities, often decades or even a century ahead of their time.

As taxonomists we are usually prepared to utilize any data, from whatever source, which will help us to separate groups – the process of *analysis* so essential in recognizing species, for example—or, conversely, that will help us in uniting taxa into higher categories, genera, tribes, families, orders—the process of *synthesis*. We who are actively concerned with the Operculate Discomycetes are at that fortunate moment in time when several distinct disciplines have come to focus upon the same materials, as some of our speakers today have already pointed out. The thrust of my comments today is that, without disparaging the importance of analysis and the importance of discerning species and infraspecific taxa, our real business of the moment is synthesis.

I know that I speak for all of the panel of this session in voicing our regret that

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Mme Le Gal was unable, by reason of her health, to attend and participate today. For her studies, detailed and precise, have formed for all of us a solid foundation upon which to test our ideas of classification. The genera and many of the families which she has adopted, for which she would be the first to acknowledge her debt to the pioneering work of Boudier, were all delimited by classical morpho-taxonomic procedures. In the 25 years since she published her arrangement in the "Recherches sur les Ornementations Sporales des Discomycètes Operculés" only a few groups have seen significant changes, and these were the very groups which she recognized needed critical study. But in those 25 years new tools have been brought to bear, particularly:

1) critical microanatomical study of the apothecium, advocated by Starbäck, von Höhnel, and above all by Professor Nannfeldt,

2) cultural studies such as those outlined today by Professor Paden, and a few days ago at another session at this congress by Professor Hennebert,

3) studies of nuclear numbers in ascospores, paraphyses, and cells of the vegetative mycelium, provided us most recently by Professor Berthet,

4) ontogenetic studies of ascocarp development, quiescent since the initial studies by Corner, but as you have noted today in the papers by Dr. van Brummelen and by Professor Kimbrough, attaining new importance in the Ascobolaceae and Thelebolaceae,

5) ascus wall characters, a current area of interest of several investigators, and

6) chemotaxonomic and physiotaxonomic studies of various sorts, including the bluing reaction of certain asci in Melzer's Reagent and Dr. Arpin's critical analysis of carotenoid pigments in our group.

What is really impressive, at least to me, is that the accumulation of the data, admittedly by no means complete, has in almost all instances *reinforced* the Boudier-Le Gal classification of Operculate Discomycetes. Each independent discipline, potentially capable of telling us that our groups delimited by traditional morphological procedures are fictions or arrays of artificially arranged taxa, instead has pointed to real biological relationships at the generic and higher levels.

This is not to say there are no longer problems for us to consider! We have not so perfected our classification that we can now proceed merely to a catalogue of the species within each genus, and for a search for infraspecific variants, as is the case with some of our phanerogamic colleagues. But to my mind we have reached, in the Pezizales, a point of validity in our classification which allows us to recognize families and infrafamilial groups that are biologically sound. As new facts emerge, I feel it is safe to predict that the general outline of our classification will remain unchanged.

Though some of the many problems which confront us have already been discussed today by the participants in this program, let me briefly indicate some of the areas that seem to me to call for critical work.

First and foremost, the microanatomy of the apothecium still needs intensive study in most of the genera of Operculate Discomycetes. Too few species have been

critically examined for us yet to base our classification on what may be very useful anatomical details of taxonomic importance at the generic and higher levels.

Though I remain a staunch advocate of the monographic approach to taxonomy, I am also convinced that species analysis is, at times, not as critical a necessity for the advancement of our knowledge as is the understanding of genera, tribes, and even families. Too long, to my mind, has the concept of the species as the basic unit of evolution gone unchallenged. I am convinced from my own studies, and from the work of others on various groups of plants and animals[1], that the basic evolutionary unit may be groups of species, in some cases recognized as subgenera, genera, or even groups of genera. Natural selection, unquestionably to my mind the major evolutionary factor, may as well affect groups of species as it does individual species. Because real genera are physiologically related, through their evolutionary ancestry, in *many* attributes, they may evolve simultaneously in one direction or another under the stress of a particular natural selection pressure. We need not assume in the classical way that a single species evolves to form a new species or genus, but rather may take a broader view, that related species simultaneously respond and change with time. It is for this reason that I advocate intensive study of what constitute generic, as opposed to specific, characters. Such characters cannot, therefore, be arbitrarily chosen, but must reflect phylogeny. Species, when aggregated into genera on the basis of phylogenetic similarity, begin to make a valid classification.

Clearly, we must avoid excessive generic splitting. Our colleague, Professor Berthet, recently wrote me of his very real concern that there seems to be a tendency, at least in the Sarcoscyphineae, to recognize a separate genus for nearly every species. I must admit that I share his concern. For how many genera with one or a few species can we tolerate with, say, a *Conoplea* imperfect state? We know it in *Urnula*, in *Plectania*, and in *Korfiella*, and I suspect, unlike Professor Paden, that in time we shall find a species of *Pseudoplectania* that also yields a *Conoplea* imperfect state. Have we not gone too far in recognizing so many genera of similar Discomycetes when perhaps one, *Urnula*, would suffice?

Though it seems fair to state that there is rather general agreement today on generic limits in the Pezizales, clearly there are points of real disagreement. For example, as taxonomists we disagree among ourselves on the generic limits of the *Discina-Neogyromitra-Maublancomyces-Paradiscina-Gyromitra-Pseudorhizina* complex of genera. To the non-specialist on Discomycetes, our taxonomic indecision in this area must seem incredible, compounded by the fact that these are large fungi, not infrequently collected, and for which names are therefore actively sought in our books and papers.

In 1970 I proposed the tribe Boedijnopezizeae within the Sarcoscyphaceae,

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[1] The thesis that I am advancing here, that the genus may represent the basic evolutionary unit, in not wholly new. I thank my student, Mr. Paul Powell, for calling to my attention the recent paper by Darlington (*1971*) on group selection in carabid beetles, a beautifully executed case in point.

based on three genera, *Boedijnopeziza*, *Cookeina* and *Microstoma*, differing from all other members of the Pezizales in having their asci maturing simultaneously within the apothecium. In all other genera of the order—and in my recent classification (Korf, *1972*) I recognized over 90 genera—asci mature *seriatim*, that is to say, asci of various ages and states of maturity will be present in any mount. I know of only one other case of simultaneous ascus maturation among Discomycete-like fungi. This is in the genus *Cyttaria*, the type and only genus of the Cyttariaceae, a family shunted about from Pyrenomycetes to Operculate Discomycetes to Inoperculate Discomycetes in various classifications. This peculiar genus is found only parasitic on the southern hemisphere beeches of the genus *Nothofagus*. It produces large, spherical or pyriform ascostromata, usually in clusters on a swollen canker of a branch or trunk. Each ascostroma produces 20 to 100 or more large cavities lined with a hymenium. In the species I have studied, these asci are all at the identical stage of development in any one apothecial cavity, but each cavity will be at its own developmental stage. The ascostroma is thus not an apothecium, but a compound structure bearing individual apothecia. The asci are cylindrical, flattened at the apex, which is thickened in youth and provided with a broad apical ring which, in some species, turns blue in Melzer's Reagent. The ring is sufficiently large that it recalls that seen in many species of *Peziza*, rather than the tiny blueing pore seen in many Helotiales. The thin, flattened apex ruptures, sometimes giving the appearance of an operculum, but whether one should call such asci operculate or inoperculate remains, at least for me, an unanswered question. The ascospores of *Cyttaria* recall in their form those of the Pezizales rather than of the Helotiales. But pycnidia, perhaps better thought of as spermagonia, are found in young ascostromata of at least some species of *Cyttaria*, and no member of the Pezizales is known to produce either pycnidia or spermagonia. Despite the simultaneous ascus maturation recalling that in the Boedijnopezizeae, I think it best to treat the Cyttariaceae as a separate order, Cyttariales, and to place it in the Inoperculatae, probably representing a line of development quite unrelated to the Helotiales, Phacidiales, or Ostropales, and not too divergent from the Pezizales.

I would also call your attention to another anomalous fungus which appears to have affinities with the Operculate Discomycetes. This is the monotypic genus *Medeolaria*, described by that master discerner of the odd fungus, Roland Thaxter, almost exactly 50 years ago. It occurs on the stems of a small, North American, herbaceous wild plant in the woods, *Medeola virginiana*, where it causes fusiform swellings and a shortened internode. Through these swollen areas the previously completely internal hyphae emerge in a palisade of paraphysis-like elements, among which eventually are formed asci with 8 huge, brown ascospores, flattened on one side and longitudinally ribbed as in *Phillipsia* or *Wynnea*. To the best of my knowledge, the fungus was never again collected until last year, when a former student, Dr. Donald H. Pfister, and I made a special trip to search for it in one of three areas where Thaxter had reported it. After searching in vain for six hours among thousands of *Medeola* plants, we luckily were able to find several diseased

plants bearing the *Medeolaria* in various states of development. We are, however, scarcely any closer to a knowledge of the life history of this peculiar parasite than we were before, and our hope of studying the asci and their dehiscence mechanism was frustrated by the discovery that they disappear very early in development. The large, inequilateral, ribbed asospores recall, among Ascomycetes, only those of the Sarcoscyphineae, yet the parasitism and simple structure of the ascocarp, little more than a felt of asci and paraphyses, lead me to propose that *Medeolaria* deserves not only a separate family, but a new order, Medeolariales, of which it is the sole representative. Needless to say, I hope that some of my colleagues here will take up the study of Thaxter's fungus, to prove its relationships and to determine whether I am justified in assigning it a position close to the Pezizales despite its evanescent asci, for which no operculum has been demonstrated.

Lack of an operculum is all that has kept us today from treating the order Tuberales in our discussions, for here is another group that very clearly represents probably the closest relatives to the Pezizales that we know. Loss of a functional operculum is surely to be expected when an Operculate Discomycete takes to an underground life and to dispersal of its ascospores by some other means than air dispersal. The selection pressures to retain the complex apical mechanism of the operculum, operating on all members of the Pezizales, no longer affects such a fungus when its spores have a suitable means of dispersal by some other agent. Despite the lack of an operculum, those of us who work with Operculate Discomycetes are content to include the Tuberales among the Operculates!

In summary, let me note that it is our good fortune to be working in the area of Operculate Discomycetes. Our genera appear, for the most part, to be sound. Our groups of genera, at several taxonomic levels, also appear to have a basis in phylogeny. The challenges to us are to refine our system, to apply the new techniques as they appear – the scanning electron microscope being a current example – but also to proceed with the detailed study of all of our taxa to ensure that they are biologically defensible.

References

Darlington, P. J., Jr. (1971). Interconnected patterns of biogeography and evolution. In Proc. nat. Acad. Sci., USA **68**: 1254–1258.

Korf, R. P. (1972). Synoptic key to the genera of the Pezizales. In Mycologia **64**: (in press).

INDEX

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

Abies 75, 233, 245; excelsa 213; pindrow 246
Absidia blakesleeana 111, 115; corymbifera 111, 115; cuneospora 111, 115; cylindrospora 111, 114, 115; pseudocylindrospora 111, 113, 114*
Acer, 52, 173, 338; negundo 106
Acervus 435
Acetabula aestivalis 426
Achillea 52; millefolium 3, 24
Acremonium 108, 367, 378; verticillatum 97
Acrostalagmus 189
Aesculus 52
Agarico-igniarium foliaceum 201, 202
Agaricus 261; arrhenii 128-134, 147; bifrons var. semitinctus 251; blattarius 129-134, 147, 152; candicans 128; cereolus 128; corrugis 259, 261, 265, 266*; esculentus 203; faciculus 203; glaucopus 105; gracilis 251, 257, 265; intybaceus 203, 206, 208; mesodactylus 129-131, 133, 134, 147; microrrhizus 269; mycenoides 134, 337; ombrophilus 128; pellospermus 261; pelosporus 259; pygmaeus 132; recedens 158, 241; subatratus 261; togularis 127-134, 147, 152; togularis var. filaris 123, 156, 158; unicolor 132; xanthoderma 103
Agathis 242
Agrocybe 127-129, 131, 133-135, 283, 284, 314; erebia 285; praecox 128, 129, 285
Ajellomyces 379
Aleuria 396, 410; aurantia 406, 410, 411, 430, pl. 22
Alliaria 22
Allium 172, 173
Alnus 52, 173, 321, 338
Alternaria 7, 171; polymorpha 171, 172
Alytosporium roseum 100
Amauroascus 371, 374, 377, 379; **albicans 376; aureus 375; echinulatus 375;** pl. 14; **kuehnii 376;** niger 375; **reticulatus 375,** 376, pl. 14; verrucosus 374, 375, 378, pl. 14
Amylocystis lapponica 210
Anethum foeniculum 31; graveolens 24
Angelina 395
Ansonia salicifolia 25
Anthericum liliago 25
Anthracobia 410; macrocystis 411; melaloma 411
Anthurium 57
Antirrhinum 52; majus 25
Antrodia serialis 217
Aphanoascus 396, 397
Aphanocladium 189
Apinisia 379
Apium 52
Aposphaeria caricae 50, 54; mori 50; pezizoides 50, 54; pomi 49, 55; violacea 18, 21
Arachniotus 345, 351, 371, 374, 377-380; albicans 376; **aurantiacus 373;** aureus 375; citrinus 372; confluens 372; dankaliensis 372, 373, pl. 14; flavoluteus 373; glomeratus 371, 376; hebridensis 373, 378; hyalinosporus 374; intermedius 378; lanatus 378; lectardii 371, 378; marginosporus 374; niger 375; **punctatus 373;** purpureus 379; reticulatus 376; ruber 345, 372, pl. 14; striatisporus 371, 377; trisporus 351, 353, 379; verrucosus 375
Arachnotheca 371, **376,** 377, 379; **glomerata 376**
Aradus cinnamomeus 186
Araucaria 173
Arborum fungi auriculae . . . 201, 207
Arctium 34
Argynna 365-368; polyhedron 368
Aristolochia durior 25, 26; sipho 25
Armillaria mellea 101, 103, 105
Artemisia 26; absinthium 23; campestris 26
Arthroderma 380
Ascobolus 389, 391-393, 395, 396, 411, 412, 440; § Ascobolus 390, 393; § Ascozonus 396; § Dasyobolus 390, 393; § Gymnascobolus 390, 392, 393; § Heimerlia 390, 393; § Pseudascodesmis 390, 393; § Pseudosaccobolus 390, 393; § Sphaeridiobolus 390, 393; crenulatus, pl. 22; immersus 394; magnificus 412

Ascochyta 15-17, 32; dianthi 29; pinodella 8; pisi 15, 16
Ascocoryne 59; sarcoides 63, 82*, 83
Ascodesmis 378, 390, 394, 412
Ascophanus 395-397, 399, 400; carneus 400; cinereus 399; granulata 399; subfuscus 400
Ascozonus 396-399, 401, pl. 19 figs. 31-45
Asparagus officinalis 72
Aspergillus 199, 200, 347; carneus 347
Asteroma scrophulariae 40
Asteromella 34, 37, 173; mali 50
Athelia 96
Aubrietia 25
Aurantioporellus 216
Aurophora 434-436, 441
Auxarthron 379
Avena 172

Beauveria 185, 188
Berberis 52, 173
Beta 52, 173
Betula 173; lutea 74; verrucosa 353
Bjerkandera adusta 100, 101
Blastotrichum 99; confervoides 99; pucciniodes 97-99
Boedijnopeziza 434-436, 440, 441, 448
Bolbitius 283; aleuriatus 284; reticulatus 284; variecolor 283; vitellinus 283
Boletus 202, 205, 209; abietinus 208, 209; calceolus 215; edulis 97; elegans 204, 215; frondosus 202-204, 206, 207; giganteus 206; imbricatus 202; intybaceus 202, 205, 207; nummularius 215; purpurascens 208, 209; ramosissimus 204, 206; rubiginosus 210; squamosus 202
Borago 173
Botryophialophora 190
Botrytis 100, 405, 410, 441; § Corymbosi 96; agaricina 96, 97; carnea 103; dendroides 104; macrospora 104, 105; varia 100; variosperma 100, 101
Boudierella 396, 397
Brassica 26; oleracea 17, 20
Bryonia alba 18, 21
Bulgaria platydiscus 408
Byssoascus 371, **377,** 379; **striatisporus 377**
Byssochlamys 341-343, 345, 349, 351, 353, 356, 379; fulva 341, 352*-354; musticola 351, 353; nivea 341, 349, 350*, 351, 353, 379; nivea var. lanugucilariae 351, 353; trisporus 351; zollerniae 354, 356

Caccobius 396, 398, 399, 401, pl. 19 figs. 31-45
Cacumisporium capitulatum 108
Cadophora 61, 62; americana 90, 92; brunnescens 87-89*, 90; fastigiata 62, 71, 73*; heteroderae 75, 78; lagerbergii 81; lignicola 84; melinii 73*, 74; obscura 66, 67*, 68; repens 82, 83; richardsiae 87-89*
Callistephus 3
Calluna 173, 174
Calocybe gambosa 103
Caloscypha 410; fulgens 406, 411
Calystegia sepium 26
Camarophyllus niveus 103
Campanula 3, 173
Candelabrella 196
Cannabis sativa 27
Capnophialophora 108
Capparis spinosa 27
Carpinus betulus 314; orientalis 314
Carya pecan 174
Castanopsis 233, 247
Catalpa 27, 52, 55
Cedrus 172; atlantica 288
Cephalosporium 189
Ceratocladium microspermum 83
Cereus 172
Chaetomidium 365
Chaetomium 365
Chamaecyparis 52, 173
Cheilymenia 396, 399, 410
Chenopodium 52; album 18, 28
Chloridium 108
Choanephora circinans 111, 115; infundibulifera 111, 115
Chorioactis geaster 440
Chrysanthemum 52, 172, 173; corymbosum 28; indicum 10; leucanthemum 3; morifolium 10
Chrysosporium 378
Chusquea culeou 238
Ciboria batschiana 441
Ciliaria 396
Citrus 172, 176
Cladobotryum 95, 96, 99*, 101-103, 106-109; agaricinum 96; **apiculatum** 96, **97,** 98*, 99, 106, 108; binatum 104, 105; **dendroides** 96, 101, **103,** 104*-108; **leptosporum** 96, **106,** 107*; macrosporum 96, 104, 105, 107; **mycophilum** 96, **102***, 103; ternatum 104, 105; ternatum var. binatum 104; terrigenum

104, 105; thuemenii 96; variospermum 96, 100, 101; varium 95, 96, 100-102; verticillatum 96-98*, 99
Cladotrichum ternatum 100
Clavaria 219; aequivoca 206; cardinalis 227; holmskjoldii 223; laeticolor 229; longispora 228; luteoalba 224; pulchra 227, 229; pulchra f. coccineo-basalis 228
Clavulinopsis 219, 226*, 227; appalachiensis 221; aurantio-cinnabarina 221, 225, 227; aurantio-cinnabarina var. amoena 221, 225; citrino-alba 227; corniculata 219-222*, 223, 226*; dichotoma 220, 223; fusiformis 221, 223; gracillima 219, 220, 224; helvola 220; holmskjoldii 220, 223, 224; laeticolor 219, 221, 226*-229; laeticolor var. antillarum 221; laeticolor f. bulbispora 221; laeticolor f. **coccineo-basalis** 219, 221, **228**; miniata 221, 225, 227; pulchra f. coccineo-basalis 228; **subaustralis** 219, 220, **225**, pl. 8; subtilis 220, 223; umbrinella 220, 223, 224
Cleistophoma 40
Clematis 173
Codinaea 108
Cokeromyces 113
Colutea 52; arborescens 55
Coniochaeta 59, 79; ligniaria 79; tetraspora 79; velutina 79
Coniothyrium 44; ruscicola 23
Conocybe 119, 121, 122, 125, 128, 131-133, 137, 280, 283-289, 295, 313-315, 323, 327, 328, 334, 337, 338; § Conocybe 281, 286*, 287, 322*, 328; § **Intermediae** 119, 121, 122, 313, 322*, **328**, 329; § Ochromarasmius 328; § Pholiotina 119, 120, 123, 124, 126, 127, 281, 282, 284, 286*, 287, 313, 314, 318, 327-329; § Piliferae 122, 287, 328; § Vestitae 329; antipus 121; **aporos** 119, 120, 123-127, 135, 136, 138*, 142, **144**, 145*, 146, 151*, 152, 156, 281, 282, 286*, 287, 323, 324*; **appendiculata** 121, 123-125, 289, 313, 328, **329**, 330*, 333; appendiculata f. annulata 125; appendiculata var. macrospora 125, 333, 334; **arrhenii** 119, 123-127, 131, 132, 134-137, 139, 141, 146, **147**, 150, 156, 158, 285, 287, 328, 333, 337; arrhenii var. arrhenii 120, 140*, 142, 148, 149*; 150; 151*; arrhenii f. dentata 124; arrhenii var. **hadrocystis** 119, 120, 123, 127, 135, 136, 140*, 142, **150**, 152, 153*; blattaria 119, 120, 125-127, 129, 131-139, 141-143*, 147, 150, 152, 154, 155*, 156, 158, 160, 285, 287, 288, 328, 337; blattaria f. dentata 120, 124, 125, 150; blattaria f. exannulata 123, 136; blattaria f. typica 120; **brunnea** 124, 125, 286-289, 316*-**318**, 321, 322*-324*, 327-329, 333; coprophila 121, 287, 328; exannulata 124; farinacea 121, 122, 286*, 287; **fibrillosipes** 313, 320*, 322*, **325**, 328; filaris 119, 120, 123, 126, 127, 129, 139, 142, 143*, 152, 156, 158, 159*, 283, 287, 288, 336; filaris var. exannulata 158; filaris var. Kühneri 158; filaris var. ochracea 158, 283; filaris var. recedens 158; filaris var. recedens f. subochracea 158; filaris var. rugosa 123, 158; **fimicola** 313, 332*, **335**; **flexipes** 313, 332*, **336**, 337; hebelomatoides 121; intermedia 315, 316*, 318, 321, 322*, 323, 325, 327, 328; intermedia var. brunnea 313, 314, 318, 323; laricina 287, 328; magnicapitata 322*; percincta 119, 120, 125, 136, 138, 139, 141, 142, 160, 161*, 162, 323; peronata 142, 288; **pinguis** 313, 332*, **338**; pubescens 121, 122, 287, 321; rickeniana 286; rugosa 123, 158; spicula 286; **stercoraria** 313, 332*, **334**; subovalis 121, 122; subpubescens 122, 287; tenera 121, 122, 284, 287, 328; **teneroides** 119, 120, 125-127, 135-143*, 158, **160**, 161*, 281; togularis 119, 120, 131, 133, 134, 137, 139, 141, 142, 147, 152, 160, 317; vestita 147, 288, 328; vexans 119, 120, 125, 136, 137, 139, 141, 152, 156
Conoplea 405, 408, 441, 447; fusca 408; geniculata 408; globosa 408; juniperi 408; juniperi var. robusta 408
Convallaria 52, 173
Convolvulus sepium 26
Cookeina 407, 434-436, 440, 442, 448; sulcipes 407, 436, 440; tricholoma 407
Coprinarius corrugis 259; gracilis 251
Coprinus 284, 297; § Setulosi 318; narcoticus 307; velox 297
Coprobia 396, 399, 410; granulata 410
Coprobolus 396, 398, 399, 401
Coprotus 396, 398-401, pl. 19 figs. 31-45; lacteus 402
Coriolus sector 216
Cornus 52
Corticium radiosum 106

Cortinarius mucosus 103
Corylus 52
Coryne dubia 83; sarcoides 83
Costantinella 405, 406, 410, 411
Cotoneaster 52
Crataegus 52
Cristulariella 190
Ctenomyces 380
Cubonia 396, 397, 399
Cucumis 52, 172, 173
Cunninghamella batistae 111, 116; elegans 111, 116; phaeospora 111, 116
Cyathea dealbata 242
Cyathipodia 426
Cyclamen 72; persicum 71
Cyclopus 131
Cylindrodendrum 190; album 190
Cylindrophora 99; apiculata 97-99
Cytispora abnormis 55, 57
Cyttaria 386, 445, 448

Dactylaria 108, 193, 195; **lanosa 193,** 194*, 195; purpurella 195
Dactylium 96, 107, 108; agaricinum 104; boletorum 104; dendroides 96, 97, 104, 106; leptosporum 106; macrosporum 96, 104; melleum 100; mycophilum 102, 103; rennyi 100; varium 96, 100
Dahlia 28
Daphne 52
Datisca cannabina 28
Datura stramonium 29, 41, 42
Daucus 172, 173
Delphinium 25
Dermatophytes 380
Descolea 231, 233, 234*, 235, 237, 241, 243, 248; antarctica 231-234*, 236, 237*, 239, 242; **flavo-annulata** 232, 233, 236, **246,** 247*, 248; **gunnii** 232-234*, 236, **242,** 243*, 245; **majestatica** 231-234*, 235, 236, **239,** 240*, 241, 246, 248; **pallida** 231-234*, 236, **237,** 238*, 239, 242; **phlebophora** 231-234*, 236, **243,** 244*, 245; **pretiosa** 231-234*, 236, **245,** 246*, 248; recedens 231-233, 236, 239, 241*, 242
Desmazierella 435-437; acicola 406-408, 436
Dianthus 29, 172, 173; caryophyllus 29, 70; lusitanicus 29
Diaporthe arctii 26, 32, 34, 35, 41, 45; eres 32, 35, 54, 56, 57; medusaea 57; oncostoma 57; perjuncta 57; pustulata 57; sociabilis 54; tulasnei 35; verbenae 45
Dicentra 52
Didymella glumicola 175; winteriana 37
Didymocladium 96; ternatum 100
Didymosphaeria 366
Digitalis obscura 18, 19, 37
Diplodia 24, 31; perpusilla 31
Diplodina 32; helianthi 32
Diplorhinotrichum 195; affine 195
Dipocladium 96; elegans 102, 103; majus 102, 103; melleum 100; minus 100, 101; penicillioides 100; rennyi 100
Dipsacus sylvestris 18, 29
Discina 411, 423, 425, 428-430, 447; perlata 428
Disciotis 411; venosa 411
Dracaena 173
Drosophila corrugis 259; gracilis 251; gracilis f. corrugis 259; jerdonii 305; microrrhiza 269
Dysoxylum decandrum 30

Elaeagnus 52
Eleutherascus 371, **377-379; lectardii 378**
Emericellopsis 349
Entoloma clypeatum 103
Eragrostis 176; cynosuroides 174, 176
Erica 173, 174
Eriobotrya 174
Erysimum vulgare 18, 30
Eucalyptus 233
Euonymus 22
Eupatorium sessilifolium 30
Eupenicillium 341
Euphorbia guyoniana 30
Euphrasia 31; officinalis 31
Exochora 52

Fagopyrum 173
Fagus 72, 75, 210, 317; sylvatica 65, 72, 74
Fastigiella 429
Ficus 54
Fimaria 396, 399, 400, 410
Florum fasciculus 202-204
Foeniculum vulgare 31
Fomes foliaceum 201; fomentarius 202
Fonsecaea 62
Forsythia 52
Fragaria 52, 172, 173, 246
Franseria 362

Fraxinus 52; excelsior 25
Freesia 52
Fungi esculenti 202, 203
Fungus alius interaneis . . . 206; cinereus 206; intybaceus 205-207; maximus Ungaricus 203; multis laciniis . . 203
Fusarium 367; oxysporum 184
Fusicoccum depressum 57

Galanthus 173
Galera 154, 314, 318; appendiculata 329; brunnea 318, 323; mycenoides 313; pusilla 156; ravida 318, 331; togularis 134, 152, 158
Galerina 132, 154, 337; jaapii 337; marginata 132; mniophila 156; mycenoides 337; nana 152; paludosa 337; praticola 337; unicolor 327
Galiella rufa 408
Galinsoga 52
Galium 32
Gaeumannomyces 59; graminis 60, 63
Genosperma 410
Geodina 434-436, 441
Geopyxis 405, 410; carbonaria 410; majalis 410, 411; vulcanalis 410
Geotrichum 376
Gladiolus 173
Glycyrrhiza 32; echinata 32
Grifola 205-207; frondosa 201-203, 206-208; umbellata 204
Gymnoascaceae 371, 379
Gymnoascus 380; aureus 375; ruber 372; sudans 351, 353; verrucosus 375
Gymnopilus 231, 235
Gyromitra 425, 428, 429, 447; ambigua 428; californica 428; esculenta 411, 428, 440; infula 411, 428; infula var. apiculatispora 428; sphaerospora 428; tasmanica 428

Hamamelis 52
Hamigera 341, **342,** 343, 345, 349, 351, 379; **avellanea** 343, 344*, **345,** 347, 349; **striata** 343, **347,** 348*, 349
Harposporium 189; anguillulae 189; baculiforme 189; helicoides 189; sicyodes 189
Harziella capitata 189
Hedera 25, 52; helix 51
Heleococcum 365
Helianthus 32; annuus 20, 21; tuberosus 18
Helichrysum 32
Helicostylum 113
Helminthospora tenera 104
Helvella 387, 411, 425-428; acetabulum 430, pl. 22; aestivalis 426, 427; branzeziana 426, 427; lacunosa 427; macropus 427
Helvellella 425
Helvellula 428
Heracleum 52
Herpotrichia 366
Hesseltinella 111; vesiculosa 111, 112*, pl. 7 figs. 1-3
Heterobasidion annosus 215
Hexagonia 201
Hirneola auricula-judae 100
Hirschioporus abietinus 208, 209
Hirsutella 190
Humaria 396
Humarina 396
Humulus lupulus 18, 32, 33
Hyacinthus 172
Hydnum 216; fulgens 216
Hydrangea 52
Hylophila blattaria 152; ombrophilus 131; togularis 128, 131, 136, 147
Hymenoclea 362
Hyoscyamus 33
Hypericum 52, 173
Hypocrea rosea 103
Hypomyces 95, 96, 106, 108, 109; armeniacus 99; aurantius 100, 101; cesatii 100; lateritius 108; ochraceus 99; odoratus 95, 101, 103, 105, 109; rosellus 95, 103, 109; roseus 102, 103; trichothecioides 96, 101
Hysterium samarae 50, 54

Inermisia 410
Inocybe 302
Inonotus 210; dryophilus 210; rheades 210; rubiginosus 209; vulpinus 210
Iodophanus 396, 399, 400, 405, 409
Ipomoea coccinea 33
Iris 173

Jafnea 410
Jafneadelphus 410
Juglans 52, 172
Juniperus 173

Khaya 88
Korfiella 441, 447

Laburnum 52
Lactarius 97, 98, 365; blennius 97; mitissimus 97, 103; rufus 97

Lactuca 52; sativa 34
Lamprospora 409, 410
Langucularia racemosa 353
Lappa 34
Lapsana communis 34
Larix 233, 247
Lasiobolus 391, 392, 396, 397, 399-401, pl. 18 figs. 21-30; cainii 400
Lavas 25
Lecythophora 61, 62; lignicola 61, 62, 84, 86
Leiosepium 108
Lepidium graminifolium 35
Lepidosphaeria 365-368; nicotiae 368
Lepiota procera 154, 162
Leporina 396
Leptopodia 426
Leptoporus destructor subsp. sericeo-mollis 213; revolutus 213
Leptospermum 233, 242-245; ericoides 242; scopiarum 242, 243
Leptosphaeria 20; acuta 43; lindquistii 20; maculans 20; rusci 23
Leptosphaerulina 359
Leucocortinarius 231, 235
Leucoscypha 410
Lignosus aureus querci . . . 201
Ligustrum 52, 55, 173
Lilac 35, 55
Lilium 173
Lotus 35; corniculatus 35; creticus 35
Lunaria 173
Lupinus 172
Lychnis 173
Lycium 52
Lycopersicum 172, 173
Lycopus exaltatus 35
Lythrum salicaria 39

Macrophoma graminella 38
Macroventuria 359; anomochaeta 362; wentii 359, 360*, **361**
Magnolia 52
Mahonia 52, 173
Malus 52, 172, 173
Mangifera indica 174
Marcellcina 410
Marchaliella 367; zopfielloides 367
Margarinomyces 59-62; atrovirens 65; bubaki 61, 62, 66, 68; decumbens 80; fasciculatus 80; hoffmannii 79, 80; luteoviridis 80; microsperma 83; mutabilis 80
Marrubium 35
Martinia 441
Masseeola 207
Maublancomyces 447
Medeola 448; virginiana 448
Medeolaria 445, 448, 449
Medicago 36; sativa 36
Melampyrum 36; sylvaticum 36
Melanospora 365, 392
Melastiza 410; chateri 406, 410
Mercurialis annua 37
Meripilus 205, 207; giganteus 203-206
Mespilus 52
Microstoma 434, 435, 448
Microthecium 365
Midotiopsis 440
Mirandina 195
Mollisia 59, 75; cinerella 63, 73*, 75
Monacrosporium 99
Monilia 441
Monosporium agaricinum 97
Montagnella 172
Morchella 405, 406, 410, 411; elata 411
Mortierella hyalina 111, 116
Morus 52, 54
Mucor 104; dendroides 104, 105
Musa 174
Mycena 267, 269
Mycogone 108; puccinioides 97; verticillata 97
Mycolachnea 387, 410
Mycosphaerella § Didymellina 359; cruciferarum 37
Myrioconium 190
Myxofusicoccum mali 173
Myxotrichum 380

Nannizzia 379, 380
Nanoscypha 434-436
Narasimhella 371, 373, 374, 377, 379; **hyalinospora 374,** pl. 15; poonensis 374
Naucoria tremulenta f. typica 319
Nectria 108, 365; albertinii 103; aurantia 100; cesatii 100, 101; rosea 103, 105; rosella 103
Nemophila 173
Neogymnomyces 380
Neogyromitra 423, 425, 428-430, 447; caroliniana 429; gigas 429, 430, pl. 22
Neophoma graminella 38
Neotestudina 365-368; rosatii 367
Neournula 441; nordmanensis 408
Neslia paniculata 37
Nicotiana tabacum 37, 38

Nodulosporium 405, 410, 411
Nothofagus 83, 231, 233, 235-237, 239, 241-245, 248; cliffortioides 239, 240, 244; dombeyi 238; fusca 239, 240, 242, 244; menziesii 239, 240, 244; pumilio 236
Nothojafnea 410

Octospora 396, 410; euchroa 411
Oedocephalum 400, 405, 406, 409
Oidiodendron 377
Oligoporus 201, 212, 214; farinosus 201, 210, 212-215; **rennyi** 210, **214**
Onobrychis viciifolia 17
Ophiobolus graminis 60
Ornithogalum 173
Oryza sativa 174
Ostracoderma 405, 409
Otidea 410, 415-423; alutacea 418-422; alutacea var. microspora 418; bufonia 416, 419-421; caligata 418-422; concinna 418-423; felina 418-422; grandis 420, 421; kauffmanii 418-422; leporina 416-422; leporina var. minor 417-423; onotica 416-422; platyspora 420; rainierensis 418; smithii 419-421

Pachybasium 189; niveum 189
Pachyella 409
Pachykytospora tuberculosa 217
Paecilomyces 190, 341, 342, 345, 349; **fulvus** 353, **354; leycettanus 342; niveus 351;** todicus 354; variotii 354; **zollerniae** 355*, **356**
Panaeolus 282
Papulaspora 412
Paradiscina 429, 447
Parietaria officinalis 38
Patella 396
Paxina 426
Pedicularis hirsuta 42
Pelargonium 144, 173
Penicillium 62, 64, 81, 197, 200, 341-343, 345-347, 362, 378, 379; avellaneum 341, 345, 347; daleae 200; **inflatum 197,** 198*, 200; ingelheimense 341, 347; janthinellum 200; leycettanum 342; luteum 341; nigricans 200; striatum 343, 347
Peniophora subulata 106
Peyronellaea 171; glomerata 7; herbarum f. chrysanthemi-corymbosi 28; indianensis 175; nicotiae 9; prunicola 9
Peziza 395, 396, 399, 400, 405, 409, 448; ampliata 406; anthracina 409; anthracina var. muricata 409; brunneoatra 406, 409; cerea 406; echinospora pl. 22; fimeti 430, pl. 22; leiocarpa 409; micheli pl. 22; ostracoderma 409; petersii 409; praetervisa pl. 22; repanda 406; saniosa 406, 409; trachycarpa 409; vesiculosa 405
Pezizula 396
Phaedropezia 440
Phacotrichum 365
Phaseolus 172, 173
Phialophora 59-62, 75, 82*, 83, 108, 367; alba 63, 64*; americana 90; atra 76, 77*, 78; **atrovirens** 63, **65***; aurantiaca 79, 80; brunnescens 87, 90; **bubakii** 61, 63, **66,** 67*, 68; caliciformis 87, 88, 90; cinerescens 63, 68, 69*; cyclaminis 63, 70*; **decumbens 80; fasciculata 80;** fastigiata 61, 63, 71, 73*, 74, 77*, 78; goidanichii 76, 77*, 78, heteroderae 75, 77*, 78; **hoffmannii** 60, 64, **79,** 80; lagerbergii 63, 81, 82*, 83; lignicola 61, 63, 84, 85*; lutea-olivacea 76; luteo-olivacea 76, 77*; **luteo-viridis** 79, **80;** malorum 63, 75, 77*, 78; melinii 64, 74, 75; mustea 64, 86, 87*; **mutabilis 80,** 86; obscura 66, 68; radicicola 60, 63; repens 63, 82*, 83; richardsiae 63, 87, 89*, 90; verrucosa 59-63, 84, 90, 91*, 92
Philadelphus 52, 173
Phillipsia 435, 436, 440-442, 448
Phleum 38
Phoenix 172, 173
Pholiota 129, 131, 336; arrhenii 129, 131, 147; blattaria 131, 132, 134-137, 141, 147, 150, 152, 160, 162; dura 129; erebia 129, 314; filaris 123, 156, 314; intermedia 313-315, 318; mycenoides 336, 337; ombrophila 129; praecox 129; pusilla 156; recedens 241; rugosa 156, 158, 314; septentrionalis 313-315; teneroides 137, 138, 141, 142, 160, 162; togularis 129, 131, 132, 134-136, 141, 144, 147, 152
Pholiotina 121-125, 133, 137, 139-141, 146, 150, 158, 231, 235, 314, 334, 337; appendiculata 329, 334; blattaria 136; filaris var. kühneri 156; filaris var. ochracea 156; filaris var. rugosa 156; intermedia 315; intermedia subsp. brunnea 318; septentrionalis 314, 315, 319; septentrionalis subsp. brunnea 318; septentrionalis subsp. smithii 315; septentrionalis subsp. vasilievae 325; togularis

152; togularis f. bispora 138, 160; togularis var. filaris 156; verrucispora 235
Phoma 1, 2, 6-8, 10, 11, 15-17, 21, 22, 25, 26, 31, 33, 39-44, 49, 51, 171, 173-175; abnormis 55; aceris-negundinis 55-57; acuta 43; alternariaceum 7; anethicola 24; bismarckii 55, 57, 172, 174; chartae 175, 176; charticola 17, 23; chrysanthemicola 1-4, 10, pl. 1 fig. 1, pl. 3 figs. 3, 4, pl. 6 figs. 1, 2; cicatricum 49, 54; cinerascens 50, 54; complanata 24; depressa 55, 57; depressitheca 174, 176; elliptica 50, 54; ellipticum 50, 51, 54; euonymella 50, 54; Euphorbiae Guyonianae 30; eupyrena 1, 3, 4, 11, pl. 4 figs. 1, 2, pl. 6 fig. 3; eupyrena f. dulcamarae 11; exigua 2, 4, 6, 15, 19-21, 23-34, 36-45, 50, 51, 55, pl. 1 fig. 2, pl. 4 figs. 3, 4; exigua var. minor 17, 19; exigua var. ranunculorum 17; exigua var. sambuci-nigrae 39; fimeti 1, 2, 4, 6, 7, 11, pl. 1 fig. 3, pl. 2 figs. 1, 2, pl. 5 figs. 5, 6; fraxinifolii 55, 57; friesii 50, 55; fumaginoides 7; glomerata 1, 4, 7, 8, 28, 31, 171, 172, pl. 2 figs. 5, 6, pl. 6 fig. 5; glumarum 171, 174-176; glumicola 174, 175; herbarum 1, 2, 4, 7, 8, 15, 17, 19-24, 29, 30, 33, 36, 39, 40, 42, 43, pl. 1 figs. 4, 5, pl. 2 figs. 3, 4; herbarum § Tetragoniae 18, 19, 42; herbarum f. absinthii 23; herbarum f. achilleae 24; herbarum var. anethi 24; herbarum f. ansoniae-salicifoliae 25, 39; herbarum f. antherici 25; herbarum f. anthirrhini 25; herbarum f. aristolochiae-siphonis 25; herbarum f. Artemisiae 26; herbarum f. artemisiae-campestris 26; herbarum f. blattariae 26; herbarum f. brassicae 26; herbarum f. calystegiae 26; herbarum f. cannabis 27; herbarum f. capparidis 27; herbarum f. catalpae-capsularum 27, 49, 51, 55; herbarum f. chenopodii-albi 18, 19, 27; herbarum f. chrysanthemi-corymbosi 28; herbarum f. convolvuli 26; herbarum f. dahliae 28; herbarum f. datiscae-cannabinae 28; herbarum var. daturae 29; herbarum f. dianthi 29; herbarum var. dianthi-caryophylli 29; herbarum f. dipsaci 20, 29; herbarum var. dulcamaricola 30; herbarum var. dysoxyli 30; herbarum var. erysimi 18, 19, 30; herbarum eupatorii-sessilifolii 30; herbarum var. euphorbiae-guyonianae 30, 31; herbarum f. euphrasiae 31; herbarum f. foeniculi 31; herbarum f. galiorum 32; herbarum f. glycyrrhizae 32; herbarum var. helianthella 32; herbarum f. helichrysi 32; herbarum f. humuli 18, 19, 32, 33; herbarum f. hyoscyami 33; herbarum f. ipomoeae 33; herbarum var. lactaria 18, 20, 34; herbarum f. lactucae 34; herbarum var. lappae 34; herbarum f. lapsanae 34; herbarum f. laptanae 34; herbarum f. lepidii 34; herbarum f. lilacis 35, 49, 55; herbarum var. loti-cretici 35; herbarum f. lycopi 35; herbarum f. marrubii 35; herbarum f. medicaginea 36; herbarum f. medicaginis 36; herbarum f. medicaginum 36; herbarum α melampyri 36; herbarum f. melampyri 36; herbarum f. mercurialis 37; herbarum f. minor 18, 19, 37; herbarum f. Nesleae 37; herbarum f. nesliae 37; herbarum f. nicotianae 37; herbarum f. parietariae 38; herbarum f. Phlaei 38; herbarum f. phlei 38; herbarum f. phytolaccae 38; herbarum f. rubi 38, 49, 51, 55; herbarum f. salicariae 39; herbarum var. sambuci 18, 19, 39; herbarum f. sambuci 18, 39; herbarum f. sambuci-nigrae 39; herbarum f. sarothamni 39, 40; herbarum f. schoberiae 40; herbarum f. scrophulariae 40, 41; herbarum f. sempervivi-tectorum 40; herbarum var. sii 41; herbarum f. solani-nigricantis 41; herbarum f. solidaginis 41; herbarum f. strammonii 41; herbarum f. stramonii 41, 42; herbarum var. tageticola 42; herbarum var. tetragoniae 18, 42; herbarum var. thulensis 42; herbarum var. tulostomatis 43; herbarum var. urticae 43; herbarum f. urticae 43; herbarum f. valerianae 43, 44; herbarum f. verbasci 44; herbarum f. verbenae 44, 45; herbarum f. verbenae-paniculatae 45; herbarum f. vincae 45; herbarum f. ypomeae 33; hibernica 7, 8, 18, 21, 22; indianensis 171, 175, 176; jolyana 174; Lactucae 34; lignicola 18; limitata 27, 39, 50, 51; lingam 20, 26; loticola 35; macdonaldii 15, 21; macrostomum 27, 35, 38, 39, 49, 51, 53*-57; macrostomum var. **incolorata** 49, 51, 52, **55**, 56; macrostomum var. macrostomum 49, 56, 57; malvacearum 54; medicaginis 36; medicaginis var. pinodella 1, 4, 8, pl. 4

figs. 5, 6, pl. 5 figs. 1, 2, pl. 6 fig. 4; mespili 55, 57; monocytogenetica 171; morearum 50, 54; mori 50, 54; mororum 49, 54; musae 174; oleracea 7, 17, 20, 21, 37; oleracea f. bryoniae 18, 21; oleracea var. dipsaci 18, 20, 29; oleracea var. helianthi-tuberosi 18, 20; oleracea f. nesliae 37; oleracea var. scrophulariae 18, 21; oleracea var. urticae 18, 21; petiolorum 55, 57; petiolorum f. juglandis 55, 57; phyllostictoides 49, 51, 54; pigmentivora 18, 21; planiuscula 55, 57; platanoidis 50, 54; polymorpha 171, 172, pomi 49, 54, 55, 57; pomorum 171-174; prunicola 1, 4, 9, 27, 43, 55, 57, 171-173, pl. 3 figs. 5, 6, pl. 6 fig. 6; pyrina 173; radicis 174; salicina 50; samarorum 25; saprophytica 7; siliquastri 55, 57; silvatica 37; solanicola 6; striaeformis 54-57, 174; trifolii 8; urticae 17, 21; Tulostomatis 43; valerianellae 44; violacea 7, 18, 21

Phomopsis 26, 30, 32-35, 41, 44, 54, 56, 57, 174; cinerascens 54; morearum 54; petiolorum 57; planiuscula 57; platanoidis 54; pustulata 57

Phragmites 172

Phyllosticta 175; cruenta 175; decidua 6; glumarum 174, 175; glumicola 174, 175; hypoglossi 23; limitata 50, 51, 55; mali 50, 51, 55; oryzina 174; prunigena 173; pyrina 9, 173; robiniaecola 50, 55; robinicola 50, 55; ruscicola 23; ruscigena 18, 23; saxifragae 50, 54; taxi 50, 55

Phyllostictina 175; hypoglossi 23

Physocarpus 52

Phytolacca decandra 38

Picea 74, 188, 233, 245; abies 72, 78, 193, 195, 197, 199, 200; excelsa 72, 83; smithiana 246

Pindara 435

Pinus 3, 72, 172, 173, 233, 247; contorta 186; nigra var. austriaca 9; resinosa 186; strobus 72; sylvestris 9, 72, 81, 83, 213

Pisum 173

Pithya 435-437, 440; vulgaris 407

Platanus 52

Plectania 405, 408, 440, 447; coccinea 407; nannfeldtii 408

Plenodomus 54; acutus 43; cannabis 27; lingam 26; salicum 54

Pleospora capparidis 27

Plicaria fulva 409

Podospora 365

Polyopeus 51; purpureus 51, 57; purpureus var. incoloratus 55, 56; purpureus var. latirostratus 55, 56; purpureus var. nigrirostratus 55, 56; purpureus var. verus 50, 51, 54, 56

Polyporus abietinus 208, 209; albo-carneo-gilvidus 216; amorphus 212; apalus 211, 213; cespitosus 203; cinerascens 215; cuticularis 210; dryadeus 210; dryophilus 210; elegans 215; fibrillosus 216; fissilis 210; floridanus 216; frondosus 201-206, 208, 209; fulvus 210; giganteus 203, 206, 208; imbricatus 202, 203; intybaceus 201-206, 208; lapponicus 210; lindbladii 215; melanopus 101; picipes 101; póris albidis 203; ramosissimus 205, 206; rennyi 201, 210-214; resinosus 210; rubiginosus 209, 210; sericeo-mollis 211-214; spadiceus 203; squamosus 101, 202; subfuscus-flavidus 215; subsericeo-mollis 212; umbellatus 208; varius 101, 215; versatilis 216

Populus 3, 52, 148, 173, 210; tremula 68, 72

Poria 214; cinerascens 215, 216; lindbladii 215, 216; rennyi 210, sericeo-mollis 213

Preussia 365, 366

Protium heptaphyllum 356

Prunella 246

Prunulus gracilis 257

Prunus 9, 52, 173, 174

Psathyra 261; corrugis 259, 261; gracilis 251; gracilis var. corrugis 259; microrrhiza 269; squamifera 269

Psathyrella 261, 284, 295, 297, 299, 302, 305, 307; § Homophron 302, 303; § Psathyrella 257; **amstelodamensis** 295, 296*, 297, 298*, **299,** 300*, 303, 305, pl. 9; candidissima 311; caudata 277; cernua 303, 305; corrugis 259, 261; flexispora 305; fulvescens 297; gossypina 311; gracilis 249, 250*, 251, 252*, 257, 261, 264*, 266*, 273, 274, 277, 279, 295, 297; gracilis f. **albolimbata** 249, 256*, **265,** 273, 275*, 277, 297; gracilis f. **clavigera** 249, 256*, **265,** 274*, 277, 297; gracilis var. corrugis 259; gracilis f. corrugis 249, 254*, 261; gracilis f. gracilis 249, 251, 259, 261, 265, 267, 268*, 273; gracilis f. **substerilis** 249, **267;** hirta 311; hydrophila 128; macquariensis 303; microrrhiza 249, 251, 257, 258*, 260*, 262*, 263*, 269, 270*, 272*,-274, 276*, 277, 278*,

279, 297; microrrhiza f. pseudobifrons 273: muricellata 305; **narcotica** 295, 296*, 304*, **305;** odoratus 307; olympiana 302, 303, 305; pennata 311; **pervelata** 295, 308*, **309,** 311, pls. 10, 11; polycystis 277; pseudogracilis 277; pygmaea 132, 305; saponacea 307; spadicea 305; spadiceogrisea 295; squamifera 269, 274; subcernua 303; xanthocystis 305
Pseudoarachniotus 371; aurantiacus 373; citrinus 372; echinulatus 375; flavus 372, 373; halophilus 372, 373; hyalinosporus 374; marginosporus 371, 374; punctatus 373; reticulatus 375; roseus 372, 373; terrestris 372, 373; thirumalacharii 372, 373
Pseudogymnoascus 379
Pseudombrophila 410
Pseudophaeotrichum 365-368; sudanense 368, pl. 13
Pseudopithyella 435, 437
Pseudoplectania 408, 440-442, 447; nigrella 441, 442
Pseudorhizina 425, 447; sphaerospora 428
Pteridium aquilinum 187
Pterocatleya 52
Ptychogaster 212; albus 212; citrinus 201, 210, 212-214
Ptychoverpa 411; bohemica 411
Pulvinula 410; archeri 411
Pustularia 410
Pustulina 410, 425; catinus 410; ochraceus 430, pl. 22
Pycnoporellus 201, 216; fibrillosus 216; **fulgens 216**
Pyreium fomentarium 202
Pyrenochaeta 10, acicola 1, 2, 4, 9, 10, pl. 3 figs. 1, 2, pl. 5 figs. 3, 4; spinaciae 9, 10
Pyrenopeziza 59, 75; laricina f. microsperma 63, 73*-75
Pyrenophora 359
Pyronema 409, 410; domesticum 409; omphalodes 409, 410
Pyrus 52, 172, 173
Pythium ultimum 8

Quercus 146, 148, 233, 247; rubra 200; serrata 247

Radiomyces 113
Ranunculus 19, 172; bulbosus 17
Rhabdospora 24; pleosporoides 24
Rhinocladiella 59-62; pedrosoi 62
Rhinotrichum 409
Rhizina 425, 430; undulata 411, 429
Rhizoblepharis 410
Rhizoctonia 405, 410
Rhododendron 52
Rhodophyllus 261
Rhyparobius 398, 399
Ribes 3, 52
Rickiella 435, 436
Robinia 52, 55, 173; pseudoacacia 56
Rollandina 379; lanata 378; vriesii 377
Rosa 52, 173; multiflora 51
Rosellinia xylarispora 79
Rozites 231, 235, 241, 248; flavo-annulata 231, 246
Rubus 52, 55; idaeus 38, 74
Ruscus 23; aculeatus 23; hypoglossum 23; hypophyllum 18, 23
Russula 97, 365; coerulea 98; fragilis 97; mustelina 105; ochroleuca 97; sardonia 98
Rustroemia 441; nummiformis 440
Ryparobius 395-397

Saccobolus 389, 393-395, 412, 440; § Eriobolus 390, 393; § Saccobolus 390, 393; versicolor 430, pl. 22
Salix 52, 146, 148, 172
Sambucus 25, 52; nigra 18, 39; pudens 307
Sarcoscypha 407, 434-436, 440; coccinea 387, 407, 440-442; coccinea var. coccinea 407, 411; coccinea var. jurana 407
Sarcoscyphaceae trib. **Pithyeae 437**
Sarcosoma 408, 441; globosa 408; latahensis 408; mexicana 408
Sarcosphaera 409
Sarothamnus criocarpus 39
Sartoscypha 405
Saxifraga 54
Schoberia 40
Sclerotinia 190; tuberosa 441
Scrophularia 40, 52; nodosa 18, 40
Scutellinia 410
Secotium gunnii 242, 243
Selenaspora 397
Sempervivum tectorum 41
Sepedonium 108
Septoria 25; phlyctaenoides 38; samarorum 25
Sepultaria 387, 410
Sesquicillium 190; microsporum 190
Shanorella 380
Sium 52; latifolium 41

Skeletocutis amorphus 212
Solanum 52, 172, 173, 181; dulcamara 11, 30; nigrum 41; tuberosum 11
Solidago 41, 52
Sorbus 52, 173
Sorosporella 190; uvella 190
Sowerbyella 410
Spadicoides atrum 79
Sparassis 207; laminosa 207
Sphaeria aurantia 100; aurantiaca 100; aurea 100; rosea 103, 105; rosella 103, 105; tageticola 42
Sphaerospora 410; minuta 410
Sphaerosporella 410
Sphagnum 337
Spicaria musticola 351
Spiromastix 379
Sporormia 365, 366; acmulans 366
Sporotrichum 179, 181, 184; agaricinum 97; aureum 179, 180*, 184; boletorum 104; candidum 105; carpogenum 76, 78; cerebriforme 179, 184; cylindrosporum 100; **dimorphosporum** 179, **181,** 182*; malorum 75, 78; **sporodochiale** 179, **182,** 183*; thermophilum 184
Stagonospora 25; **samarorum** 15, **25,** 29, 39
Stemphylium 9
Stephanoma 108
Stereum 106; hirsutum 101
Strangulidium 214; rennyi 210, 214, 215
Stranvaesia 52
Streptotheca 396, 398
Stropharia 128
Strumella 408
Suaeda 40
Syngliocladium 190; cleonis 190
Syringa 35, 52, 55, 173

Tagetes 42
Talaromyces 341-345, 351, 379; avellaneus 341, 342, 345; emersonii 342; leycettanus 342; luteus 342; striatus 341, 342, 347; thermophilus 342; vermiculatus 341
Taxus 52, 55, 233, 245, 246
Testudina 365-367; terrestris 366, 367, pl. 12
Testudinaceae 365, **366**
Tetragonia expansa 18, 42
Thecotheus 395, 396-399, 401, 409, pl. 19 figs. 31-45; cinereus 409; pelletieri 399, 401
Thelebolus 391, 392, 395-401, pl. 16 figs. 1-8; microsporus pl. 17 figs. 9-11; stercoreus 394, 395, 397-401; subfuscus 401; zukalii 397, 398, 400
Thelephora 100
Thermoascus 343, 345, 351; crustaceus 345; thermophilus 345
Thindia 434-437, 441
Thomasiniana theobaldi 38
Tilia 52
Togaria blattaria 152; togularis 129
Tolypocladium 185, 188-190; **cylindrosporum** 185, 186*, **187,** 189, 190; **geodes** 185, **187,** 188*, 190; **inflatum 185,** 186*, 189
Tomentella 106
Torula heteroderae 75, 76, 78
Torulomyces 378
Tradescantia 25
Trametes hispida 217; micans 217; morganii 216, 217; rigida 216; serialis 217; Trogii 217; versicolor 101
Tremella 207
Tricharia 387, 410
Trichobolus 396, 398-401
Trichodelitschia 365
Trichoderma 189, 190
Tricholoma saponaceum 309
Trichophaea 387, 405, 410; abundans 410; confusa 410
Trichosporiella 179, 184; **cerebriformis 184;** hyalina 184
Trichosporium populneum 76, 78, 79
Trichothecium 101, 106; agaricinum 104; candidum 104, 105; roseum 106
Trifolium 52
Triticum 172
Tsuga 225
Tulipa 52
Tulostoma volvulatum 43
Tyromyces 214; fissilis 210

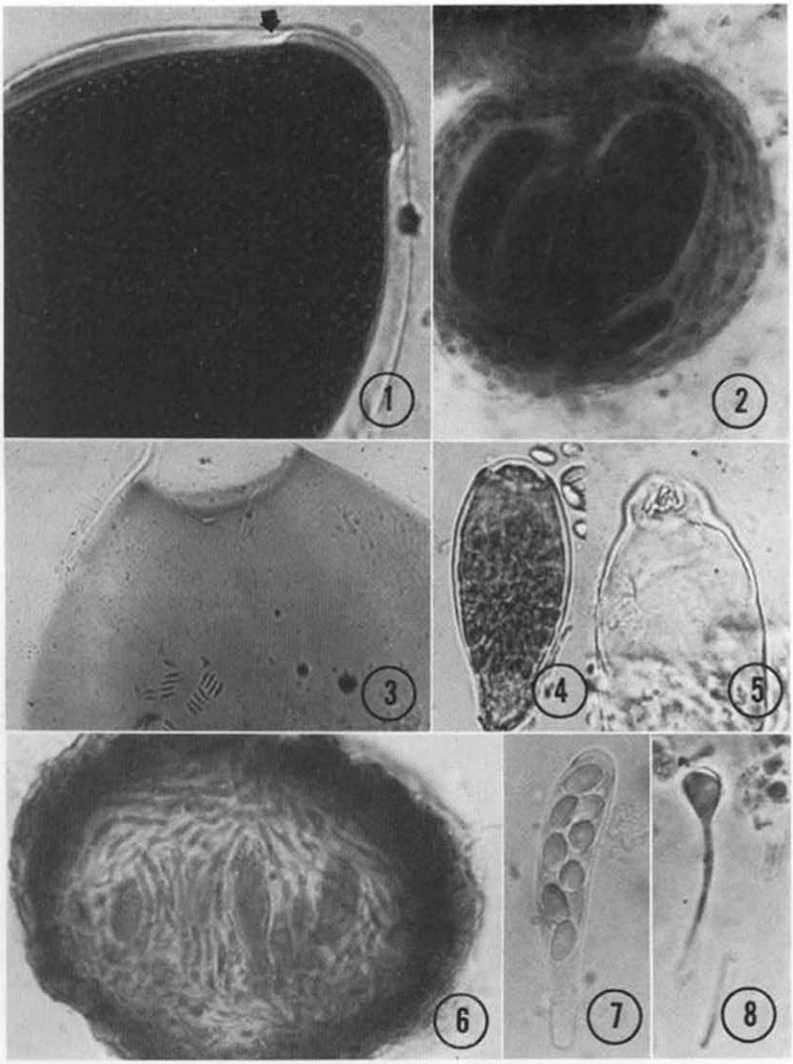
Ulmus 52
Uncigera 190
Underwoodia 425, 427, 428; beatonii 427; columnaris 427; fuegiana 427
Urnula 405, 408, 440, 441, 447; craterium 408; geaster 440
Urtica 25, 43, 52, 173; dioica 17, 21, 43; urens 18

Valeriana 43
Valerianella 172

Venturia 359
Verbascum blattaria 26; thapsi 44
Verbena 44, 45; paniculata 45
Vermicularia acicola 9
Veromessor 362
Verpa 411
Verticicladium 406-408, 441; trifidum 408
Verticillium 69, 106, 108, 189; agaricinum 97; cinerescens 68, 70; lactarii 97; nigrescens 6
Viburnum 25, 52
Vicia 173
Vinca 45, 52; major 45
Viola 172
Vitis 52, 172

Waldemaria 371; pernambucensis 372
Westerdykella 365, 366
Wettsteinia 359
Wolfina 408
Wynella 411, 425, 427; silvicola 427
Wynnea 434, 435, 440, 441, 448

Zollernia illicifolia 356
Zopfia 368; rhizophila 368
Zopfiella 365
Zukalina 396, 399
Zygocactus 172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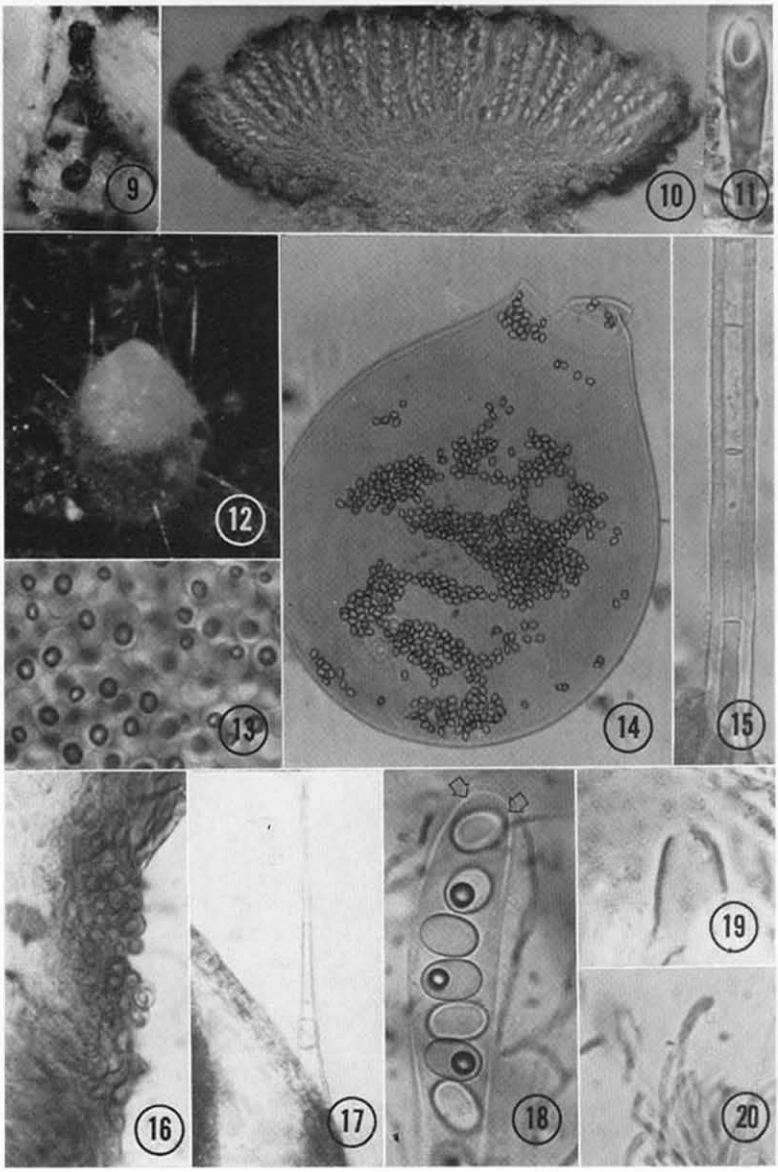
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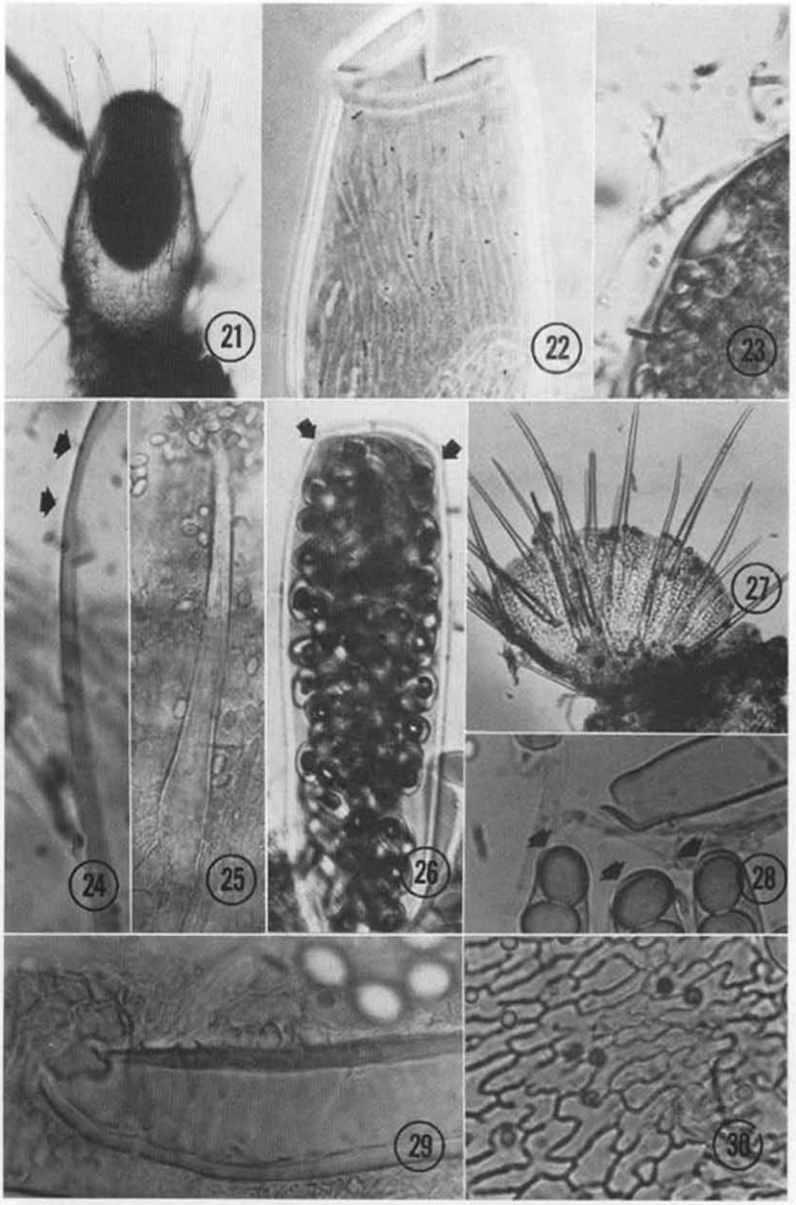
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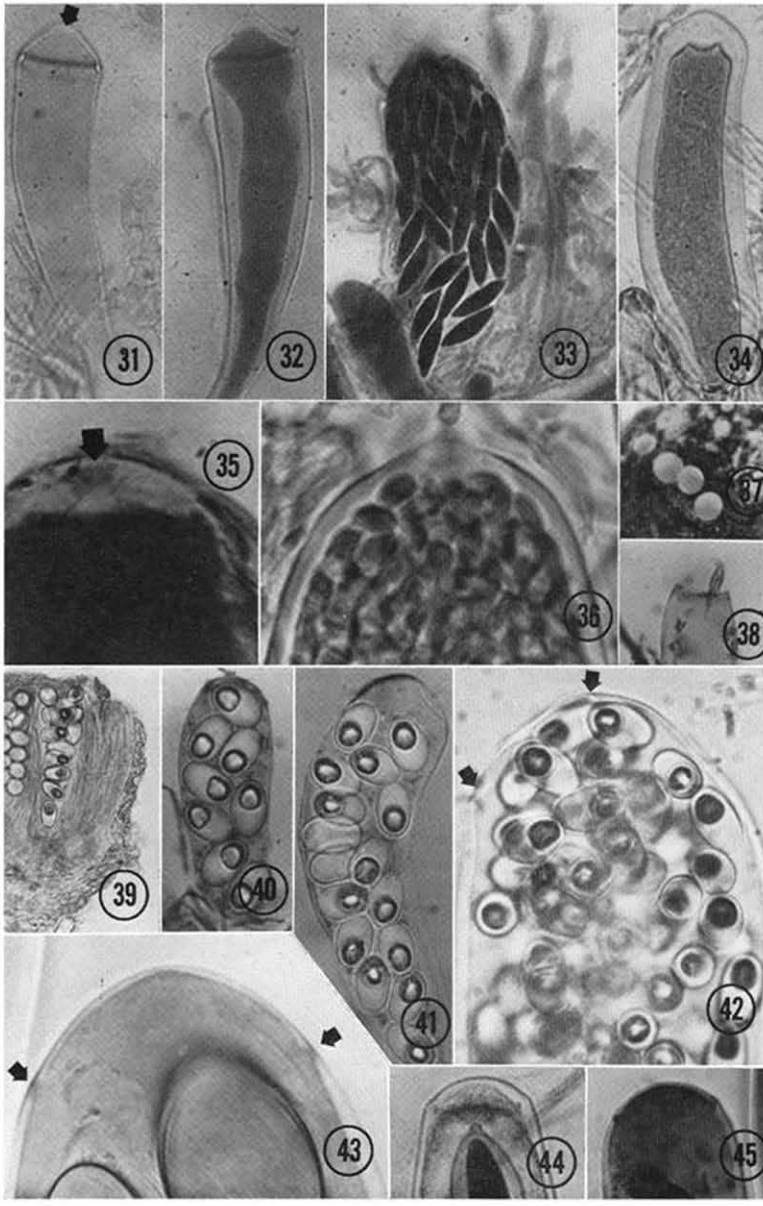
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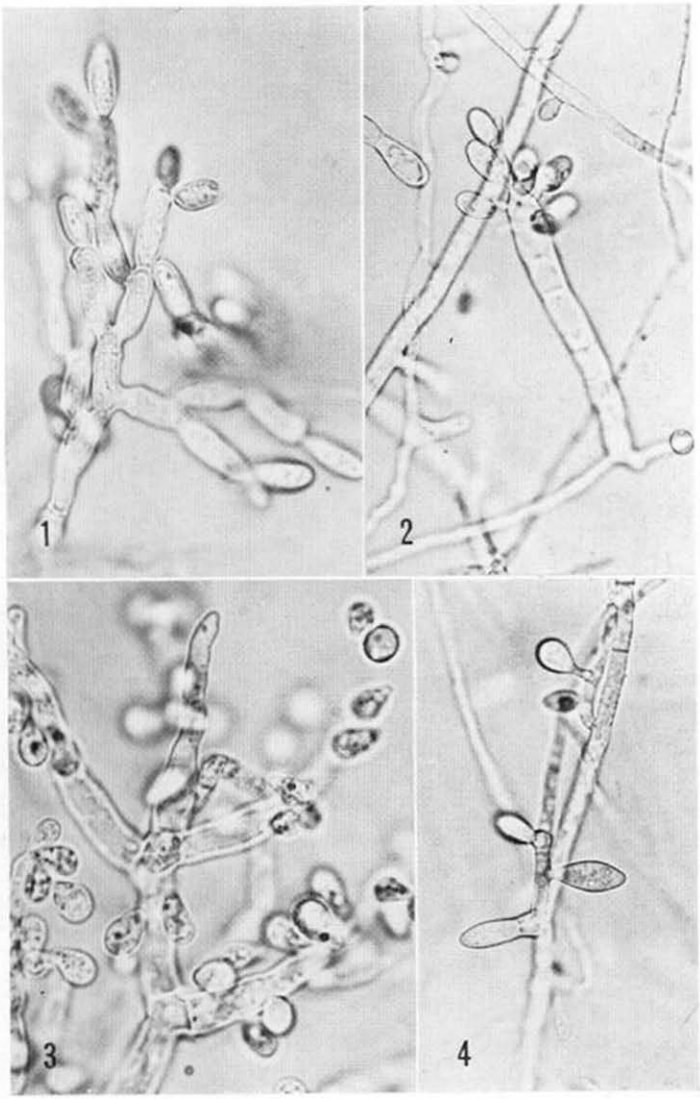
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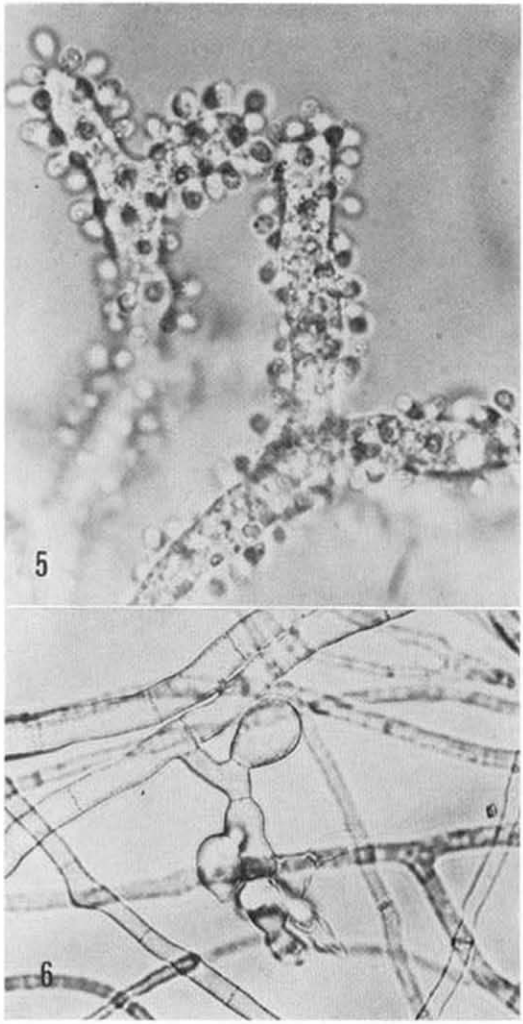
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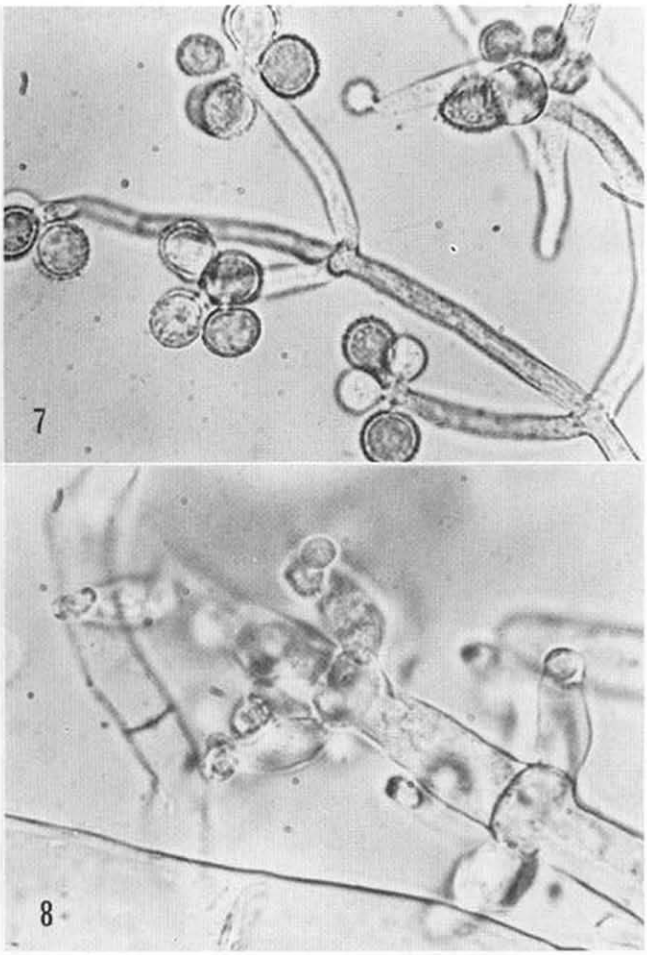
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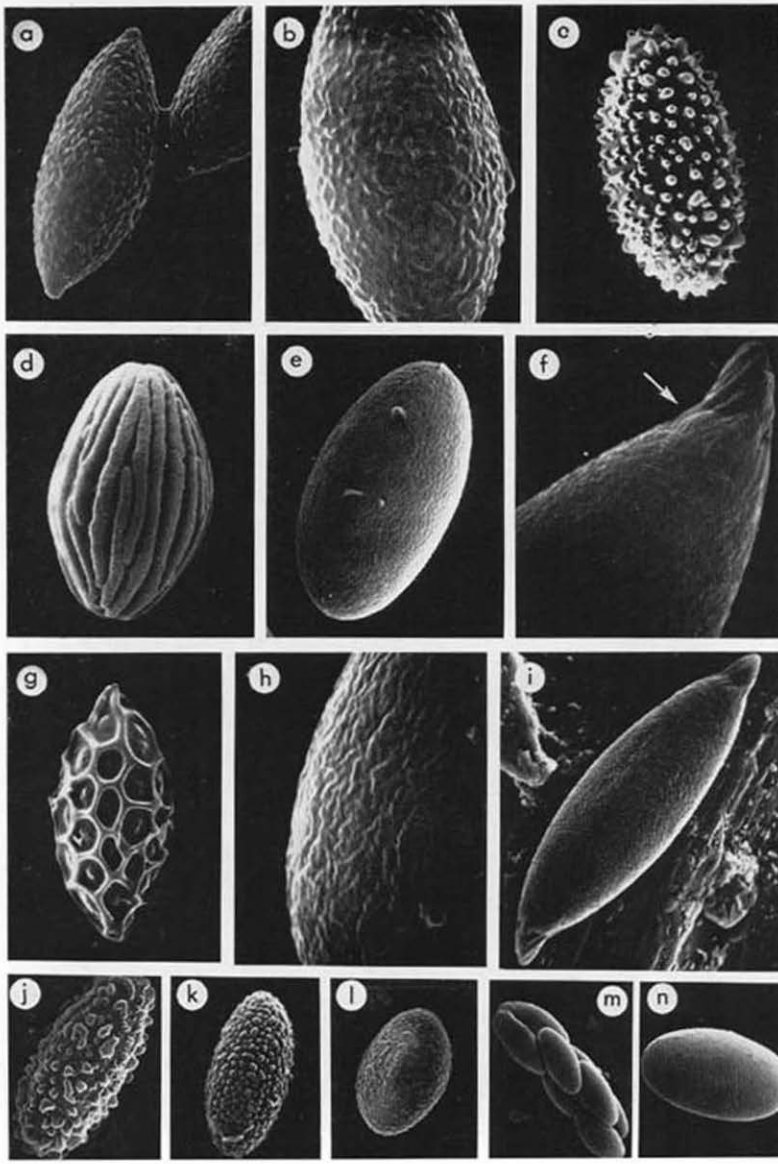
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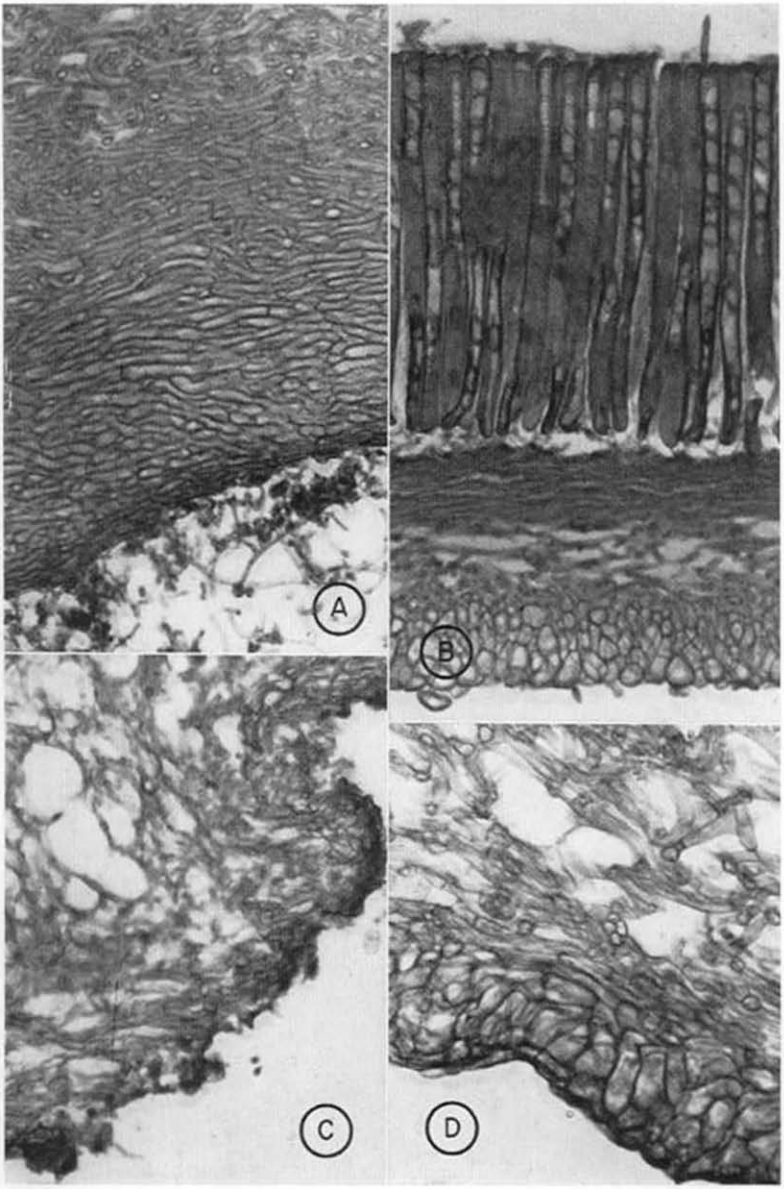
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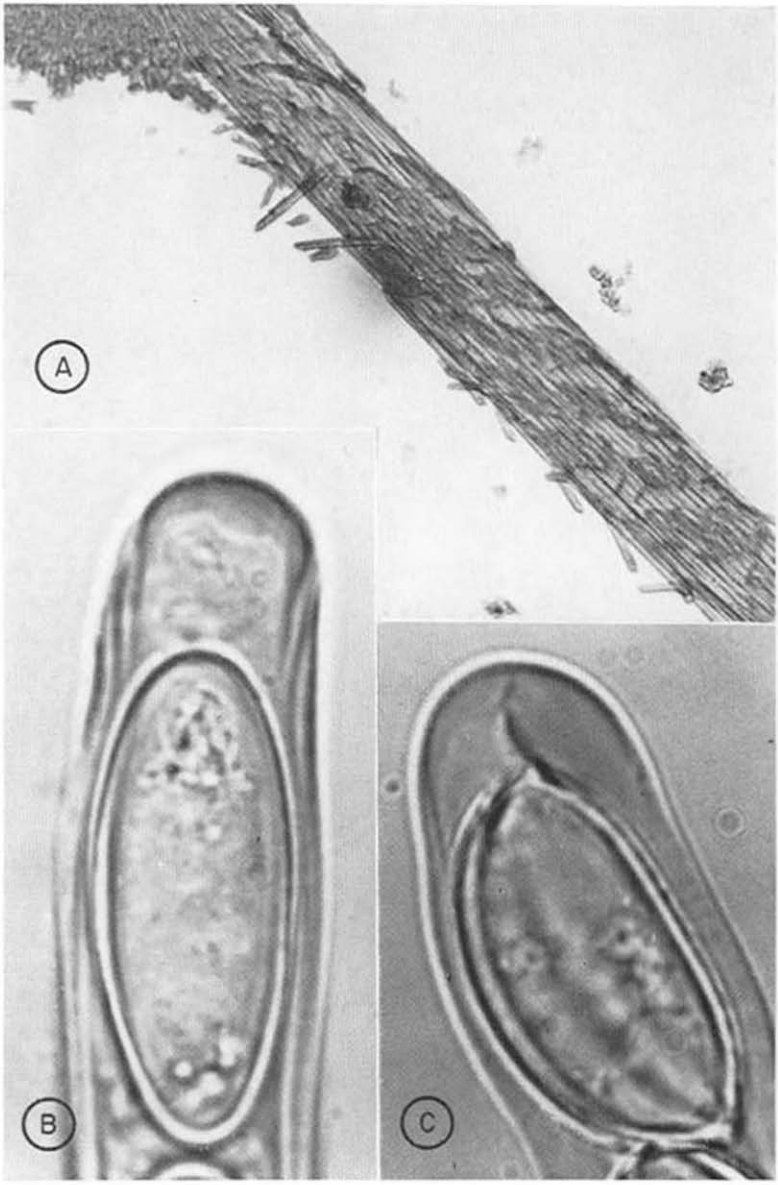
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