

verwendet and statt xeric

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Convergent evolution in discomycetes from bark and wood

"lignicolous" and "dry weathered lignum" here means arid wood and bark

domini meint sie in der Höhe.

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Dapas versteht unter "auf Binde" stets in der Höhe, meint an noch lebende Stämme.

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Dry ^{verwittertes Holz} weathered wood (lignum) and ^{dieße Rinde} arid bark support a discomycete flora which is taxonomically extremely diverse and contains a high percentage of species with characters not found in Discomycetes of more mesic habitats. A large proportion of filiform-spored, and all muriform-spored non-lichenized Discomycetes occur in this habitat. Most lignicolous Discomycetes have either a pigmented epithecium or a dark margin which covers the hymenium when dry and many have reviving, gelatinous ascomata. Their asci often have a simplified structure difficult to interpret. Weathered wood is a niche which has long continuity in geologic time but is relatively unfavourable for fungi because of exposure, aridity and low nutrient levels. Strong selective pressure has consequently been exerted on those fungi able to colonize it, resulting in a high incidence of convergent evolution.

KEY WORDS:— bark – Discomycetes – evolution – fungi – wood.

CONTENTS

| | |
|----------------------------|----|
| Introduction | 15 |
| The environment | 17 |
| The organisms | 19 |
| The characters | 22 |
| Conclusions | 31 |
| Acknowledgements | 33 |
| References | 33 |

INTRODUCTION

The identification and classification of Discomycetes which grow on dry lignum (wood) and the bark of living and standing dead woody plants is a source of continuing problems to mycologists, perhaps rivalled only by those in the taxonomy of lichenicolous fungi. Individual species often have distinctive characters not found among non-lignicolous ascomycetes, and it has been tempting to include all species with one or more of these in common in a single genus without investigating closely to ascertain if the genus is really natural.

means xerophile

Recently there has been renewed interest in the classification and biology of some of the taxa involved, as many of the reported cases of genera containing both lichenized and non-lichenized fungi occur on weathered lignum. As a result

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it has become obvious that out-dated generic circumscriptions founded on single, albeit distinctive, characters comprise fungi belonging to different families, orders, or even subclasses of ascomycetes. This situation equally applies to many long-established genera in other groups of fungi, but the extent to which it has occurred in lignicolous discomycetes and the unusual nature of some of the characters is remarkable, suggesting that morphology alone might provide valuable clues to the understanding of the biology of these organisms.

Corticolous and lignicolous discomycetes are extremely diverse taxonomically. They include a few indubitable members of the Helotiales, such as *Pezicula* Tul., *Tympanis* Tode ex Fr. and *Godronia* Moug. & Lév. Corticolous and lignicolous members of the Hypodermataceae (Rhytismatales) are also not uncommon; their present inclusion in *Coccomyces* de Not., *Colpoma* Wallr. and *Xyloschizon* H. Sydow fails to give a proper impression of their diversity which is more comparable with that seen in the better known foliicolous forms. The Tryblidiaceae (which certainly merits recognition as a distinct family) is exclusively corticolous on thick arid bark. The Stictidaceae and Odontotremataceae are predominantly corticolous and lignicolous. Both lichenized and non-lichenized species of Lecanorales occur in this habitat, as well as lichenized and non-lichenized discoid loculoascomycetes belonging to the Hysteriales. Finally, there is quite a number of genera which cannot be confidently assigned to any order in current classifications; these include *Xylopezia* Höhnelt and *Winteria* Rehm, which seem to be loculoascomycetes with unitunicate asci, and the propoloid fungi (*Propolomyces* Sherw., *Propolidium* Sacc., *Melittosporiella* Höhnelt and *Melittosporium* Corda).

Every large genus and many of the smaller genera of lignicolous discomycetes which have been investigated by modern taxonomic methods (Groves, 1952, 1965; Hafellner, 1979; Sherwood, 1977a, 1980) have been shown to be a complex of species from two or more families, with or without the addition of the thelotremataceous lichens whose ascomata superficially resemble those of the Stictidaceae and are often confused with them. To give an extreme example, Hafellner (1979) concluded that the species formerly included in *Karschia* Körber included both Loculoascomycetes and members of the Lecanorales, and belonged to fourteen genera.

Conversely, the same or closely related organisms have frequently been described in four or more genera which have traditionally been considered distinct. A classic example is *Durella atrocyanea* (Fr.) Höhnelt, an erumpent greenish-black discomycete, common on dry wood; this has thick-walled, iodine-negative asci, large, three-septate ascospores, a thick pigmented epithecium and a margin of dark radiating hyphae immersed in a gel. As *Durella* Tul. this species is classified in the Helotiales: Leotiaceae because the asci are neither bitunicate nor operculate and the margin is hyphal. As *Cryptodiscus* Corda it is assigned to the Dermateaceae in some systems of classification and the Stictidaceae in others. It also has names in *Stictis* Pers. ex Fr. (Ostropales: Stictidaceae), *Patellaria* Fr. (Hysteriales: Lecanactidaceae) and *Odontotrema* Nyl. (Ostropales: Odontotremataceae). Existing discomycete keys are unsatisfactory for identifying a *Durella*, as shown by the fact that the only specimen filed under 'Durella' in a certain reputable mycological herbarium until recently was *Pseudographis elatina* (Ach.) Nyl.

Another commonly misunderstood immersed discomycete is *Karstenia*

lonicerae Fr. which, with a few closely related species, has a hyaline covering layer of characteristic small-celled angular pseudoparenchyma (*textura angularis*) which splits open by teeth to expose the hymenium, thin-walled asci which do not react with iodine and long multi-septate ascospores. This species complex has synonyms in *Stictis*, *Phragmonaevia* Rehm, *Coccomyces*, *Cryptodiscus* and *Melittosporium*. It is obviously a natural genus whose affinities remain obscure.

From the above it will be evident that *Cryptodiscus* as currently circumscribed contains species which are not closely related. As interpreted by Dennis (1978) it included a *Karstenia* Fr. and (with reservations) *Durella atrocyanea*, as well as its type, *C. pallidus* (Pers.) Corda, a colourless, deeply immersed discomycete with capitate asci unchanged in iodine, a hymenium which stains blue in iodine and relatively large three-septate spores. Species which remained in the genus when I began studying it in 1975 also included several thelotremataceous lichens and a lichenized *Arthonia* Ach. (a loculoascomycete). If such extraneous material is removed, *Cryptodiscus* remains as a natural assemblage of closely related lignicolous species differing in ascospore and paraphysis characters.

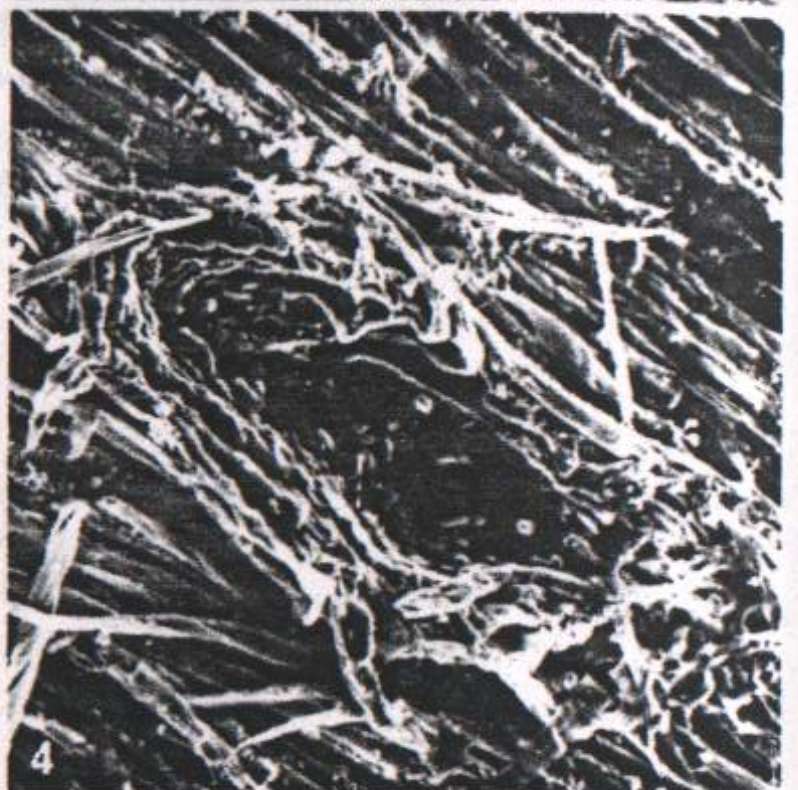
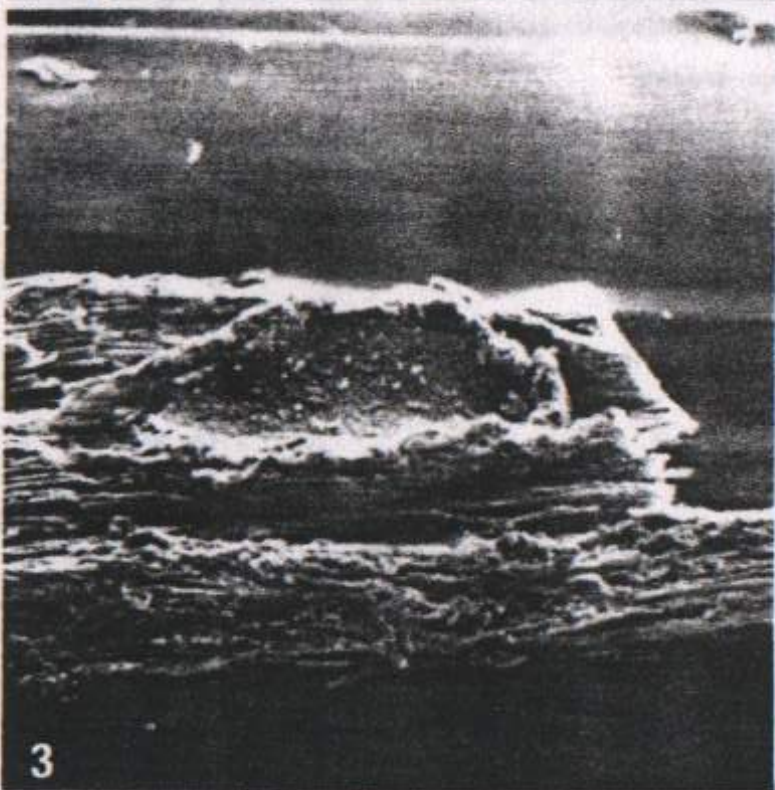
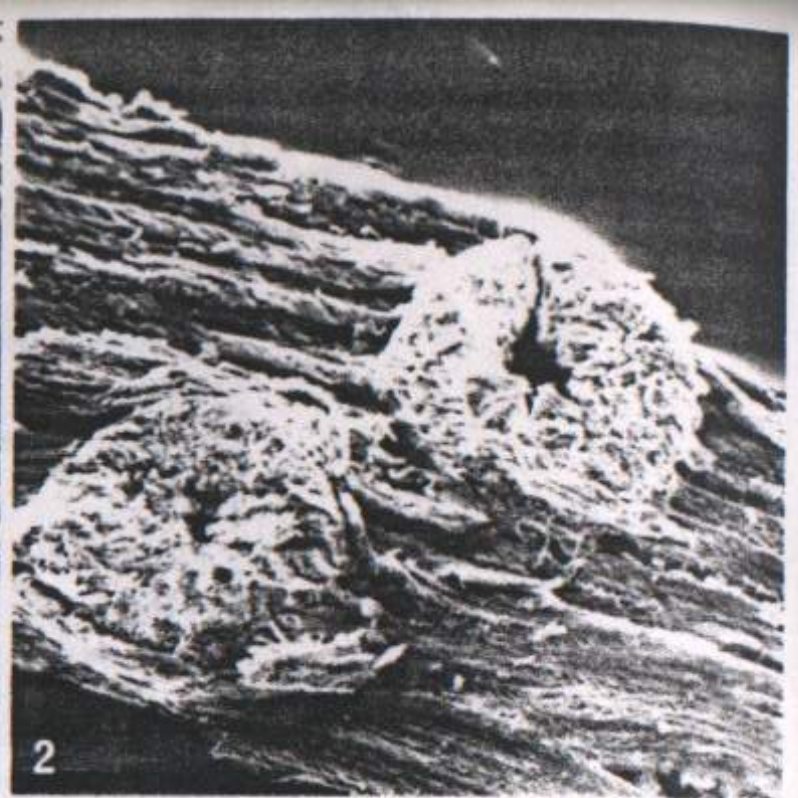
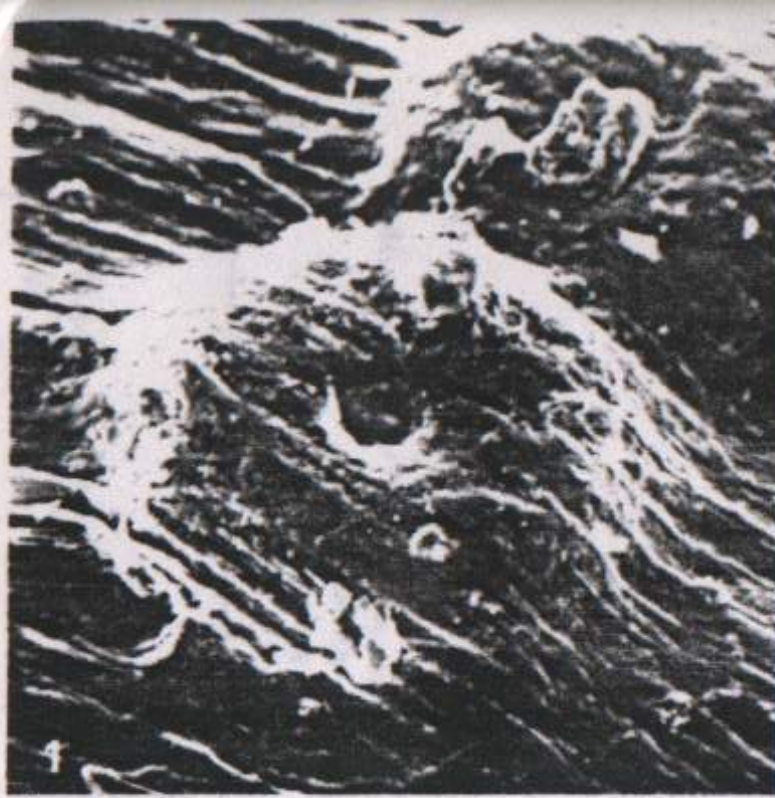
Hypodermataceous fungi with discoid ascomata are also a source of difficulty to systematists. Emphasis on filiform ascospores as a taxonomic criterion and a lack of attention to ascus structure has led to the inclusion of *Coccomyces* species in *Stictis* and *Godronia*. *Godronia*, typified by a corticolous helotialean discomycete with long acicular spores, has at one time or another included the type species of *Discocainia* J. Reid & Funk, which is almost certainly hypodermataceous, a species of *Cerion* Masee, also hypodermataceous, and a *Robergea* Desm. species (Stictidaceae).

The catalogue of misclassified lignicolous discomycetes is almost inexhaustible but the preceding examples serve to illustrate the confusion that abounds. A great phylogenetic diversity where fundamental characters of ascus structure and ascocarp development are concerned, coupled with a high degree of convergence in gross morphology and ascospore characters, is a taxonomic maze, but it also poses the question as to why this should have occurred to such an extent in this particular ecological niche.

Convergent evolution is characteristically exhibited by assemblages of organisms adapted to harsh environments, such as deserts. It is therefore reasonable to hypothesize that the environment of weathered lignum imposes unusually severe constraints on fungal adaptation. By considering the characteristics of the physical environment and relating them to the observed morphology, it is possible to suggest a partial ecological explanation for the taxonomic riddles posed by lignicolous discomycetes.

THE ENVIRONMENT

The environment on weathered, standing dead wood, especially of twigs and small branches, is an extreme one for fungi. Even in humid climates dead twigs are desiccated for much of the time, as well as being exposed to marked temperature fluctuations and, especially on dead trees, high light intensities. Fungi growing in the outer layers of thick, arid bark, such as that of *Pseudotsuga*, are only slightly more protected from environmental extremes. Lignicolous fungi on standing dead wood are exposed to much the same rigours as epiphytic lichens and lichenicolous fungi, and it would consequently not be surprising if they



Figures 1-6. Fruitbodies of lignicolous discomycetes as viewed with the scanning electron microscope. Fig. 1. *Xylopezia hemisphaerica* (Fr.) Höhnelt. Fig. 2. *Odontotrema minus* Nyl. Fig. 3. *Melittosporium propolidioides* (Rehm) Rehm. Fig. 4. *Durella atrocyanea* (Fr.) Höhnelt. Fig. 5. *Odontotremopsis pikei* Sherw. ined. Fig. 6. *Stictis radiata* Pers. ex Gray. Figs 1-3, 6 $\times c.$ 50; Figs 4,5 $\times c.$ 100.

exhibited some characters commonly regarded as lichen-like. Furthermore, accumulations of weathered dead wood are more abundant in cold and arid habitats than in warm mesic situations where wood is rapidly degraded. Many of the most distinctive and taxonomically interesting lignicolous discomycetes occur in areas such as the western Himalayas which are both cold and arid. In western North America the communities seem richest in forests near the timberline or on dry exposed sites. This may indicate an inability to compete in favourable environments with faster growing fungi, especially Hymenomycetes and pyrenocarpous fungi. *L. Leo Hales*

Weathered dead wood is also low in readily available nutrients. The extent to which the fungi discussed in this paper are capable of degrading cellulose and lignin is unknown. In general, ascomycetes are not aggressive wood-rooting fungi, although some, notably the Xylariaceae, are evidently capable of degrading lignin. Many lignicolous discomycetes appear to scarcely alter the structure or appearance of the wood on which they grow, indeed the possibility that the wood itself is not the main source of nutrients for all cannot be excluded. Often the wood also supports substantial populations of algae with which the fungi seem to be more or less casually associated. Foliage leachates, resin, leachates from epiphytic lichens (cf. Carroll, Pike, Perkins & Sherwood, 1980), insect exudates and bird droppings are also possible sources of fixed carbon and especially nitrogen in an aerial, nutrient-poor environment.

Convergent evolution in widely separated lines requires that strong directional selection operate over a considerable period of time, implying a harsh but stable environment. Weathered wood in semi-arid temperature montane areas, although quite different from the lush tropical rain forests where many mycologists would look for evolutionarily isolated ascomycetes of potentially ancient lineage, is one that has a long continuity in geologic time in some areas. This is not in itself convincing evidence that the organisms which occupy this niche today are ancient, but rather provides the long time scale necessary for convergence between isolated lines.

THE ORGANISMS

The genera listed in Table 1 do not constitute an exhaustive list of discomycetes which occur on wood. They have been selected to illustrate the taxonomic diversity which exists in this habitat, as well as the prevalence of unusual characters which may represent adaptations to specific environmental stresses. The list has been limited to genera which I have studied personally, since the inclusion of data gleaned from the literature in a compilation of this type almost invariably serves to perpetuate old errors in little-known groups.

The standard general reference works on the taxonomy of discomycetes are those of Nannfeldt (1932), Korf (1973) and Dennis (1978). Korf (1973) provides a clear account of the arrangement of orders and families according to the system used by most contemporary mycologists and gives a useful bibliography of most of the important references on the subject to that date. Unfortunately none of these generally excellent works is particularly satisfactory where the lignicolous genera under discussion are concerned, and to obtain fuller information it is necessary to consult the original literature.

Most non-lichenized discomycetes studied by mycologists belong to the

Table 1. Distribution of characters in lignicolous discomycetes *means xerotolerant on wood & bark!*

| | Mode of ascocarp dehiscence | Ascocarps black | Ascocarps gelatinous | Hyal cells and/or spores small (< c. 2 x 1 μm) | Shape and septation of ascospores | Anamorph produced | Number of spores per ascus | Mode of ascocarp development | Ascus type |
|----------------------------|---|-----------------|--|--|--|-------------------|--|---|---|
| <i>Orbilina is missing</i> | covering layer splitting longitudinally covering layer splitting radially ascocarp opening by a gysigenous pore | | margin gelatinous hymenium gelatinous | | filiform spores spores unusually large muriform spores | | fewer than 8 delimited some ascospores regularly abort asci initially polysporous primary ascospores <u>fragment</u> <u>ascoconidia</u> produced | ascohymenial ascolocular intermediate | hypodermataccous ostropalcan pseudopericulate verruarioid operculate? annulate bitunicate lecanoralean |
| HELOTIALES | | | | | | | | | |
| <i>Claussenomyces</i> | | + | + | | | | + | + | + |
| <i>Durella</i> | | + | + | | | + | | + | + |
| <i>Godronia</i> | | + | | | + | + | + | + | + |
| <i>Pezicula</i> | | | | | + | + | + | + | + |
| <i>Tympanis</i> | | + | + | + | + | + | + | + | |
| RHYTISMATALES | | | | | | | | | |
| <i>Ascodichaena</i> | + | + | | | + | + | + | + | + |
| <i>Cerion</i> | + | | | | + | | + | + | |
| <i>Coccomyces</i> | + | + | | + | + | + | + | + | |
| <i>Colpoma</i> | + | + | | | + | + | + | + | |
| <i>Discocainia</i> | + | + | + | | + | + | + | + | |
| <i>Odontotremopsis</i> | + | + | | | + | | + | + | |
| <i>Therrya</i> | + | + | + | | + | | + | + | |

Orbilina is missing

Y +

| Genus | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 |
|------------------------|---|---|---|---|---|---|---|---|---|----|----|----|----|----|----|----|----|----|----|----|
| OSTROPALES | | | | | | | | | | | | | | | | | | | | |
| <i>Conotrema</i> | | + | + | | + | | + | ± | | + | | ± | | + | | | | + | | + |
| <i>Cryptodiscus</i> | | + | | | + | | | | | | | | | + | | | | + | | + |
| <i>Odontotrema</i> | | ± | ± | | + | | ± | + | | | | | | ± | | | | + | | + |
| <i>Odontura</i> | | ± | | | + | | ± | + | | | | | | | | | | + | | + |
| <i>Ostropa</i> | + | | | | + | | | | + | | | | | | | | | + | | |
| <i>Pseudographis</i> | + | | | | + | | | | | | | | | | | | | ? | | + |
| <i>Robergea</i> | + | | | | + | | | | + | | | | | | | | | | | + |
| <i>Schizoxylon</i> | | | + | | ± | | ± | + | | + | | | | ± | | | | + | | + |
| <i>Stictis</i> | | | + | | ± | | ± | + | | + | | | | ± | | | | + | | + |
| <i>Tryblidium</i> | | + | | | + | | | | | + | | | | ? | | | | ? | | + |
| <i>Xerotrema</i> | | + | | | + | | | | | + | | | | + | | | | + | | + |
| GRAPHIDALES | | | | | | | | | | | | | | | | | | | | |
| <i>Leptotrema</i> | | | + | | | | | | | | | | | | | | | + | | + |
| <i>Thelotrema</i> | | | + | | | | | | | | | | | | | | | + | | + |
| LECANORALES | | | | | | | | | | | | | | | | | | | | |
| <i>Agyrium</i> | | | | | | | | | | | | | | | | | | + | | + |
| <i>Dactylospora</i> | | | | | + | | | | | | | | | | | | | ± | | + |
| <i>Sarea</i> | | | | | ± | | | | | | | | | | | | | + | | + |
| HYSTERIALES | | | | | | | | | | | | | | | | | | | | |
| <i>Bactrospora</i> | | | | | + | | | | | + | | | | | | | | + | | + |
| <i>Eutryblidiella</i> | | | | | + | | | | | | | | | ± | | | | + | | + |
| <i>Lecanidion</i> | | | | | + | | | | | | | | | | | | | + | | + |
| <i>Tryblidaria</i> | | | | | + | | | | | | | | | | | | | + | | + |
| ORDER UNCERTAIN | | | | | | | | | | | | | | | | | | | | |
| <i>Karstenia</i> | | | | | | | | | | ± | | | | | | | | ? | | ± |
| <i>Melittosporium</i> | + | + | | | + | | | | | | | | | | | | | ? | | + |
| <i>Propolomyces</i> | | + | | | | | | | | ± | | | | | | | | ? | | ± |
| <i>Winteria</i> | | | | | + | | | | | | | | | | | | | + | | + |
| <i>Xylopezia</i> | | | | | + | | | | | | | | | | | | | + | | ± |

⊕
anamorph of Propolis?

Pezizales (operculate discomycetes) or Helotiales (inoperculate discomycetes). None of the Pezizales occurs on standing dead bark or weathered lignum, but the Helotiales includes a number of genera which produce ascomata on relatively dry bark and lignum; to some extent these latter exhibit similar morphological adaptations found in other groups which occupy the same habitat. Groves (1952, 1965) published reliable monographs of *Tympanis* and *Godronia* and also on several other similar Helotiales. Ouelette & Korf (1979) provide detailed information on *Claussenomyces*.

The Hypodermataceae is a large family of immersed discomycetes, usually assigned with the Phacidiaceae to the Phacidiales, but probably best placed in a separate order, the Rhytismatales, as was proposed by Barr (1976). The general accounts of the Hypodermataceae of Darker (1932, 1967) provide a good introduction to the family, although his emphasis is on foliicolous species. Reid & Cain (1961) give a thorough account of *Therrya* Sacc., Reid & Funk (1966) of *Discocainia* and Sherwood (1980) of *Coccomyces*. The Stictidaceae (Ostropales) has been the subject of a recent critical revision (Sherwood, 1977a, b). Schmidt (1970) and Tibell (e.g. 1975) have published important accounts of members of the Caliciales. Comments on the Odontotremataceae and Tryblidiaceae included below are based on my own, so far unpublished, observations.

THE CHARACTERS

The characters in Table 1 are listed in a more or less increasing order of significance as viewed by modern taxonomists; all are used by reputable taxonomists at or above the generic level. Each character is analyzed and its possible adaptive significance discussed here. In view of the arbitrary selection of genera and the gaps in the data set, it is fruitless to analyze the information statistically, but a general pattern of lack of correlation of secondary characters with those considered to be of primary significance in classification can be noted.

Ascomata, immersed or partially erumpent with a mechanism for opening and closing in response to changes in hydration

A large proportion of corticolous and lignicolous discomycetes have reviving ascomata in which the hymenium is covered by marginal or stromatic tissue except when conditions are favourable for ascospore discharge. This character is most prevalent in the Hypodermataceae, but occurs in other families as well. The mechanism is the same in all cases, functioning like the bimetallic conductor of a thermostat. The hymenium remains covered by a layer of fungal tissue until late in development, when it opens either by splitting the overlying tissue radially or longitudinally (Hypodermataceae, Tryblidiaceae, *Karstenia*) or by a circular pore (Stictidaceae, Odontotremataceae). The inner portion of the margin or covering layer consists of gelatinous tissue which may be either hyphal or pseudoparenchymatous and which swells markedly on rehydration; the outer layer consists of non-gelatinous fungal tissue or host tissue and does not swell when wetted. Consequently, upon rehydration the triangular flaps of *Coccomyces*-like ascomata curl backwards and the torus in the orifice of *Stictis*-like ascocarps swells and stretches the opening. The hymenium is thereby protected unless the asci are mature and conditions are favourable for ascospore discharge. The process is not dependent

on physiological activity as it can be observed even in old herbarium specimens. Since ascospore discharge is also at least partly a mechanical process these fungi can discharge spores at short notice after long periods of dormancy—an advantage in arid, unpredictable habitat.

Ascomata black with a covering layer, dark epithecium, or both

Orbilia not

With the exception of the tropical genus *Cerion*, with a brilliant red hymenium, the lignicolous discomycetes found on dry wood are almost all dark coloured and look very much alike to the unaided eye. The dark pigmentation probably serves as a shield against strong light, particularly in species with an epithecium, but this is not necessarily its primary function. Many are winter-fruiting and grow in areas (such as the Rocky Mountains) where winter temperatures rarely exceed freezing; the black coloration could conceivably be an adaptation for warming ascomata quickly during a brief winter thaw.

In the Stictidaceae, the degree of epithecium development is correlated with the degree to which the hymenium is exposed. In the perithecioid genera *Ostropa* and *Robergea* the paraphyses are colourless and undifferentiated, whereas in the apothecioid genus *Schizoxylon* Pers. ex Fr. the paraphyses are apically branched, pigmented and form a prominent epithecium. In the intermediate genus *Stictis*, the species with a pigmented epithecium tend to be those with relatively discoid, erumpent ascocarps and those which grow in exposed habitats.

Presence of gel in marginal tissues and/or hymenium

Gelatinous tissues are common in fungi with persistent fruitbodies exposed to alternate wetting and drying, notably the Tremellales. Ingold (1959) suggested that water stored in gelatinous tissues functions as a reservoir which maintains metabolic activity and allows spore discharge even after the surrounding environment has become depleted of water, at least in *Bulgaria inquinans* Fr. (*Phaeobulgaria inquinans* (Fr.) Nannf.). It may also be significant that many winter-fruiting fungi are gelatinous. A fruitbody whose structure is determined by extracellular colloidal material is less likely to be disrupted by freezing than one whose structure is determined by the turgor of precisely orientated cells.

The hymenial gel in the Lecanorales and Ostropales commonly, although not invariably, turns blue in iodine due to the presence of unidentified soluble polysaccharides. As both orders produce persistent fruitbodies in exposed habitats it is not surprising that they have also evolved a gelatinous hymenium; compounds that produce blue colours with iodine are so widespread in nature that their co-occurrence in these two groups cannot on its own be considered evidence for any relationship between them. The amyloid reaction of the hymenium of the Ostropales may merely emphasize their lichen-like ecology.

Mycelium and spores with very small cells

Orbilia not

The size of ascomycete cells varies over six orders of magnitude, from a volume of slightly less than $1 \mu\text{m}^3$ in some spermatia to globose cells in the excipular tissue of Pezizales which occasionally reach $100 \mu\text{m}$ diameter (and therefore a volume exceeding $100\,000 \mu\text{m}^3$) and few very large lichen spores. Hyphae more

than 10 μm diameter, however, are usually restricted to reproductive structures, either ascomata or conidiomata. The minute size of spermatia is not too surprising, since they need contain little more than a nucleus. The minute size of the cells of vegetative hyphae, excipular structures, and ascospores in some lignicolous discomycetes, particularly the Stictidaceae, sometimes seems to violate the theoretical limit for a eukaryotic cell. Given small nuclei, small mitochondria, and other small organelles it is just possible to construct eukaryotic mycelium of units 1 μm broad and 0.85 μm long, but such extreme compartmentalization and lack of cytoplasm must impose severe limits on the transport of materials between cells. It is also theoretically possible in an ascomycete, where the cytoplasm is continuous through septal pores, to have viable cells without the full complement of organelles. Unfortunately nothing is known of either the cytology or the ultrastructure of the Stictidaceae. Manton (1959) has demonstrated a full complement of organelles, including a chloroplast, in an alga with cells only 1–1.5 μm diam.

The hyphal diameters of lignicolous discomycetes are almost all in the range 1–4 μm . The disadvantages of having very narrow assimilative hyphae include the large amount of wall material which must be synthesized per unit active cytoplasm and a slow rate of transfer of cell components down the hyphae, since resistance to flow is necessarily directly proportional to the radius of a cylinder, while the flow itself is proportional to the square of the radius.

There is, however, at least one possible physical explanation why narrow hyphae would be advantageous in a dry or exposed environment. The mechanical strength of a cylinder is a function of the strength of its walls, the number of cross partitions and the square of its radius. Both Oomycetes which grow in water and members of the Pezizales which occur on water-soaked logs, produce coarse, thin-walled vegetative hyphae and a large, thick-walled propagule able to survive unfavourable periods. Fungi of mesic situations, especially Hymenomycetes, produce hyphae of average diameter and medium-sized propagules which are also differentiated to survive unfavourable periods, but not so sharply as those of aquatic and semi-aquatic fungi. Non-ephemeral fungi which grow in normally arid habitats have narrow hyphae and propagules made up of small units which may, however, form large spores. This generalization has many exceptions and merits more investigation, but is both supported by many observations and theoretically reasonable.

Mycelium subject to arid and freezing conditions needs to be structurally strong or it will collapse and become non-viable; a narrow diameter is one way of achieving this end.

Unusual ascospore characters

Filiform spores: Filiform ascospores, threadlike spores with a length/width ratio greater than 20:1, are particularly prevalent in the Stictidaceae. There is no sharp demarcation between long-cylindrical or acicular and filiform spores. Many Helotiales, Sphaeriales and Pleosporales have long, multiseptate ascospores, especially in the tropics, but there are relatively few genera of ascomycetes which have ascospores with a length substantially greater than 20 times their width, and these are confined to a very few families. Since it is probable that discharge of an ascospore much longer than 90 μm is difficult, the advantage to *Robergea*

cubicularis (Fr.) Rehm of producing ascospores $2000 \times 2 \mu\text{m}$, and why this and two other species of *Robergea* Desm. have ascospores four times as long as any other known ascomycete, remain obscure.

Part of the answer may be a need to impact on a substrate of narrow diameter, so narrow, in fact, that the *Robergea* ascomata must grow with their hymenium orientated lengthwise on the twig or grass blade because the fruit body is completely immersed and the spores are longer than the diameter of the part of the host on which it occurs. However, it is easy to envisage that filiform ascospores, especially those of the Hypodermataceae which have a gelatinous sheath, are well designed for sticking to plant surfaces, including leaves as well as twigs.

Interestingly, looking beyond the lignicolous discomycetes for ascomycetes with very long ascospores, the extreme for lichenized fungi, *Bacidia marginalis* (Vainio) R. Sant. ($320\text{--}510 \times 2\text{--}2.5 \mu\text{m}$; Santesson, 1952), is foliicolous, and that for loculoascomycetes, *Glyphium elatum* (Grev.) Zogg ($160\text{--}400 \times 1.5\text{--}3 \mu\text{m}$) often grows in association with *Stictis radiata* Pers. ex Gray.

Large ascospores: A complex of factors governs the maximum size of ascospores, different combinations of them resulting in different maxima for different groups. Few ascomycetes with annelate, inoperculate asci produce spores much broader than $10 \mu\text{m}$, making those of an undescribed corticolous species of *Therrya* ($98 \times 8 \mu\text{m}$) large for this group. The structure of operculate asci, with a lid instead of a pore plug, makes the passage of larger ascospores possible. In the Pezizales the next limiting factor appears to be either the structural instability of large unicellular ascospores, which can only partially be overcome by thickening the wall, the limited time available for maturation of an ephemeral fruitbody, or the energetics of the ascus jet mechanism itself. The maximum size for non-hypogeous Pezizales, c. $60 \times 30 \mu\text{m}$, is also the maximum size for large muriform spores in both the Pleosporales and Tryblidiaceae. The addition of transverse and longitudinal septa increases the structural stability of the spore and eliminates the need for a very thick wall. Comparing the Pezizales and Pleosporales, the similar limit in spore size, despite a different ascus discharge mechanism and ascospore architecture, suggests that larger ascospores present difficulties to the active spore discharge mechanism itself. With one exception, all known very large ($>60 \times 30 \mu\text{m}$) ascospores occur in lichenized fungi (especially prevalent in the Thelotremataceae), with some approaching this size in lichenicolous fungi (e.g. *Norrlinia peltigericola* (Nyl.) Theiss. & H. Sydow), all characteristic of xeric habitats. The only known exception is *Xerotrema megalospora* Sherw. & Coppins, a recently recognized rare inhabitant of dry wood, which has muriform ascospores $90\text{--}170 \times 22\text{--}40 \mu\text{m}$ in one-spored asci. There is, as might be expected, a negative correlation between ascospore size and the number per ascus in most ascomycetes.

The production of large propagules increases the chance of survival of individual propagules but decreases clutch size. The effective clutch size of *Xerotrema* may be as low as 20 or 30 ascospores per generation, a peculiar reproductive strategy for a fungus. The genetics of this species must also be unusual as all eight nuclei seem to be enclosed in the developing ascospore membrane so the resultant mycelium must always be heterokaryotic. This fungus has been found growing with *Melittosporium propolidioides* (Rehm) Rehm, which also has muriform spores in one-spored asci. Four-spored asci occur in some species of *Tryblidium* Rehm. ex Wallr. and *Eutryblidiella* (Rehm) Höhnelt; perhaps heterokaryosis is advantageous in the environment on hard lignum.

Muriform spores: All known muriform-spored, non-lichenized discomycetes occur on bark, dry lignum, or resin. In the case of *Claussenomyces*, the species which grow on damp well-rotted wood are not muriform-spored. Large compartmentalized spores are clearly advantageous in a harsh environment where the large number of cells both increases mechanical strength and makes it possible for some cells to survive if a spore is damaged; large size also increases impaction efficiency and the amount of mycelium that can be produced in the absence of a fresh nutrient source. It is not clear, however, why non-lichenized discomycetes fail to produce muriform-spored taxa in other habitats. The same contrast exists in (at least the British) Pleosporaceae; here the large-spored species that occur on standing dead herbaceous debris and dead limbs of trees have muriform spores, whereas the dung-inhabiting taxa generally have only transversely septate spores with large cells.

Anamorphs

Knowledge of the anamorphs (imperfect states) of lignicolous discomycetes is still very meagre. Corticolous Helotiales (e.g. *Tympanis*), some of which are parasitic, tend to have a pycnidial phase in their life cycle and to produce relatively large phialoconidia which are able to reproduce the fungus under natural conditions. The Hypodermataceae typically produce leptostromaceous pycnidia with minute holoblastic conidia which probably merely function as spermatia. Pycnidia are more commonly produced by foliicolous than by lignicolous Hypodermataceae. Anamorphs (other than ascoconidia) are rare in the Ostropales and unknown in most other genera of discomycetes known on hard lignum.

Anamorphs are particularly prominent in the life cycles of parasitic fungi, and others which colonize ephemeral substrates. It is reasonable to suppose that the environment of weathered lignum, where competition is low and the substrate stable over long periods of time, does not exert strong selective pressures favouring rapid dispersal and colonization by means of asexual propagules. The apparent absence of anamorphs in most lignicolous discomycetes, although undoubtedly biased by inadequate data, is evidently a real phenomenon with an ecological basis.

Asci with a number of mature spores other than eight

In ascomycetes the characteristic number of spores to be formed in each ascus is eight. Numbers fewer than eight result either from ascospore abortion (most often seen in the subterranean Pezizales, lichens and some lichenicolous fungi) or from initial delimitation of fewer than eight spores, in which case those produced are generally multinucleate. Polyspory may arise either through the initial delimitation of more than eight spores following multiple mitotic division, fragmentation of an original eight multiseptate ascospores, or the production of ascoconidia from primary ascospores.

Ascospore numbers other than eight are particularly prevalent in lignicolous discomycetes, and departures from this norm occur by almost all the mechanisms listed above. Selection has acted to produce discomycetes with very many minute spores per ascus in the Hypodermataceae (*Discocainia*), Stictidaceae, and

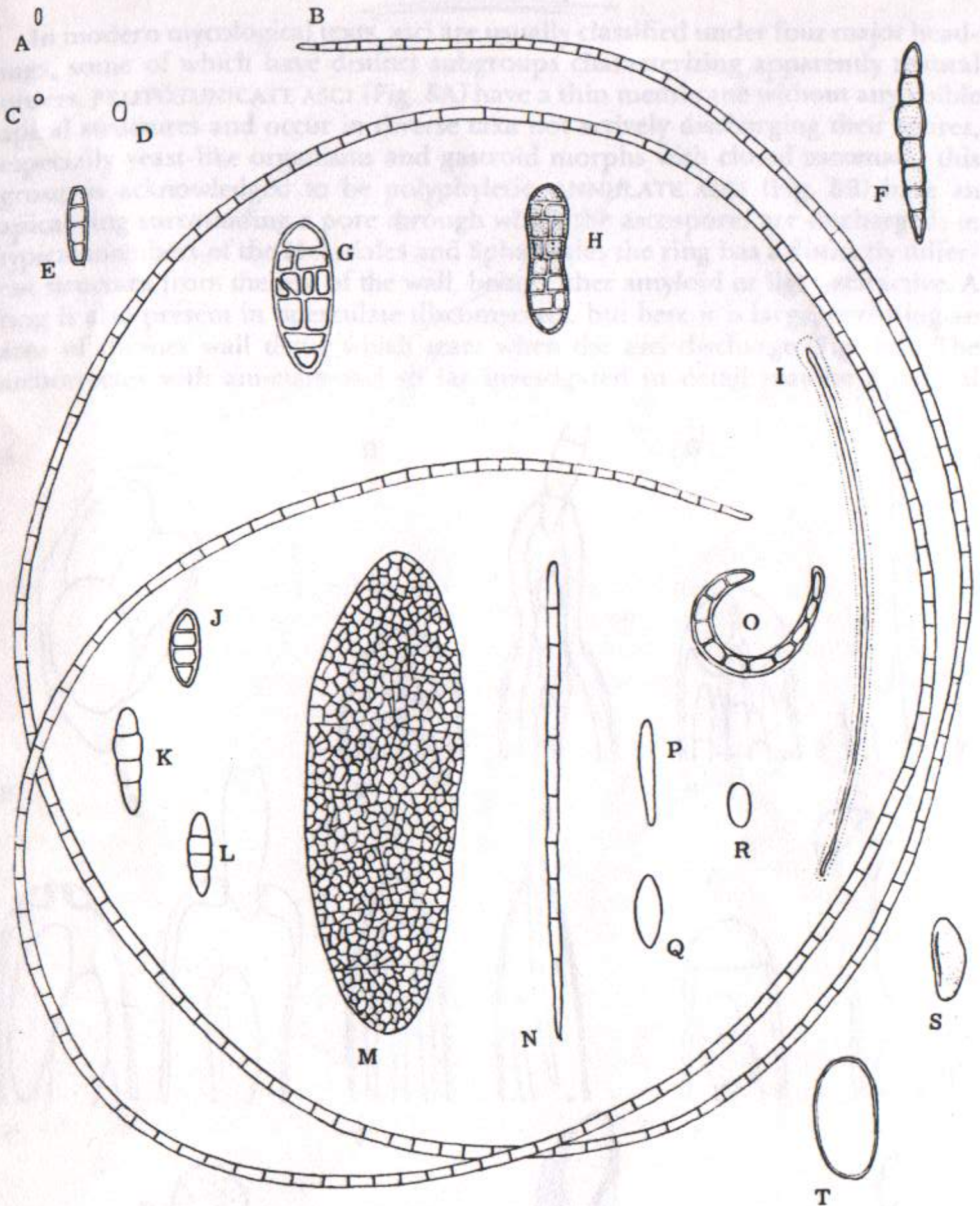


Figure 7. Ascospores, part-spores, and ascoconidia of representative ascomycetes. Starred genera are lignicolous or corticolous. A. *Tromeropsis microtheca* (P. Karsten) Sherw.*. B. *Robergea cubicularis* (Fr.) Rehm*. C. *Acarospina monilifera* (Ell. & Ev.) Sherw.*, part-spore. D. *Schizoxylon sepincola* Pers.*, part-spore. E. *Schizoxylon microstomum* Ell. & Ev.*, part-spore. F. *Leptosphaeria agnita* (Desm.) Ces. & de Not. G. *Pseudographis elatina* (Ach.) Nyl.*. H. *Melittosporium propolidioides* (Rehm) Rehm*. I. *Coccomyces leptosporus* Speg. J. *Odontotrema minus* Nyl.*. K. *Xylopezia hemisphaerica* (Fr.) Höhnelt*. L. *Cryptodiscus pallidus* (Pers.) Corda*. M. *Xerotrema megalospora* Sherw. & Coppins*. N. *Godronia uberiformis* Groves*. O. *Stictis sagaretiae* Cash. P. *Hymenoscyphus pileatus* (P. Karsten) Kunze. Q. *Rutstroemia luteovirescens* (Rob.) White. R. *Trochila craterium* (DC.) Fr. S. *Daldinia concentrica* (Bolt. ex Fr.) Ces. & de Not.*. T. *Lasiobolus ciliatus* (Schm. ex Fr.) Boud., x 1000.

Helotiales (*Claussenomyces*). Interestingly, all three discomycetes which commonly occur on conifer resin have polysporous asci (Hawksworth & Sherwood, 1981). Polyspored asci also occur in some lichen-forming Lecanorales on dry lignum (e.g. *Biatorella* de Not., *Strangospora* Massal.) and rock (e.g. *Acarospora* Massal.) as well as some lichenicolous fungi (e.g. *Muellerella* Hepp ex Müll. Arg.), all taxa of xeric habitats.

The unispored asci of *Melittosporium* and *Xerotrema* have already been mentioned.

Polyspory increases the number of propagules resulting from one meiotic division, while production of fewer than eight increases maximum potential spore size. Both have some adaptive value, but this being so one might well question why ascomycetes which occur in mesic environments on the forest floor so commonly have eight spored asci. A clue to the reason for this may well lie in the ascus structure of members of the lignicolous community, which is often similarly anomalous (see below).

Unusual ascomatal types

The sequence of development and differentiation of sterile and fertile elements in the fruitbody is one of the major criteria used in current ascomycete taxonomy. Most modern systems recognize two subclasses, the Loculoascomycetidae and Euascomycetidae. In Loculoascomycetidae sterile elements of the ascomata (margin and interascal tissues) are at least partially differentiated before the production and fertilization of ascogonia (if any) and are therefore regarded as having a vegetative, stromatic origin. In the Euascomycetidae the margin and interascal filaments of the ascomata all develop from cells supporting the ascogonium after it has been fertilized. Accurate developmental studies are lacking in most groups of ascomycetes, and in practice ascus structure rather than developmental criteria has been used to separate the Loculoascomycetidae (bitunicate asci) from the Euascomycetidae (unitunicate asci). Nonetheless, it is clear that the majority of ascomycetes with annellate asci have a structure indicative of ascohymenial ontogeny while the majority with bitunicate asci have the structure expected from an ascolocular developmental sequence.

Several exceptions to this rule are found amongst the lignicolous discomycetes, with the best known examples in the Hypodermataceae. There is no complete consensus on the sequences of development in this family, but the available evidence (see Morgan-Jones & Hulton, 1979) suggests that ascogonia are not produced at all, the ascogenous hyphae arising from laterally conjugating paraphyses. This development consequently might be interpreted as ascolocular rather than ascohymenial, but the asci in this family are certainly not functionally bitunicate. In *Xylopezia* Höhnelt and *Winteria* Rehm, the interthelial filaments are attached both above and below, as are the pseudoparaphyses of loculoascomycetes, but again the asci do not appear to be functionally bitunicate.

The transition between apothecia and perithecia, well illustrated by the Stictidaceae, presents no serious problem since the developmental sequence is fundamentally the same. It is conceivable that critical comparisons of other pyrenomycetes and discomycetes which have similar ascus and ascospore characteristics and occur in similar habitats could reveal other assemblages intermediate between the classic divisions 'Pyrenomycetes' and 'Discomycetes'.

Unusual ascus types

In modern mycological texts, asci are usually classified under four major headings, some of which have distinct subgroups characterizing apparently natural orders. PROTOTUNICATE ASCI (Fig. 8A) have a thin membrane without any visible apical structures and occur in diverse taxa not actively discharging their spores, especially yeast-like organisms and gastroid morphs with closed ascomata; this group is acknowledged to be polyphyletic. ANNULATE ASCI (Fig. 8B) have an apical ring surrounding a pore through which the ascospores are discharged; in typical members of the Helotiales and Sphaeriales the ring has a distinctly different structure from the rest of the wall, being either amyloid or light-refractive. A ring is also present in operculate discomycetes, but here it is large, enclosing an area of thinner wall tissue which tears when the asci discharge (Fig. 8C). The ascomycetes with annelate asci so far investigated in detail may be a natural

here
Pezizales
&
Godwinia
(Tab. 1)

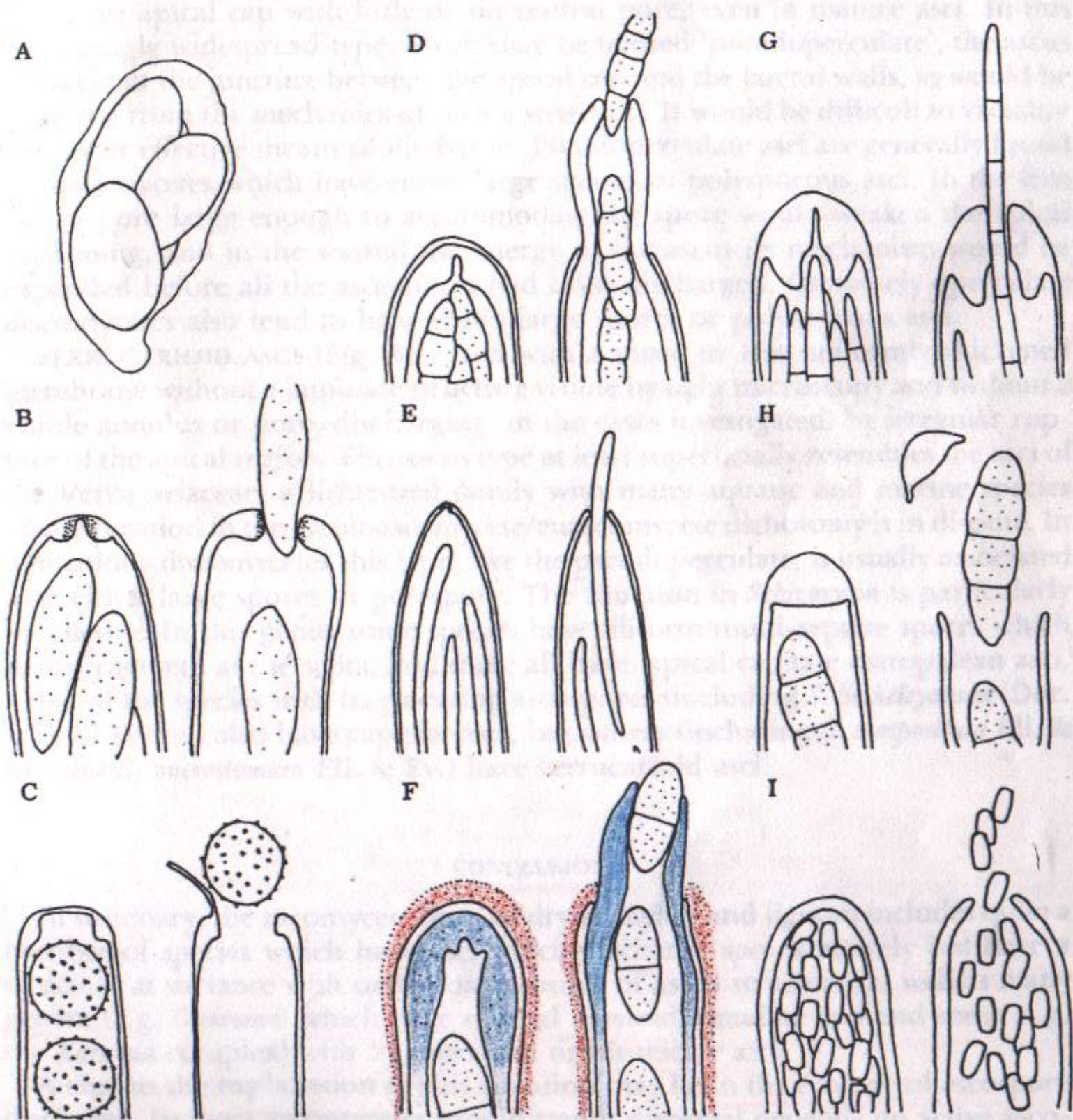


Figure 8. Structure of asci. A. Prototunicate. B. Annelate (Helotiales). C. Operculate (Pezizales). D. Bitunicate (Loculoascomycetidae). E. Hypodermataceous. F. Lecanoralean. G. Ostropalean. H. Pseudoperculate (*Odontotrema*). I. Verrucarioid (*Schizoxylon*).

group. FUNCTIONALLY BITUNICATE ASCI (Fig. 8D) have a thin, inelastic outer wall and a separable, thicker, extensible inner wall; at discharge the outer wall ruptures and the inner wall, or part of it, elongates through the rupture, the ascospores being discharged through an apical pore. Those ascomycetes which have unequivocally been demonstrated to have bitunicate asci seem to form a natural group, but there is often considerable difficulty in demonstrating whether asci are bitunicate, especially in dried material, and the status of many genera (e.g. *Acrospermum* Tode ex Fr.) provisionally assigned to the Loculoascomycetidae is quite uncertain. LECANORALEAN ASCI (Fig. 8F) of the mainly lichenized Lecanorales have thick-walled, amyloid asci and multiple wall layers visible by light microscopy in appropriate stains; these discharge apically by means of a short 'arrested-bitunicate' extension of the inner wall layers. The range of variation in ascus structure in the Lecanorales is considerably greater than in those ascomycetes with annelate asci, which is not surprising since this is the largest group within the ascomycetes and that there are good grounds for considering them the oldest surviving successful group of higher fungi. Taken in the modern lichenological sense (Henssen & Jahns, 1974), the Lecanorales are probably a natural group but one which deserves the same taxonomic rank as the Loculoascomycetes and subdivision into at least three orders.

The above discussion omits most of the details of ascus ultrastructure which have been reported in recent years, and also the controversy surrounding differences in terminology and interpretation between different schools of ascomycete systematics. It is intended only to summarize the least controversial aspects of ascus structure, and is compatible with the best documented studies in this area.

The majority of ascomycetes studied can be referred to one of the above four categories. However, there are numerous exceptions which are difficult to interpret, most of them found among epiphytic and particularly foliicolous lichens, lichenicolous fungi or fungi which grow on living or dead aerial plant parts. There are five additional types of asci which occur in lignicolous Discomycetes. These are considered below in increasing order of disparity from conventional ascus types.

HYPODERMATACEOUS ASCI (Fig. 8E): These are very thin-walled, and have an annulus which is either not demonstratable by light microscopy or is minute, inamyloid, and non-refractive. The ascospores are actively discharged. Viewed by light microscopy the asci appear to have a simple structure, with little or no trace of an apical annulus. They resemble asci of the Polystigmataceae, a family of stromatic pyrenomycetes colonizing similar habitats. Asci of the Hypodermataceae could be viewed as a poorly-differentiated type within the annelate series, but considering that they or the ascogenous hyphae have been demonstrated to develop from basal cells of the paraphyses rather than from an ascogonium (Morgan-Jones & Hulton, 1979), and that the anamorphs are distinctive and unlike those of the Helotiales, the possibility must be entertained that members of the Hypodermataceae are not 'inoperculate discomycetes' in any but the most superficial sense of the term.

The asci of *Ascodichaena rugosa* Butin, a common but taxonomically isolated inhabitant of living fagaceous bark, may represent a modification of the hypodermataceous type. This fungus has large asci and large unicellular ascospores; ascus dehiscence appears to be by means of an operculum. *Ascodichaena* is certainly not an 'operculate discomycete' in the conventional sense. The presence of a

holoblastic, pycnidial anamorph, a stromatic ascocarp and apparent absence of ascogenous hyphae would support the contention that *Ascodichaena* is distantly related to the Hypodermataceae.

OSTROPALEAN ASCI (Fig. 8G): These asci have thin lateral walls and a thick, non-refractive apical cap with a slender central pore. Ostropalean asci have also been classified as a subgroup of the annelate type. There is a close association between cylindrical, capitate asci and filiform spores; these characters appear again in the Clavicipitaceae (which have a refractive apex) and in several genera of the Pleosporales. Considering the difficulty of finding any character other than a torus of ascus wall around a central pore which would connect the Stictidaceae with the Helotiales or Sphaeriales, it cannot be assumed that this group belongs to the annelate series. The asci of the Ostropales are often mistaken for bitunicate asci, even by experienced mycologists.

PSEUDOPERULATE ASCI (Fig. 8H): Asci with thin lateral walls and a thick, non refractive apical cap with little or no central pore, even in mature asci. In this surprisingly widespread type, which may be termed 'pseudoperulate', the ascus ruptures at the juncture between the apical cap and the lateral walls, as would be expected from the mechanics of such a structure. It would be difficult to visualize any other effective means of discharge. Pseudoperulate asci are generally found in discomycetes which have either large spores or polysporous asci. In the first case a pore large enough to accommodate the spore would weaken the apical thickening, and in the second the energy of the ascus jet mechanism would be expended before all the ascospores had been discharged. Genuinely operculate discomycetes also tend to have either large spores or polysporous asci.

VERRUCARIOID ASCI (Fig. 8I): Asci with a more or less uniformly thickened membrane without a laminate structure visible by light microscopy and without a visible annulus or pore, discharging (in the cases investigated) by irregular rupture of the apical region. This ascus type at least superficially resembles the asci of the Verrucariaceae, a lichenized family with many aquatic and marine species whose position in the loculoascomycete/euascomycete dichotomy is in dispute. In lignicolous discomycetes this type, like the pseudoperulate, is usually associated with either large spores or polyspory. The situation in *Schizoxylon* is particularly instructive. In this genus some species have filiform multi-septate spores which never fragment at the septa, and these all have typical capitate ostropalean asci. Some of the species with fragmenting ascospores (including *S. berkeleyanum* (Dur. & Lev.) Fuckel) also have capitate asci, but others (including *S. compositum* Ell. & Ev. and *S. microstomum* Ell. & Ev.) have verrucarioid asci.

CONCLUSIONS

In summary, the ascomycete flora of dry branches and lignum includes quite a number of species which have asci which discharge spores actively but have a structure at variance with orthodox accounts of ascus structure, as well as many genera (e.g. *Godronia*) which have normal amyloid annulate asci and some (e.g. the *Karschia* complex) with lecanoralean or bitunicate asci.

A clue to the explanation of this situation may lie in the ecology of ascospore discharge. In most ascomycetes long-distance dispersal depends on active ascospore discharge which ensures that the spores are liberated from the ascomata and penetrate through a boundary layer of still air surrounding the substrate into

the turbulent layers of air above. In most discomycetes the ejection of spores from the ascomata is not a serious problem, but in pyrenomycetes, which have closed fruitbodies, there is a number of adaptations, including ascus types (both unitunicate and bitunicate) which elongate at discharge and also asci with diffluent stalks, to ensure that the tip of the ascus protrudes from the ostiole of the perithecium at spore discharge. An ascus without a well-defined apical apparatus would tend to discharge laterally which would be disadvantageous unless the ecology of the species favoured passive dispersal and a gastroid habit. In both unitunicate and bitunicate pyrenomycetes, there is consequently a marked division between annelate forms and gastroid (cleistothecial) plectomycete types in which active spore discharge no longer occurs.

Among the discomycetes, both Helotiales and Pezizales produce ascocarps predominantly in sheltered habitats or on large substrates and are thus faced with boundary-layer problems. Members of these orders also typically discharge ascospores over a short period of time, and as Buller (1934) has pointed out there is a need to orientate asci, paraphyses, and ascospore trajectories precisely in order to get 'puffing'. Thus, unitunicate discomycetes need a well-developed ascus discharge mechanism with a distinct pore in order to achieve the aim and distance necessary to propell ascospores through a layer of still air so that they can be dispersed; there is a strong selection pressure for certain combinations of ascospore number (usually eight), pore type and ascospore shape to produce an optimum trajectory.

A discomycete growing on a small twig attached to a tree has minimal boundary layer problems and little difficulty in releasing spores from the ascomata. If it fruits on the underside of a twig, dispersal can occur even if the ascus disintegrates and the spore simply falls out of the hymenium under gravitational pull. This may occur in some members of the Caliciaceae, at least those which occur in exposed situations. Tibell (personal communication) suspects that invertebrates also play a role in the dispersal of calicelean ascospores, although firm evidence is lacking. Perhaps the Caliciales should be viewed as a gastroid counterpart of the Helotiales!

(Still considered)

The remaining discomycetes discussed in this paper have not, as far as is known, lost all traces of an active spore discharge mechanism, but it is reasonable to assume that there has been no strong selection pressure for aim or long distance trajectories in ascospore discharge. Instead, selection has favoured optimum ascospore type, particularly either large, filiform, or numerous spores (in polysporous asci) and the asci have become modified to suit the spore, even if this does not allow a precise trajectory and barely releases the spores from the hymenium. Annuli in large-spored species lose their structure and become 'pseudoperculate' or 'verrucarioid'.

Loss of annuli

Another factor favouring the modification of asci in lignicolous discomycetes is the presence in nearly all of a dense palisade of paraphyses of pseudoparaphyses cemented in a gelatinous matrix, and also the fact that relatively few asci discharge at any one time. Even if the ascus bursts irregularly the spores can only be discharged outward. If the ascus disintegrates, lateral pressure exerted when the hymenial gel and paraphyses swell on rehydration may well force spores, especially large ones, out of the hymenium to be dispersed by gravity, water splash, water trickles or invertebrates.

A consideration of ecological factors is a valuable aid to the understanding and



resolution of taxonomic problems posed by the varied assemblage of fungi inhabiting dry bark and lignum. It is reasonable to explain the non-annulate, inamyloid asci of *Tympanis*, which on the basis of its other characters seems to be a good member of the Helotiales, by regarding the ascus as a modified form suited to the discharge of the very numerous ascoconidia of this genus. It is possible that functionally bitunicate asci have also given rise, by modification, to the ascus types now found in *Xylopezia* and *Winteria*.

ascoconidia
occur only
in xerophytic
taxa and
always in
inamyloid
asci

Knowledge of both the ecology and taxonomy of lignicolous discomycetes is unfortunately still in a very incomplete state. However, the fungi which inhabit this ecological niche merit further study both from the ecological and the taxonomic points of view, as they provide striking examples of a complex of morphological adaptations to an extreme environment. Their study may also have parallel implications for the lichenized and lichenicolous fungi which also occupy xeric habitats, not least on dry lignum. However, as my main experience is with lignicolous discomycetes more detailed comparisons with these are better left to other authors.

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