

# The Ascomycota – Introduction and Glossary



*Gibellula pulchra*, a perithecial species parasitic on spiders from Thailand. The ascomata are the small yellow flask-like structures with darker tips to the left and below the centre of the colony. Conidia are formed from the powdery, paler yellow hyphae on the edge of the colony.

## Classification of the Kingdom Fungi

The true fungi contain species in four phyla (major divisions), the **Ascomycota**, **Basidiomycota**, **Chytridiomycota** and **Zygomycota**. Many true fungi produce both mitotic and meiotic spores, often from distinct fruiting structures which appear at different times and are associated with different symptoms. Structures producing mitotic spores (or conidia) are referred to as anamorphs, and those producing meiotic spores (ascospores, basidiospores etc.) as teleomorphs. For historical reasons, the different spore-bearing forms have frequently been given separate names. In many cases fungi are most prominent as anamorphs, and are traditionally referred to using their anamorph names. In some instances the sexual stage is not known: the fungus may have a purely mitotic life cycle, or the teleomorph may simply not have been recognized. Linkages between anamorphs and teleomorphs can be established using various methods (especially sequencing),

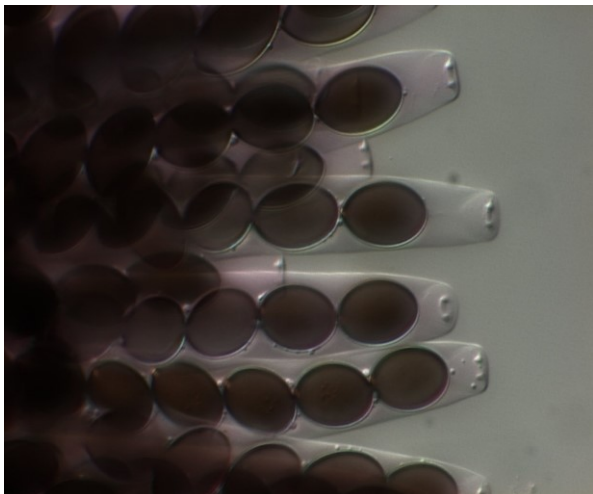
but many have still not been identified. Until recently, when the sexual morph is known the fungus as a whole should be referred to by the teleomorph name, but in applied mycology circles the anamorph name is frequently used even though the meiotic phase is known. The dual nomenclature system has now been formally abolished, but the system is in flux and in many cases the correct name is yet to be established under the new nomenclatural rules.

Species of *Ascomycota* probably constitute around 70% of all fungal species – between 2.5 and 3.8 million according to the latest estimate (Hawksworth & Lücking, [DOI](#)). The great majority of fungi of significance in environmental and industrial applications, including almost all potential contaminant species, belong to the *Ascomycota*. Species of *Ascomycota* are also the causal organisms of a very substantial proportion of economically important plant diseases. Species of the *Ascomycota* are also prominent as symbionts, especially as lichens but also mycorrhizal species and endobionts of plants.

Fungi (with the exception of yeasts) are filamentous organisms with their vegetative tissues composed of tube-like *hyphae*, usually with cross-walls (except in the *Zygomycota*) with pores through which water, nutrients etc. can pass. Hyphae are often branched and anastomosed, and collectively form a network known as the *mycelium*. This is often difficult to detect as it may be immersed within substrata, but becomes easier to observe in culture. Yeasts are fungi also, and collectively form a biological strategy group rather than a homogenous group in taxonomic terms. Environmentally significant species may have affinities with both ascomycetous and basidiomycetous fungi.

## Major groups of Ascomycota

The *Ascomycota* are immensely diverse in morphological and phylogenetic terms, and major taxonomic groupings are still regularly being discovered. The classification remains fluid but is becoming more stable as the result of many molecular phylogenetic studies. The focus in this document is on recognition of key morphological structures, and no attempt is made to encompass the extent of diversity within the group.

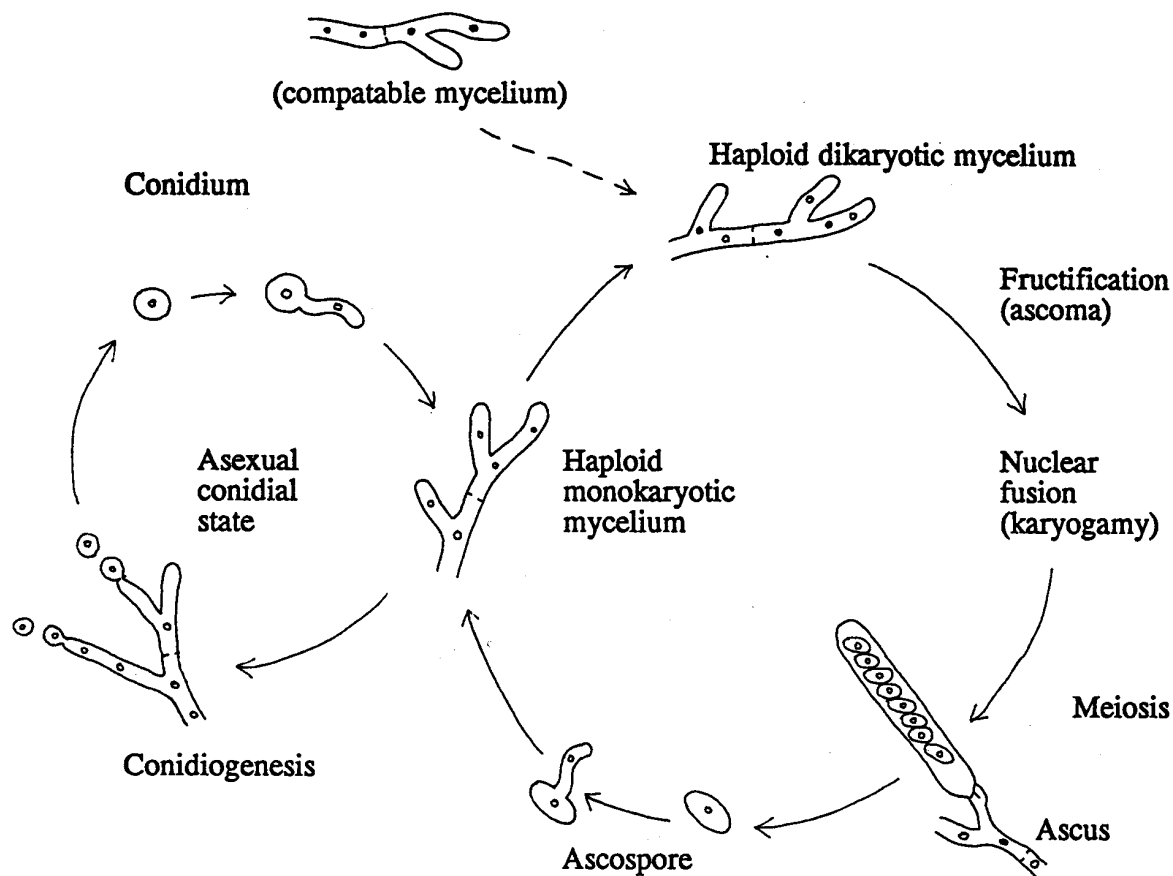


The ascospores (meiospores) of *Sordaria humana* are formed within cylindrical asci, specialized cells with a sophisticated opening mechanism enabling their discharge into the atmosphere.

The hyphae (where they occur) are septate and sexual propagation occurs by means of ascospores, uni- or multicellular spores produced

by free cell formation within specialized globose to cylindrical cells, the *asci* (singular: *ascus*). In most groups the asci are protected by a fruit-body called an *ascoma* (plural: *ascomata*). Ascomata are variable in form. Forms in which the asci are totally enclosed and in which the ascocarp has no special opening are termed *cleistothecia*. Cleistothecia are found in a number of ascomycete orders including the *Eurotiales* (the group to which *Aspergillus* and *Penicillium* belong) and the powdery mildews (*Erysiphales*). Cup-shaped ascocarps, which are called *apothecia*, have a mass of non-fertile hyphae supporting a layer of asci, which line the upper side of the fruit-body. These cup fungi belong to the groups *Pezizales* and *Helotiales* and to many groups of lichenized *Ascomycota*. With this arrangement of the asci, the fungus is free to discharge all of its spores at the same time. In other groups of ascomycetes, the asci are surrounded by a flask-shaped ascocarp with a narrow opening, the *ostiole*, through which the asci can discharge their spores, usually one at a time and sometimes explosively. These ascocarps are called either *perithecia* or *pseudothecia*. Perithecia are associated with the *Sordariales*, *Hypocreales* and some other orders (including the lichenized *Verrucariales*), whilst pseudothecia occur in the loculoascomycetous groups (especially the *Capnodiales* and *Pleosporales*). Whilst the ascomata of these two types may look alike, there is an important distinction, the internal cavity develops in a different fashion and interascal tissues (sterile hyphae accompanying the asci) are different in structure. In addition, the ascus wall is functionally single (unitunicate) in perithecial fungi, whilst in pseudothecia the ascus wall is functionally double (fissitunicate).

Although ascomycetous fungi are characterised by their meiotic state or teleomorph, they are often accompanied by asexual states (anamorphs) that produce spores by mitosis only. The majority of conidial fungi (also referred to as mitosporic fungi or fungi imperfecti) are part of the life cycles of the *Ascomycota* and are frequently found without their sexual morphs. For many the sexual morph is unknown (and may not even exist), and their classification is based on ultrastructure and overall morphological similarity to species with known ascomycetous morphs.



Typical life cycle of the Ascomycota

## Fungal vegetative structures

The normal condition of almost all fungi is as **vegetative mycelium**, the spore-bearing organs only being produced when reproduction is necessary. Ascomycete hyphae are usually regularly **septate**, and may vary markedly in diameter, pigmentation, and wall thickness. They may sometimes be warty, and are frequently covered in an envelope of mucous material. In almost all instances among the ascomycetes, the cytological condition of vegetative hyphae is **haploid**. In most cases, fusion of nuclei to produce dikaryons occurs only in special fertile hyphae, the **ascogenous cells**, in which the diploid nucleus almost immediately undergoes meiosis to produce ascospores, thus restoring the haploid state.

The wall structure of ascomycetous hyphae is relatively simple, consisting of an outer electron-dense and an inner electron-transparent layer. This contrasts with basidiomycetous cell walls, which are multi-layered. The components of cell walls which provide structural strength in most ascomycetes are **chitins**, although a few genera (notably *Ophiostoma* and *Cyttaria*, as well as

many ascomycetous yeasts) have walls composed largely of polysaccharides.

Ascomycete **septa** are in most cases **simple** in structure, in contrast to the complex dolipore septa found in many basidiomycetes. They have **simple pores** which are in some instances occluded by spherical or lens-shaped refractive structures termed **Woronin bodies**. Septa are discussed further in the section on hyphal growth and conidial development. Clamp connexions do not occur in the ascomycetes, which is not surprising considering the haploid condition of most vegetative hyphae.

Many parasitic fungi have specialized structures aiding penetration of their host, **appressoria**. These are usually produced almost directly from a hypha growing from the germinating spore, and are usually flattened and strongly pigmented.

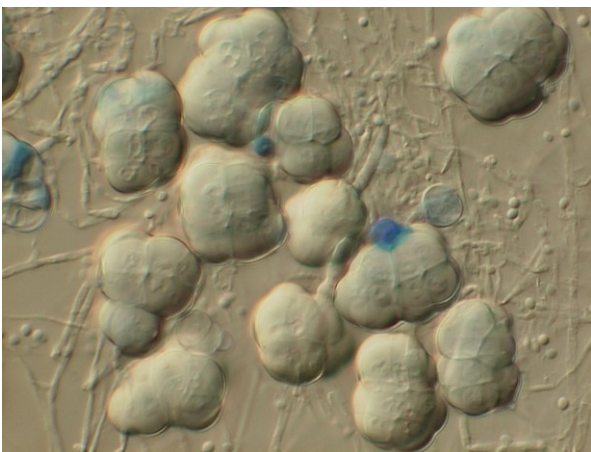
## SPORES: FORM AND FUNCTION

Spores in ascomycetous fungi may be produced simply by cell formation following mitosis, or after a meiotic division. Mitotic spores are in most instances termed **conidia** (singular **conidium**), while those formed after meiosis are referred to as **ascospores**.

There are three main functions of fungal spores; **dispersal**, **survival** and **genetic exchange**. Spores adapted for dispersal are often relatively small, thin-walled, not strongly pigmented, and simple in internal structure. Those adapted for survival are often large, thick-walled, strongly pigmented (to avoid the mutagenic effects of ultraviolet radiation), and many-celled. Dispersal- and survival-adapted spores may be produced sexually or asexually. Conidia adapted for survival purposes are often referred to as **resting-spores**, **chlamydospores** or **aleuriospores**. In some instances the resting structures may be many-celled, sometimes with more than one distinct cell layer. These are frequently overwintering organs, which germinate in the spring to produce mitotic or meiotic spores, which may or may not be contained in fruit-bodies. They are then called **sclerotia**.



*Oidiodendron reticulatum*, a fungus producing large numbers of small disseminative conidia



*Pochonia chlamydosporia*, a nematode-associated species that produces large thick-walled multicelled resting spores

Spores which perform the function of genetic exchange are referred to as **spermatia**. These are exclusively small and thin-walled. Fusion of gametes from the same or different genetic stock occurs when the spermatium comes into contact with fertile hyphae, referred to as **trichogynes**.

## Fungal reproductive structures

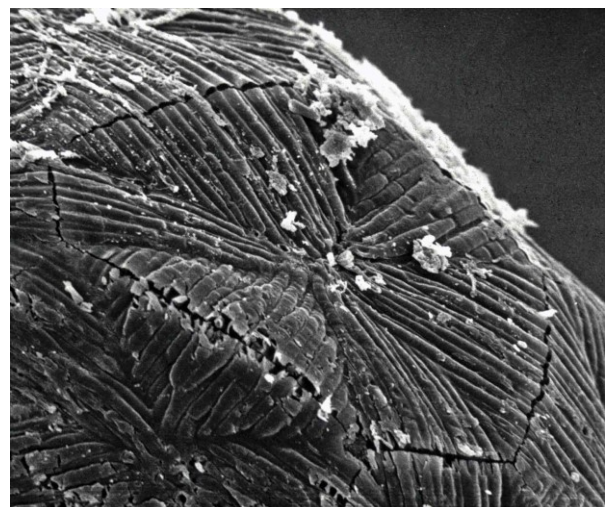
### Ascomata

#### CLEISTOTHECIA

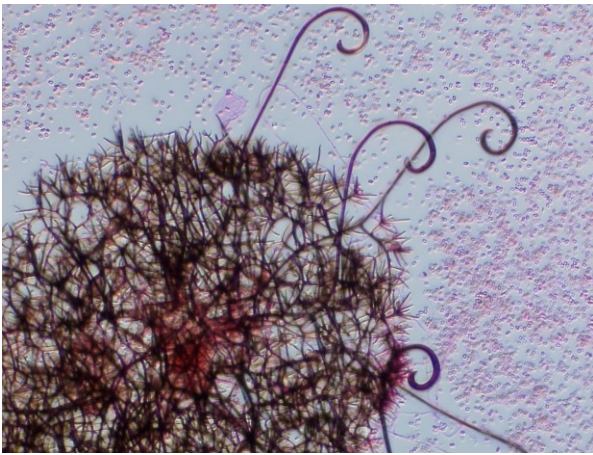
These are found in relatively few groups of *Ascomycota*; their walls need to break down to release spores which restricts their size and structural complexity. They are small, almost always globose and thin-walled, often with only two or three layers of cells enclosing the developing asci. They are almost always pale or brightly coloured, in contrast to perithecial and pseudothecial species that are mostly black due to the presence of melanin. They tend to be associated with strongly degraded plant tissues (rotten wood etc.) and can be dominant members of soil communities. In those circumstances they are rarely encountered except in culture.



*Monascus ruber*, a cleistothecial fungus used in the preparation of oriental foods, and also found as a contaminant in food products with high sugar or salt content.



In a very few species of cleistothecial fungi, the fruit-body is thick-walled, dark and rigid, breaking along predetermined fracture line to release the spores.



In *Myxotrichum chartarum*, the fruit-body wall consists only of a network of dark hyphae. The curved appendages probably have a dispersal function, the entire ascoma becoming attached to small animals etc.

### APOTHECIA

Apothecia are flat or cup-shaped fruit bodies with the asci exposed or covered only by a layer of gelatinous or crystalline material. They occur in a very wide range of clades, and are the most frequently encountered fruit body type in lichens. They are rarely melanized, but can be brightly coloured, often due to the presence of carotenoid or other pigments. In non-lichenized groups, they mostly develop rapidly in conditions suitable for spore discharge and do not persist for any length of time, but they may be long-lived and even perennial in some lichen groups. Here, the apothecia can be **lecanoroid** (surrounded by a margin composed of thallus tissue) or **lecideine** (where the marginal tissues are morphologically distinct from the thallus and do not contain the photobiont).



*Scutellinia* species (*Pezizales*) are common apothecial fungi usually associated with rotten wood or soil. The coloration is due to carotenoid pigments in the interascal tissue. In dry conditions the ascomata contract to protect the developing spores, and the spines surrounding the fruit-body may help to protect it from being eaten.



Members of the *Helotiales* tend to have small apothecia, and occur on less highly degraded plant tissues. *Hymenoscyphus fraxineus* develops on blackened petioles of *Fraxinus excelsior* – it is the causal agent of the devastating ash dieback disease.



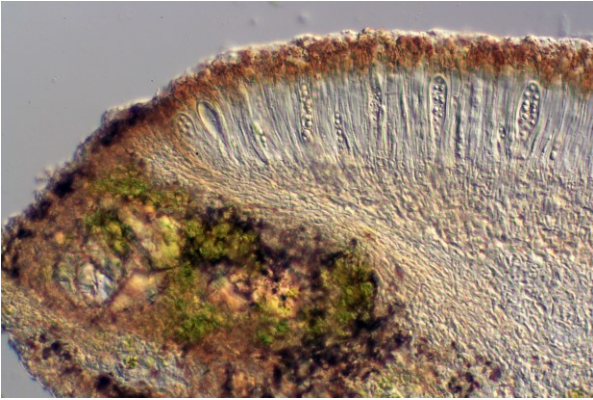
*Pannaria rubiginosa*, a cyanobacterial lichen with lecanorine apothecia. It is a typical component of wet hyper-oceanic woodland.



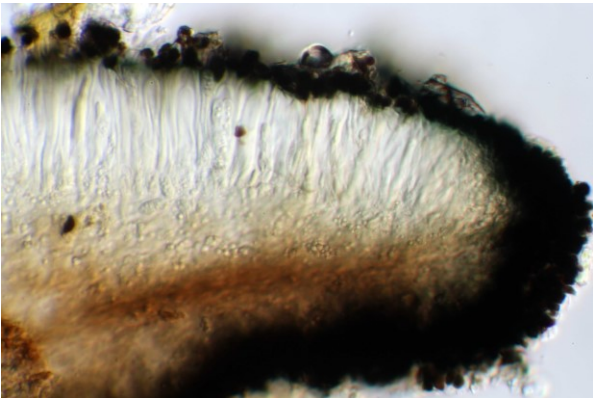
*Calogaya* aff. *saxicola*, growing on limestone in northern Greece. The brightly coloured apothecia in the centre of the thallus are lecanorine in structure, but the margin becomes excluded in older fruit-bodies.



*Mycoblastus sanguinarius*, a common lichen in northern latitudes with lecideine apothecia.



Vertical section through a lecanorine apothecium (the very common *Lecanora chlorotera*). The algal layer within the thalline margin can be seen in the left lower part of the image, and margin also contains large crystalline inclusions.



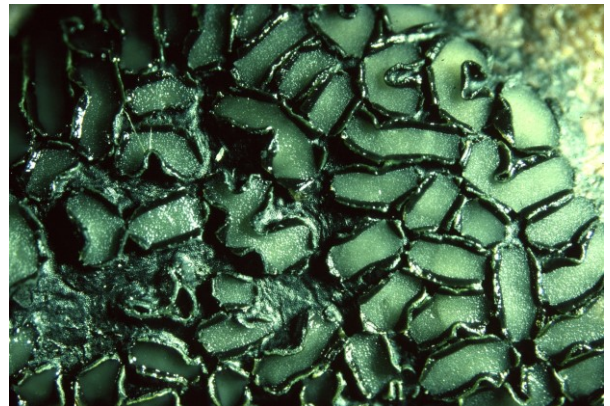
Another very common lichen is *Catillaria chalybeia*, here the apothecial margin and epithelial layer (above the developing asci) are strongly melanized and do not contain algae.

### IMMERSED AND ELONGATE APOTHECIA

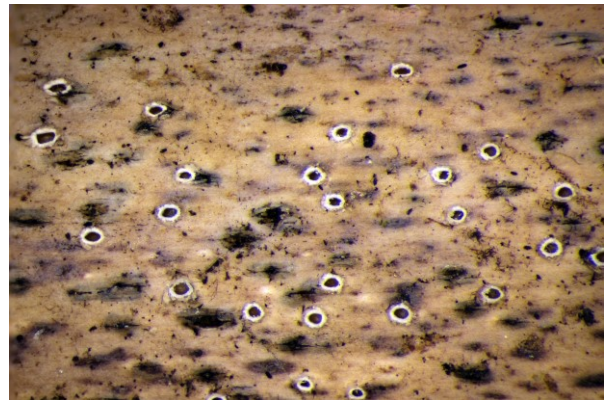
Fungi from a number of different phylogenetic clades have fruit-bodies that are apothecial in structure, but are immersed in plant tissues or lichen thalli. These may be round and open with radial or unorganized splits of the covering layer, or elongate and opening with a longitudinal split. the contents of the apothecium swell in the presence of water, pushing aside the covering layer to allow spore discharge. In conditions of drought, the covering layer protects against desiccation and also predation. The covering layer is usually strongly melanized. The split may be lined with specialized **lip cells** to aid in water retention. In lichens, such elongate apothecia are referred to as **lirellae** (singular **lirella**).



*Lirula nervisequia* is a weak pathogen of *Abies* species. It has elongate ascomata that often extend more or less the entire length of the plant leaf, with an extensive elongate split.



The very common species *Rhytisma acerinum* has compound ascomata (**stromata**) which open in wet conditions to allow spore release.



*Stictis stellata* has immersed apothecia which remain open, and rims with white crystalline deposits.



*Graphis scripta*, a very common lichen with white thalli and irregularly branched black apothecia (lirellae) that open with splits.



Species of *Umbilicaria* have leaf-like thalli with compound lrellate apothecia, which are frequently strongly contorted.

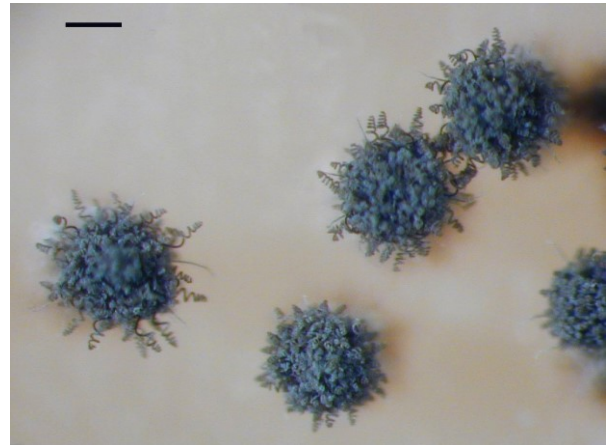
## PERITHECIA

Perithecial fungi have flask-shaped fruit-bodies with a small apical opening through which the spores are discharged. They are usually globose, but may have a papillate or elongate neck. In most cases the ascomata are strongly melanized (and therefore black), and thick-walled with a leathery or carbonized texture. There are both lichenized and non-lichenized perithecial fungi. The ascomata (perithecia) may develop on the substratum/thallus surface (and are therefore **superficial**), or within the substratum/thallus (and then termed **immersed**). They may develop initially within the substratum/thallus and then break through the surface tissues (then described as **erumpent**).

The ascomatal wall is commonly referred to as the **peridium** (or sometimes the **exciple** in lichenized species). It is frequently made up of multiple layers of cells, which may be different sizes and shapes, and may vary in pigmentation. The fruit-body wall may be smooth, roughened or covered in hairs or spines. The small hole at the apex of the fruit-body is termed an **ostiole**, and the internal wall in the ostiolar region is usually lined with upward-pointing hyphae (the **periphyses**). In most cases the asci and ascospores are formed in a cluster at the base of the perithecium, a region referred to as the **centrum**. In most cases asci elongate so that their apices enter the ostiolar region, releasing their spores directly into the atmosphere. In a small number of cases, the ascus walls break down within the fruit-body, or the ascus stalk degenerates so that asci are free within the perithecial cavity. In these circumstances spores ooze out of the ostiole like toothpaste from a tube.



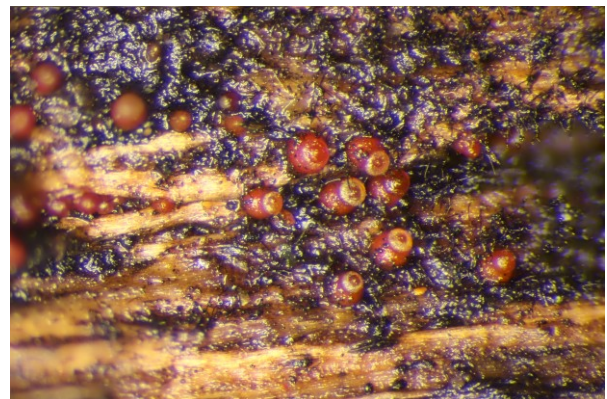
*Bertia moriformis*, a common saprobic species with very rough-walled superficial perithecia.



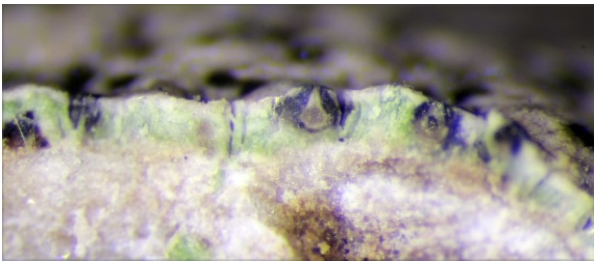
*Chaetomium robustum* growing in culture, a perithecial fungus with coiled hairs covering the peridium.



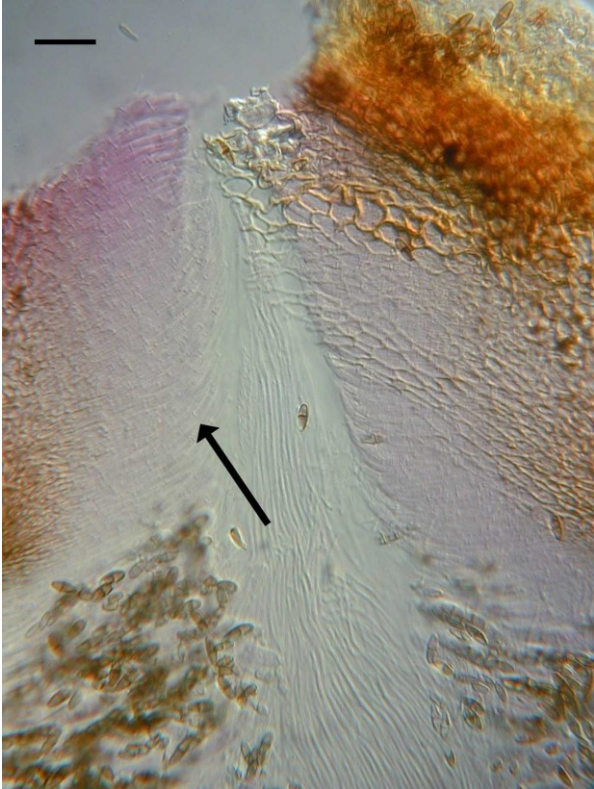
*Lasio-sphaeria ovina*, a quite common species on rotten wood. Here, the perithecia are covered in a mat of woolly hyphae, with only the region immediately surround the ostiole exposed.



*Cosmospora magnusiana* on rotten wood. This species has bright red perithecia with a paler ring around the ostiole.



*Verrucaria pinguicula*, a perithecial lichen with ascomata individually inserted in the thallus and surrounded by a black involucrellum. The algae within the thallus are clearly visible.



*Xylobotryum andinum*, section through the ostiolar region showing the upward-pointing periphyses (arrow).

## PSEUDOTHECIA

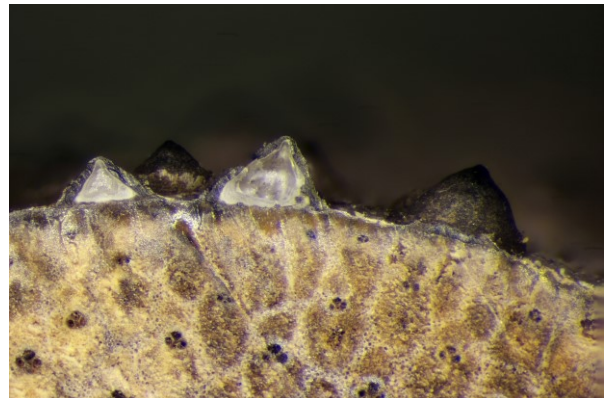
The fruit-bodies of pseudothecial fungi are mostly (but not always) perithecial in outer form, but develop initially as a solid structure with a **locule** (hole) developing within which the asci and ascospores form. These are frequently accompanied by interascal tissue, composed of chains of cells that stretch upwards and become narrower as the locule grows in size. The evolutionary divergence of pseudothecial fungi occurred at an early stage, and it is likely that the external similarities between pseudothecial and perithecial fungi are due to convergent evolution. As with perithecial species, fruit-bodies may be superficial or immersed, and sometimes may form within conspicuous mats of superficial mycelium.



*Leptosphaeria acuta*, a common species with flask-shaped pseudothecia found on old nettle stems



*Arthopyrenia analepta*, a questionably lichenized species with immersed perithecial pseudothecia.

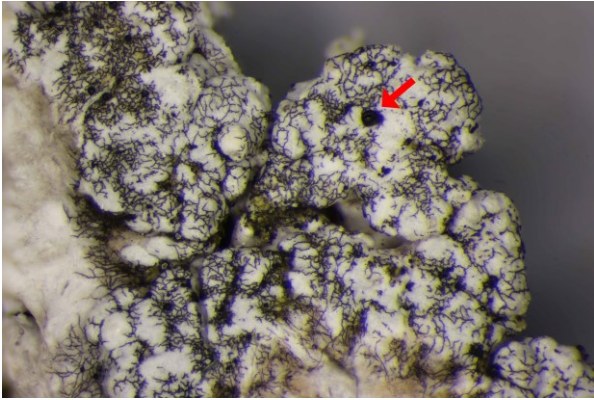


*Astrosphaeriella stellata*, a vertical section through the pseudothecia, which develop superficially on rotten bamboo canes.



*Lophium mytilinum*, an unusual pseudothecial fungus with laterally flattened fruit-bodies that open with an apical split rather than an ostiole.

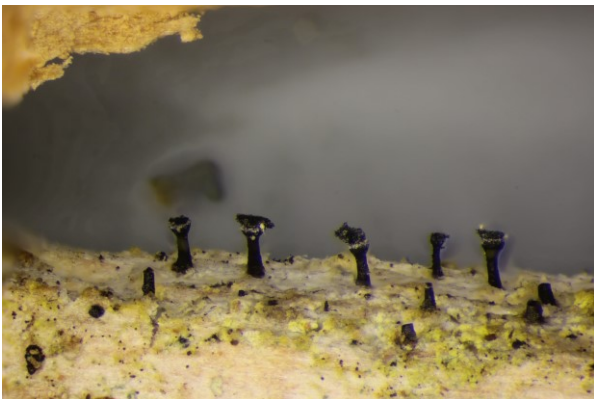




*Sphaerellothecium araneosum*, a fungal parasite on the lichen *Ochrolechia androgyna*, with minute black pseudothecia (arrowed) amongst a network of dark superficial hyphae.

### MAZAEDIA

In a small number of fungal groups, asci are formed in a powdery mass on a usually stalked fruit-body, termed a **mazaedium**. Many are lichens.



*Calicium glaucellum*, a mazaediate lichen on rotten oak wood. The black powdery masses of spores develop from the apices of the fruit-body stalks.



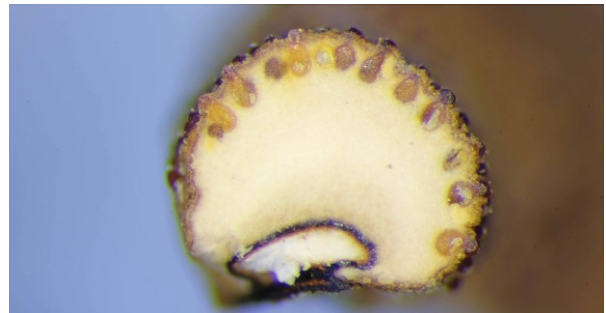
*Trichocoma paradoxa*, a mazaediate non-lichenized fungus related to *Penicillium*, in soil in a mixed woodland in eastern Bhutan.

### COMPOUND FRUIT-BODIES - STROMATA

In many species of the *Ascomycota*, reproductive structures are formed in compound assemblies. In non-lichenized fungi, these are termed **stromata** (singular: **stroma**). They may be formed from fungal tissue alone (and then referred to as **eustromata**), or a combination of fungal cells and degraded plant tissues (**pseudostromata**). The stromata may be massive and even perennial in some cases, or composed only of a cushion of cells on which ascomata develop. These last are called **basal stromata**. The stromatal structures can be highly diverse.



*Hypocreopsis rhododendri*, a species with multiple perithecial ascomata contained within finger-like stromatal lobes. The dark dots are the ostioles of the perithecia. A section through one of the lobes is below.



*Xylaria crozonensis*, with large flat strongly melanized stromata. A section is shown below, the black-walled perithecia contrasting with the white stromatal tissue.



*Diatrypella quercina* (above) and *Sillia ferruginea* (below), two species with stromata immersed in bark.



*Daldinia vernicosa*, with large reddish stromata developing from a burnt branch of *Ulex europaeus*.



*Daldinia pyrenaica*, section through a perennial stroma showing successive layers formed as new perithecia develop. There are tendrils of spores oozing from the ostioles.



*Neonectria punicea* with basal stromata erumpent from bark tissues of *Ilex aquifolium*.



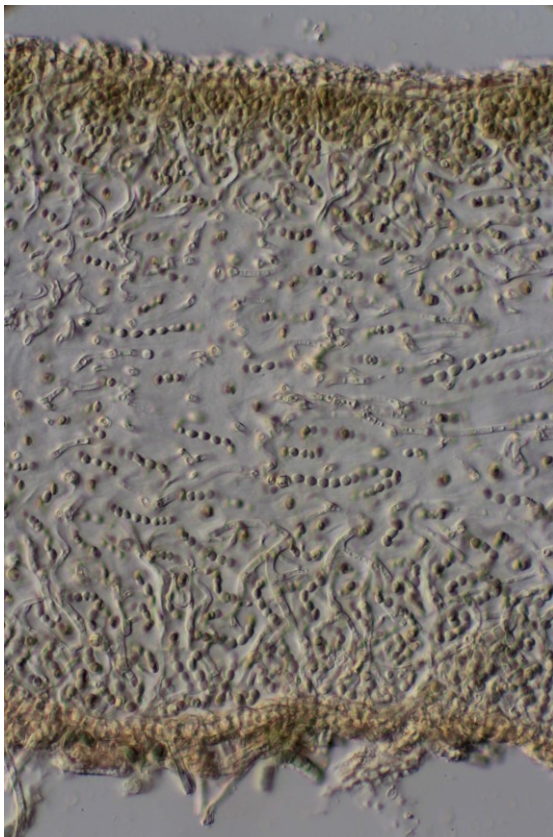
*Thamnomycetes camerunensis*, a species with branched stromata. Each of the branch apices contains a single ascoma.

## LICHEN THALLI

Lichens almost always have extensive vegetative tissues exposed to the air, as light is necessary for the algal partners (**photobionts**) to carry out photosynthesis. The photobiont may be a green alga, often a species of *Trebouxia* or *Trentepohlia* (which are actually orange). The photobiont may also be a cyanobacterium, often a species of *Nostoc*. In some cases lichen thalli harbour both green algae and cyanobacteria, the latter normally found in specialized structures known as **cephalodia**. These cyanobacteria have been shown to fix nitrogen.

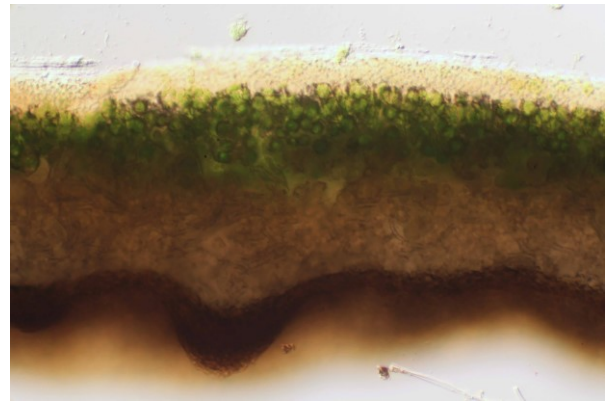
The lichen **thallus** (plural **thalli**) usually contains several layers. The outer layer exposed to the air

is the **cortex**, which is composed of specialized fungal cells, sometimes with very thick walls to protect against desiccation, through which light penetrates to the central tissues of the thallus, the **medulla**. Usually, the upper part of the medulla contains the photobiont cells, sometimes referred to as the **algal layer**. The lower part of the medulla usually consists of a loose network of fungal hyphae with air spaces between the filaments to promote gaseous exchange. There may be a lower as well as an upper cortex, providing further protection against desiccation, or this may be absent with the medullary cells exposed to the atmosphere. The lower cortex, if present, can be melanized and **rhizines** may be present, root-like structures which may help anchor the thallus to the substratum surface. The internal organization of the thallus is heavily influenced by its overall structure, and whether it is closely adhering or incorporated into the substratum below. Gaseous exchange may be further promoted by the presence of specialized cavities in the lower wall of the thallus. These may be empty (**cyphellae**, singular **cyphella**) or contain fungal hyphae (**pseudocyphellae**, singular **pseudocyphella**).



Vertical section through the thallus of the cyanobacterial lichen *Leptogium turgidum*. This has an upper cortex composed of a single layer of fungal cells, a strongly gelatinized medulla containing fungal hyphae intertwined with chains of the *Nostoc* photobiont, and a lower cortex similar to the upper layer but with small hyphae (**rhizines**) lining the lower surface.

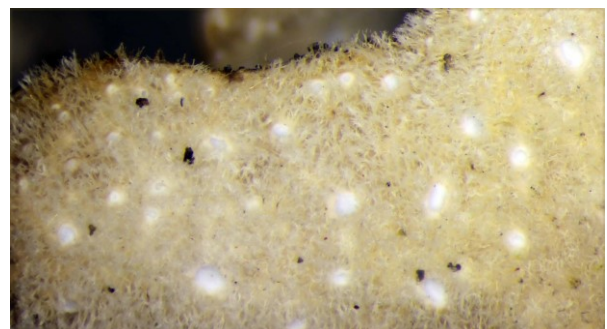
**Right** → Occasionally, lichen species can have separate morphs with different photobionts, which dramatically alters their appearance. On the left are thalli of *Sticta canariensis* containing green algae; on the right thalli of the same species contain cyanobacteria.



A vertical section through the thallus of *Parmelia submontana*. From the top, the layers are: a colourless cuticle-like **epinecral layer** composed of dead hyphae that help to protect against desiccation; a yellowish upper cortex composed of thick-walled fungal hyphae; the green algal layer of the upper medulla; a colourless (appearing brown due to trapped air) lower medulla composed of intertwined thick-walled filamentous hyphae; and a strongly melanized lower cortex.



*Lobaria amplissima*, with a green thallus containing trebouxoid algae, brown apothecia and blackish coralloid outgrowths (cephalodia) containing the *Nostoc* cyanobacteria.



*Sticta fuliginosa*, strongly tomentose lower surface of the thallus with white cyphellae which aid in gaseous exchange.

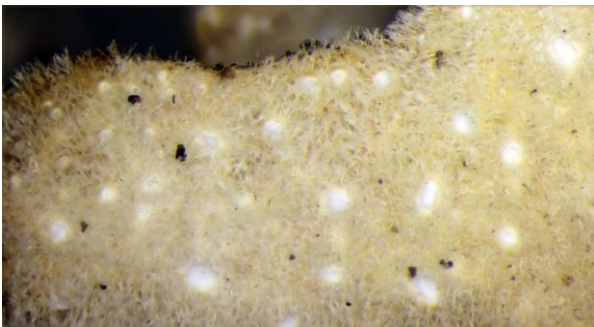




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## THALLUS FORM

Lichen thalli vary considerably in their overall structure. They may be:

- **foliose** (leaf-like, with one or more points of attachment)
- **fruticose** (minutely shrubby, usually with multiple branches)
- **crustose** (crust-like, strongly attached to the substratum; often with cracked or **areolate** thalli)
- **placodioid** (crustose but with lobes towards the margin of the thallus)
- **filamentous** (hair-like, with fungal cells surrounding a chain of algal cells)
- **leprose** (a diffuse, often unorganized mass of hyphae and photobiont cells)
- **squamulose** (minutely foliose with the individual units attached at the base but free at the edge)
- **stalked** (with fruit-bodies at the apices, often forming **mazaedia**)

In some groups of lichens, stalked secondary structures containing fruit-bodies are formed from the primary thallus units. These are referred to as **podetia**.



*Parmotrema robustum*, a large foliose lichen growing on siliceous rocks.



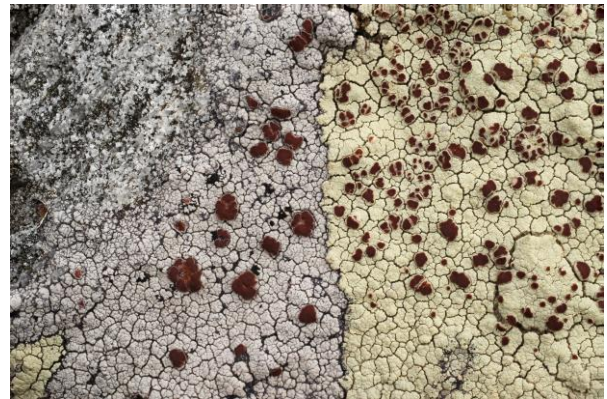
*Peltigera hymenina*, a large **foliose** cyanobacterial lichen with brown apothecia at the tips of thallus lobes.



A mosaic of *Lecanora sulphurea* and *Rhizocarpon reductum*, two common **crustose areolate** species on siliceous rocks.



*Teloschistes flavicans*, a **fruticose** lichen with bright orange-yellow frequently branched thalli. It is of conservation concern in the UK.



Two thalli of of the **crustose areolate** species *Ophioparma ventosa*; the grey thallus on the left lacks usnic acid, in contrast to the yellowish thallus on the right.



*Ramalina cuspidata*, a **fruticose** lichen on siliceous maritime rocks with tufts of elongate thalli.



*Variospora thallicola*, a **placodioid** species with lobed thallus tips. It is a common maritime species that occurs just above the tidal zone.



*Circinaria calcarea*, a common **crustose areolate** lichen on limestone



*Ephebe lanata*, a cyanobacterial lichen with a **filamentous** thallus. It occurs especially in water-filled hollows on granite boulders in upland areas.



*Lepraria lobificans*, a **leprose** lichen producing poorly-defined thalli covered in a powdery mass of vegetative propagules (soredia). It is common on the rock garden at Kew.



*Hypocenomyce scalaris*, a **squamulose** species with blackish apothecia, frequently found on coniferous wood and bark, and also on man-made substrata such as brickwork.



*Cladonia floerkeana*, with bright red apothecia on **podetia**, stalked structures derived from the primary thallus.



*Stereocaulon condensatum*, another lichen with **podetia**. It is a typical species of heavy-metal mine spoil.

## LICHEN VEGETATIVE STRUCTURES

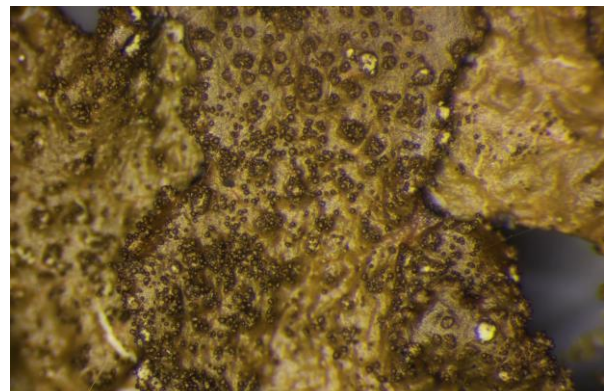
Many lichens reproduce via vegetative propagules that contain both fungal and algal cells, enabling new colonies to form without the need to locate new symbiotic partners. In many, **soredia** (singular: **soredium**) are formed, small unordered clusters of fungal hyphae and fungal cells. These develop from the medulla, and escape through cracks and cavities in the upper cortex of the thallus. The structures producing soredia are termed **soralia** (singular: **soralium**). In other lichens the vegetative propagules are formed from small outgrowths of the thallus, including the upper cortex. These are termed **isidia** (singular: **isidium**).



*Hypogymnia tubulosa*, a widespread species on bark and worked wood. Powdery clusters of **soredia** are formed from soralia at the tips of thallus lobes.



*Hypotrachyna afrorevoluta*, detail of thallus showing the rather coarse soredia.



*Melanelixia subaurifera*, detail of thallus showing copious production of isidia as pustular outgrowths.

## FRUIT-BODY ANATOMY

The structure of *Ascomycota* fruit-bodies can be quite complex. The spore-bearing structures are formed within fruit-body walls, which partially (in apothecia), almost completely (in perithecia) or completely (in cleistothecia) surround the fertile component. The wall structures are usually referred to as the **exciple** (in apothecia) or the **peridium** (in perithecia, pseudothecia and cleistothecia). There may be several distinct layers of cells involved, often with differing degrees of melanization, and the cells may be hyphal or parenchymatic in form. The asci develop in a layer termed the **hymenium** in apothecia, from a basal layer referred to as the **subhymenium**. In perithecial fungi it is more usual to refer to the asci being derived from a **centrum**.

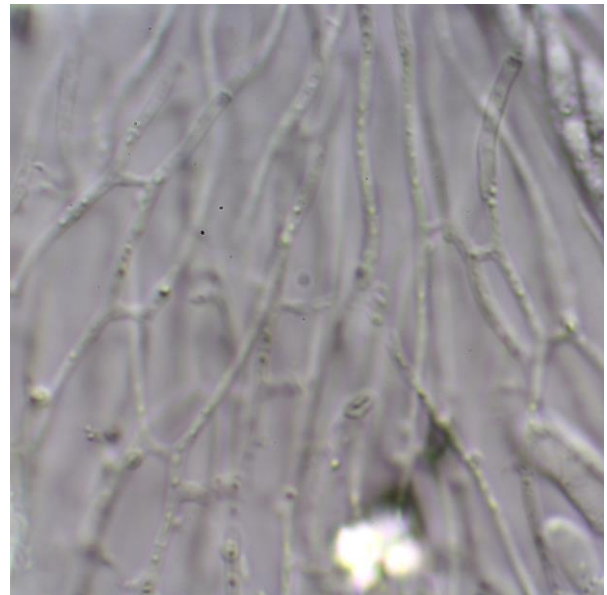
The asci are frequently accompanied by **interascal tissue** (or the **hamathecium**). This may comprise sterile hypha-like cells (**paraphyses**) which grow up from the base with free tips (in apothecia, perithecia and cleistothecia). In many pseudothecia, branched and anastomosed chains of cells (**pseudoparaphyses**) attached at both ends extend as the locule develops. Paraphyses frequently have swollen and/or branched apices, and in apothecia are frequently agglutinated in a layer of mucus and/or crystals above the asci. This layer is called the **epithecium**, and presumably functions to protect the developing asci from desiccation and predation.



Hymenium of *Rinodina sophodes*. The asci contain dark one-septate ascospores and are surrounded by paraphyses that are swollen at the apices. These are included within a dark brown gelatinous **epithelial layer**.



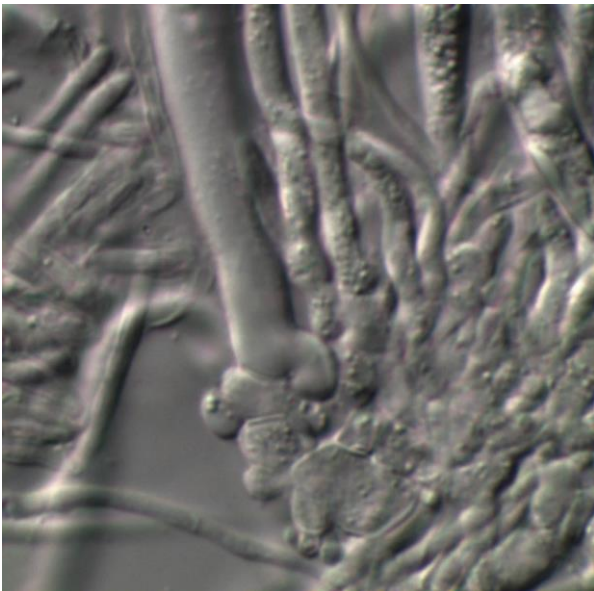
Squash mount of asci and paraphyses of *Mollisia fuscoparaphysata*. The paraphyses are swollen and branched at the apex, and surrounded by a brown mucous coat.



*Porina leptalea*, network of anastomosing pseudoparaphyses.

## ASCI

In contrast to the *Basidiomycota*, almost the entire life-cycle of species of *Ascomycota* is haploid, and meiosis is cryptic. Male gametes are referred to as **spermatia** (singular: **spermatium**), which are bacillar or filiform in shape and typically formed in small perithecium-like fruit-bodies, the **spermogonia** (singular: **spermogonium**). These are identical in structure to pycnidial conidiomata (see the section on anamorphic fruit-bodies below), and in practice it is difficult to determine whether the small conidium-like structures produced are disseminative or the agents of gene exchange. Female gametes are **trichogynes**. These are almost always very difficult to observe, and are unknown in most species. Once gametes fuse, the diploid phase is fleeting and can be detected only in the young stages of developing asci. In many members of the *Ascomycota*, asci develop sequentially via a system of **croziers**, hook-shaped structures at the base of the developing ascus.



*Hymenoscyphus fraxineus*, the base of an ascus with a well-developed crozier system.

Ascus morphology is linked to their discharge system, which can be active or passive. Actively discharging asci are elongate (cylindrical or narrowly clavate) and strongly constructed, with an apical pore through which the spores are ejected as hydrostatic pressure builds up in the ascus. The apical part is often more strongly thickened, and the spores pass through a ring-like constriction, the walls of which may stain blue in iodine indicating the presence of starch.

In some groups of *Ascomycota*, the entire ascus extends through the epithelial layer or into the ostiolar region to allow spore release directly into the atmosphere. In others, the ascus has multiple wall layers, and is usually referred to as **fissitunicate**. Here the outer wall of the ascus cracks open, and only the inner layer extends. An **ocular chamber** may be visible within the apical region of the undischarged ascus.

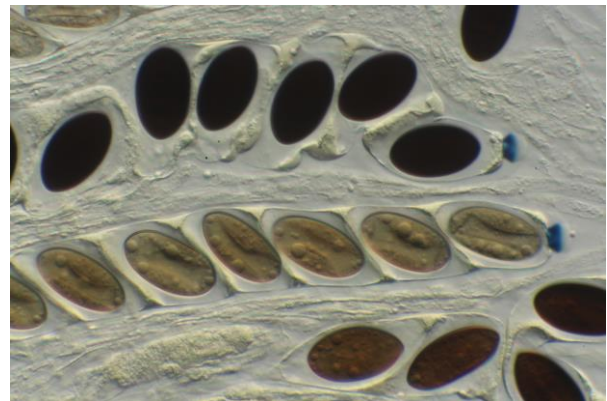
The entire ascus wall may blue in iodine in some members of the *Ascomycota*, or they may be surrounded by an iodine-positive gelatinous coating.

In passively discharging asci, the entire ascus wall has to break down in order to release the ascospores. They are almost always globose or saccate, very thin-walled and do not have any specialized apical structures.

The ascus structure is often phylogenetically significant, and many different variants have been identified.



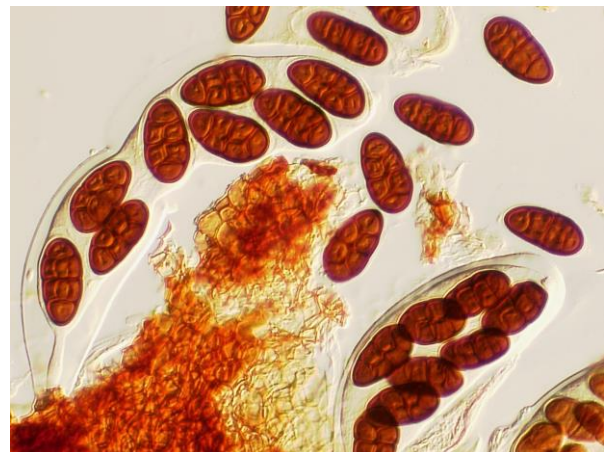
*Zignoëlla pulviscula*: cylindrical thin-walled asci without a well-developed apical structure.



*Poronia erici*: cylindrical non-fissitunicate asci with a large apical structure that blues in iodine.



*Diatrypella favacea*: multisporous asci with a small apical ring



*Clathrospora diplospora*, cylindrical fissitunicate discharge. The separate wall layers can be seen in the extended ascus to the left of the image.

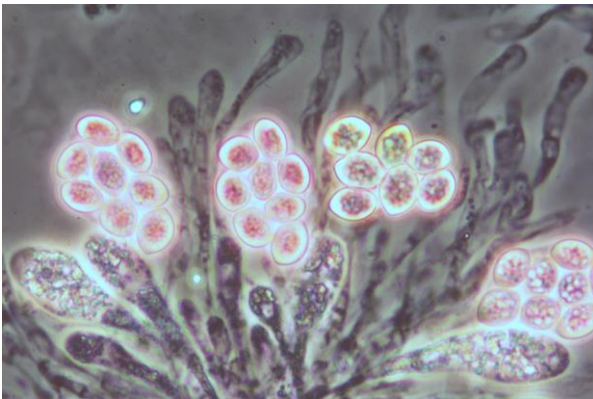




*Pseudotrachia viburnicola*: fissitunicate ascus with a broad shallow ocular chamber.



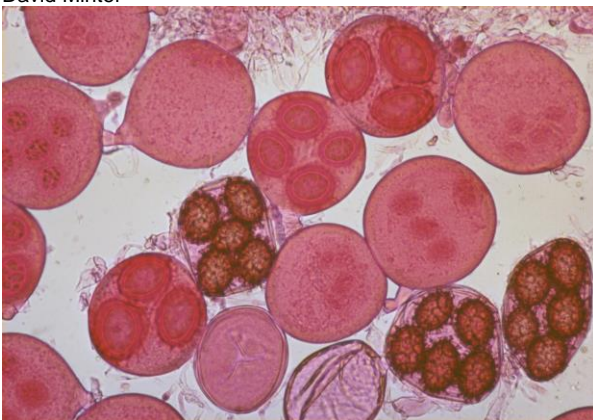
*Lecidella elaeochroma*, ascus mounted in Melzer's reagent showing the blue-staining apical region.



*Chaetomium globosum*: phase contrast image of the clavate very thin-walled passively discharging asci. The paraphysis-like structures are the remains of discharged asci. Image © David Minter



*Verrucaria squamulosa*, thin-walled but fissitunicate asci with rostrate dehiscence.



*Tuber aestivum*; globose non-discharging asci (stained in erythrosin). In truffles spore dispersal occurs when mammals eat the fruit-bodies, so no discharge is necessary. Image © David Minter.

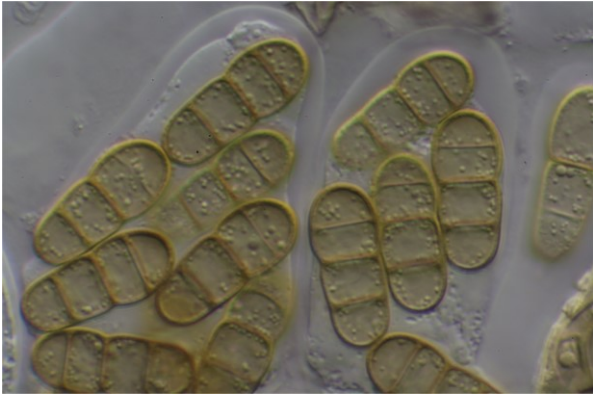


*Peziza ammophila*, discharged asci showing the broad opening with an operculum.

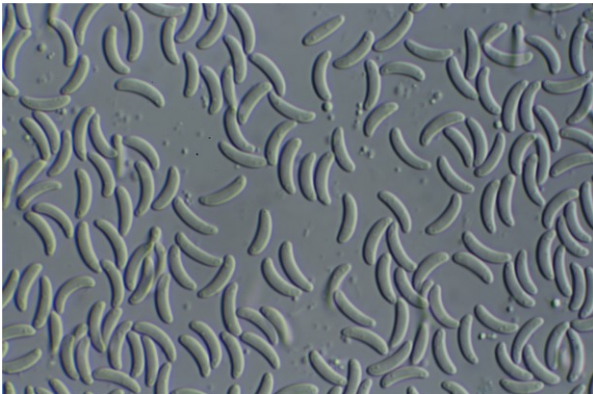
## ASCOSPORES

In a large majority of the *Ascomycota*, the meiotic division within the developing ascus that produces four daughter nuclei is followed by a single mitotic event, resulting in eight ascospores. The mitotic event may not take place, with the ascus containing four spores, or nuclei can abort to give the same outcome, or in some cases asci with variable numbers of spores. Asci with one, two and four spores are reasonably common, and multispored asci containing 16, 32 or many more spores can occur, following multiple mitotic events.

Ascospore morphology may vary greatly, partly in response to their primary function as disseminative or survival units (see section above on spore form and function). Generally speaking, a fruit body will produce large numbers of disseminative spores, which tend to be small, hyaline and thin-walled, or smaller numbers of survival spores (usually large, dark and thick-walled). Ascospores vary considerably in shape and coloration, they may be one- or multi-celled, their walls may be thick and/or ornamented. In some cases the spores have a detachable outer coat (the **episore**), a **gelatinous sheath**, or gelatinous or cellular **appendages**. Thick-walled and strongly pigmented ascospores frequently



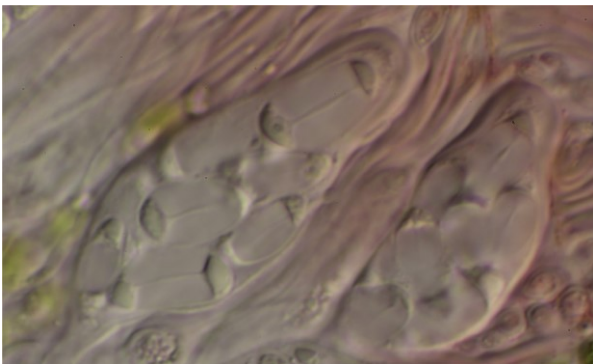
An unnamed *Venturia* species, with golden brown three-septate ascospores constricted at the primary septum.



*Leucostoma niveum*, with curved (*allantoid*) spores.



*Pyrenula chlorospila*, with very thick-walled *distoseptate* ascospores with much reduced lumina.



*Athallia cerinelloides*, with hyaline *polarilocular* ascospores.

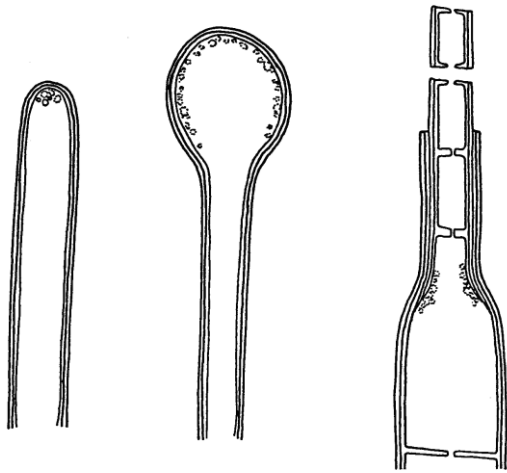
## CONIDIAL (ANAMORPHIC) ASCOMYCOTA

Much confusion may arise as the conidial fungi have historically been treated as a systematic group in their own right. This is not the case and they should be regarded as merely the conidial part of a fungal life-cycle.

Since conidial fungi exist in the environment, independent of their sexual morph, it is necessary to give them names, but in general when the sexual morph is known, that is the name which should be used. Classification of conidial fungi is primarily based on the specialized structures (*conidiogenous cells*) from which conidia are produced, and on the form of fruit body (where present) surrounding the spore-bearing structures. Other features such as the spore shape, colour, septation and ornamentation may also be significant.

### Hyphal growth and its relation to conidial development

As conidia (and indeed conidiogenous cells) are no more than modified hyphae, it is profitable to discuss hyphal growth and conidial production together. Hyphal growth involves extension of the cell wall, and a large body of research has shown that this involves special vesicles which are thought to transfer new wall material from production sites in the cytoplasm to the growing part of the wall. These vesicles are usually aggregated at the hyphal tip, which is where most active growth occurs, but they may also be found arranged in a ring some way back from the tip, or in less dense aggregations over a much wider and accordingly slower-growing area of the cell wall. These different types of cluster have been termed *wall-building apex*, *wall-building ring* and *diffuse wall-building zone* respectively, and have been observed in conidia and conidiogenous cells as well as in vegetative hyphae. Wall-building apices and rings both tend to produce new cylindrical hyphal walls (initiation), whereas diffuse building tends to act on existing walls to convert their shape (a process of maturation). Very frequently, diffuse wall building occurs together with apical or ring wall building, so that the hypha swells as it is produced.



Types of wall-building (from left): apical wall-building, diffuse wall-building, wall-building ring

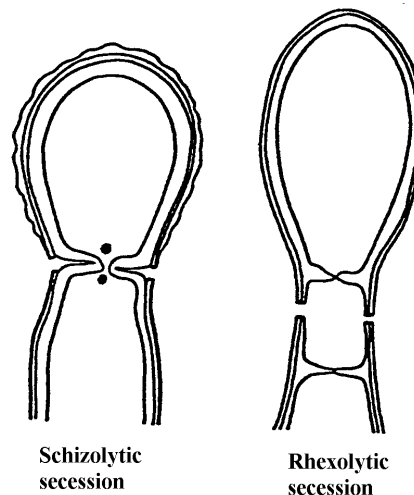
During hyphal growth, wall material gradually becomes more and more distant from the vesicle cluster which produced it. During this time, the wall material apparently becomes less flexible, and this hardening may be accompanied by the laying down of pigment, usually in an internal layer of the wall. If for some reason active wall-building ceases temporarily (such as the environmental conditions becoming unfavourable), the whole hyphal wall may harden. When wall building begins again, two things can occur: either the hardened wall is resoftened in some way and growth continues as though it had never been interrupted, or a new interior wall is laid down which then breaks out of the hardened wall and to become the exterior wall of the new section of hypha.

These two modes of growth resumption, which have been termed **holoblastic** and **enteroblastic** respectively, merely represent two ends of a spectrum, since the degree to which the wall hardens depends on how long wall building has been interrupted. When a wall is only partially hardened, the fungus will often incorporate its more plastic parts into the new interior wall. The degree to which a hardened wall is resoftened and the area over which this process takes place are further significant factors: in some fungi, a hardened wall is such a common feature of their conidiogenous cells that a specialized form of resoftening has evolved. In these fungi, conidia are produced by new enteroblastic wall extension from a minute pore in the hardened outer wall. This type of development is termed **tretic**. In the case of conidial production, even in fungi which produce conidia successively from a single meristematic locus (i.e. exhibiting enteroblastic growth), the first conidium formed must necessarily be formed holoblastically, as plastic growth and differentiation from an unmodified portion of hyphal wall.

Growing hyphae often branch at some point behind

their tip. To branch, the fungus must gather a new cluster of vesicles well behind the growing tip at the point where the branch is to begin, and the existing wall must be resoftened or burst as a new wall is laid down. The vesicle cluster then extends into the growing branch, proliferating as an independent wall-building apex. A similar phenomenon occurs when a hyphal tip is damaged or its wall-building apex is in some other way separated from the proximal part of the hypha: the fungus gathers a new cluster of vesicles at the tip of the highest intact cell, and regeneration is formed by this replacement wall-building apex.

As hyphal growth continues, septa are laid down, and as this involves the production of wall material, it is likely that vesicles similar to those involved in external wall production are active. The basic ascomycetous septum begins as an ingrowth of wall material from the main (i.e. cylindrical) part of the wall. Usually a small septal pore is left at the centre of the ingrowth, and this pore is often plugged by a Woronin body. These septa may be described as being 1-ply, because they are each composed of a single layer of wall. Their function is principally to give structural support to the hypha, but some fungi are known which produce two 1-ply septa close together at the base of each conidium, thus delimiting a small "sacrificial" cell which is destroyed as the conidium breaks away (secedes; a process of **secession**). This type of secession is called **rhexolysis**.



Another type of septum is frequently encountered in ascomycetous fungi, particularly during conidium production. This septum develops in a rather similar manner to the 1-ply septum, but it has two layers of wall and may accordingly be called a 2-ply septum. It is possible that the 2-ply septum is little more than a specialized production of two adjacent 1-ply septa, and intergrading examples are known. The principal feature of the 2-ply septum is that it has a central plane of weakness between the two layers of septal walls. This type of septum therefore provides a convenient way of allowing conidia to secede from their

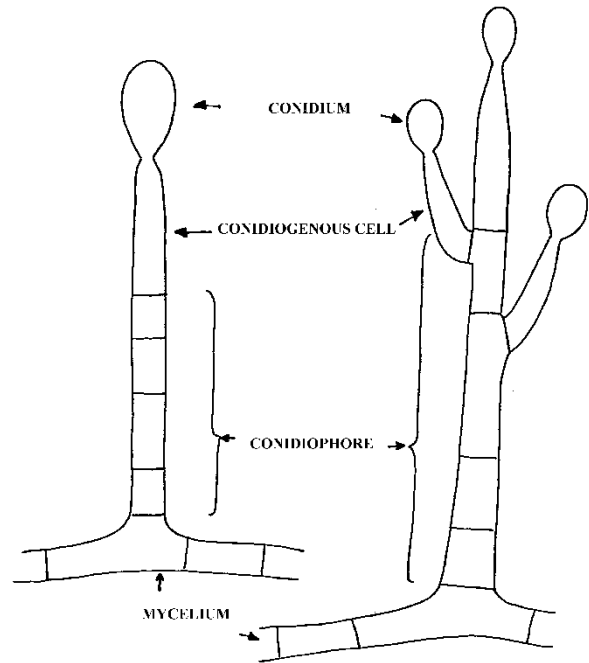
conidiogenous cell, and this type of secession is called **schizolysis**.

### Anamorphic fruit bodies

Quite large numbers of conidium-forming fungi (or fungal morphs) produce their asexual spores within fruit bodies. These to some extent parallel those of the teleomorphs, though conidia are almost always produced from the entire inner surface of the fruit-body wall, rather than from a specialized region. Flask-shaped or globose structures similar to perithecia are widely encountered, and are termed **pycnidia** (singular: **pycnidium**). Thyriothecium-like structures are also found (called **pycnothyria**; singular: **pycnothyrium**), and indeed teleomorphic forms with thyriothecia often have pycnothyrial anamorphs. The third major type of anamorphic fruit-body has no real parallel among the teleomorphic forms, and is called an **acervulus** (plural: **acervuli**). Here, the fruit body consists of developing aggregations of conidium-bearing hyphae within host tissue, which ruptures to allow spore release from the whole surface of the acervulus. **Stromata** are also commonly encountered within the anamorphic fungi, with conidia formed in or on these compound structures.

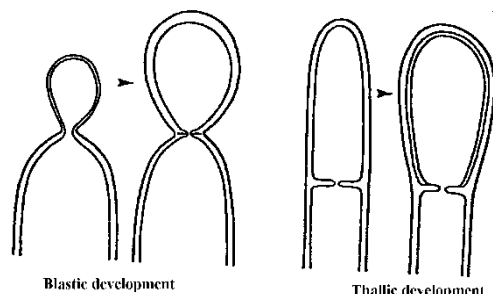
A further fruit-body type amongst the anamorphic forms is the **synnema** (plural: **synnemata**, also sometimes referred to as the **coremium**; plural: **coremia**). Here, there is no enclosed fruit-body, but hyphae are aggregated into column-like structures with conidia produced from the hyphal tips at the apex of the column. Anamorphic fungi which have some form of enclosed fruit-body (though which may eventually expose the developing conidia) are given the blanket term coelomycetes. Those where the conidium-bearing hyphae are exposed at all stages are called hyphomycetes. This last group also includes the synnematus types. Although these divisions are convenient for basic categorization, they do not properly reflect the variation present in anamorphic fruit-body types, and it is often difficult in practice to distinguish between acervular fruit-bodies and hyphomycetes with aggregated fertile hyphae.

### Conidiogenous cells and conidial development



This section should be read along with that on hyphal growth and conidial production (see above). Conidia may be formed directly from more or less differentiated hyphae, or within fruit-bodies. The first recognized classification schemes for anamorphic fungi separated groups based on presence or absence of conidiomata, and on the colour and septation of conidia. More recent studies placed much emphasis on conidial development rather than conidial morphology, and features of conidial development remain very important in classification. It must be emphasized that the plasticity of fungal growth and development is at its most extreme in conidial production, and the situation in real life is often much more complicated than the pigeon-hole type of classification still widely employed for many groups might suggest.

Conidia may be formed in a variety of ways, either by the fragmentation of hyphae, and often by the subsequent differentiation of fragments (**thallic** development) or by growth of wall material and subsequent differentiation from specialized conidiogenous cells (**blastic** development). The two modes of development are not always easy to tell apart, and are discussed further in the section above on hyphal growth.



In fungi which produce conidia through thallic development, conidiogenous cells are effectively absent, the conidia being produced from undifferentiated vegetative hyphae. This does not imply that the production of conidia is random or uncontrolled; in many cases conidia are produced from specific portions of hyphae, either as short side branches, as modifications of alternate cells within the hypha, or indeed as hyphal lengths with specific numbers of cells. Once the conidium has been delimited, further differentiation often occurs such as wall thickening or pigmentation. Where two-ply separation septa are not formed, secession (the separation of the conidium from the hypha) occurs by the breakdown of the walls of the hyphal cell adjacent to the conidium. Loss of cytoplasm and nuclei is usually avoided by the contents of that cell becoming absorbed either into the conidium or into the supporting hyphal cell.

Most fungi producing conidia through blastic development exhibit recognizable conidiogenous cells, though in some very simple forms (e.g. *Acremonium*) these may appear to be little more than side branches of hyphae with fertile tips. In most cases, conidiogenous cells are able to produce conidia successively, either in succession from the same point or locus (**percurrent proliferation**, sometimes referred to as **phialidic production**) or singly from successive points (**sympodial proliferation**). In others, the benefits of producing a succession of relatively small and simply constructed conidia are overcome by those of generating large and complex structures, and a conidiogenous cell may produce only a single conidium.

Especially in cases where conidia are separated by wall breakage between pairs of one-ply septa rather than by two-ply septa, a **scar** may remain on the conidiogenous cell composed of the remnants of separating cell wall, showing the position of previous conidial production. In some cases in fungi employing percurrent conidial proliferation, this wall material may be relatively extended, producing a cylindrical or funnel-shaped structure known as a **collarette**. This is thought to protect the vulnerable meristematic region as successive conidia are produced.

Where conidiogenous cells exhibit percurrent proliferation, the successive production of inner wall layers at the conidiogenous locus results in a local wall thickening, with only a narrow pore connecting the conidiogenous cell with the developing conidium. This is termed **periclinal thickening**, and is one of the surest ways of detecting percurrent proliferation.

It is not uncommon for conidiogenous cells to exhibit a mixture of sympodial and percurrent proliferation. Frequently, this appears to be a more or less random process with one type of

proliferation dominating. In a few genera the two types of proliferation are clearly controlled; in such cases the conidiogenous cells are sometimes referred to as **polyphialidic**.

In some cases in conidiogenous cells which exhibit percurrent proliferation, there is a small degree of proliferation (growth) of the fertile apex of the conidiogenous cell itself in between production of successive conidia. This gives the apex of the conidiogenous cell a banded appearance due to the successive breakages of the cell wall as conidia succeed and growth of the inner wall layers through the scar. This is often referred to as **annelidic proliferation**.

The morphology of conidiogenous cells is quite variable, ranging from almost unmodified hyphal branches to clearly distinguishable cylindrical, flask-shaped or barrel-shaped cells. They are only rarely strongly pigmented, due to the difficulty of proliferating through a dark and hardened cell wall. The **conidiogenous loci** (i.e. the parts of the cell from which conidia are actually produced) are usually attenuated to some degree, especially where percurrent or annelidic proliferation is employed. In fungi forming conidia within fruit-bodies, the conidiogenous cells are necessarily smaller and less differentiated due to the restriction of space for development.

### Conidiophores

Frequently, conidiogenous cells are located singly or in clusters on specialized hyphae known as **conidiophores**. These may be largely similar in appearance to vegetative mycelium, though maybe oriented vertically rather than horizontally, or strongly differentiated. They may be branched irregularly or verticillately, or have swollen apices, and are often strongly pigmented. The conidiophores themselves may be clustered together into cylindrical structures known as **synnemata** or **coremia**. Conidiophores are only well-developed in fungi producing conidia without fruit-bodies, though in these instances it is not uncommon for conidiogenous cells to be inserted singly or in small clusters on supporting cells.

### Conidia

Propagules which are formed without a preceding meiotic division are given the blanket term **conidia** (here including spermatia and resting-spores; see above). Conidia are not constrained by production within asci, and thus show an even wider range of form, especially those formed without a protective fruit-body, and those dispersed in water rather than air. Many (especially those functioning as spermatia) are small, hyaline, thin-walled and aseptate. Dispersal conidia are much more varied

in form, and may be transversely and also longitudinally septate, strongly and homogeneously or differentially pigmented, and variously ornamented. They are immensely varied in shape, branched or coiled, and may have cellular or gelatinous appendages from the apex, base, sides or all three of these positions. Survival conidia (or resting-spores) are usually dark and thick-walled, and may be unicellular or multicellular, in the latter case intergrading with sclerotia.

The non-specialist sometimes has difficulty distinguishing conidia from ascospores, especially where material that is not in ideal condition is examined. The mistake is often made where asci are not observed that the material must therefore be of an anamorphic fungus. However, it is rare for a specimen or culture to show conidia without conidiogenous cells, as conidial production frequently occurs over an extended period. In the absence of asci or conidiogenous cells, the most reliable way to distinguish the two types of propagule is to look for the scar where the wall between the conidium and conidiogenous cell has broken. However, many conidia are separated with double septa (see above), and the scar may be difficult to distinguish. Other pointers are that conidia tend to be more variable in size and shape than do ascospores.

### Types of conidia



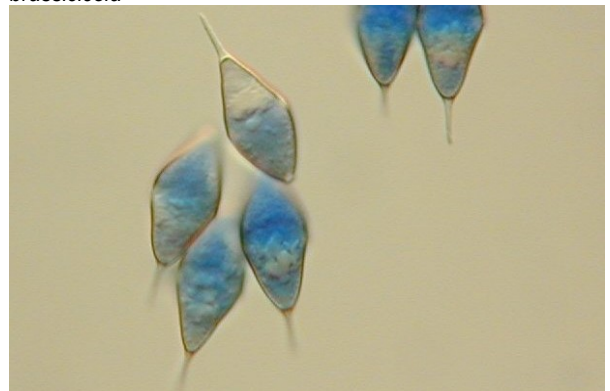
Brown aseptate spinose conidia of *Periconia atropurpurea*



Small hyaline conidia formed from simple conidiogenous cells in *Acremonium* sp.



Complex conidia formed in branched chains in *Alternaria brassicicola*



Biconical conidia with spinose appendages of *Beltrania rhombica*



Distoseptate conidia of *Bipolaris hawaiiensis*



Dark resting spores produced by *Ceratocytis paradoxa*

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