Module on
Peziza- Important Features and Life Cycle
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Taxonomy

Peziza Dill. ex Fr. 1822, with over 100 species (Korf, 1973), is the most common genus of Pezizaceae. According to classification of Alexopoulos and Mims (1979) the taxonomic position of Peziza is as:

Division: Amastigomycota
Class: Ascomycetes
Order: Pezizales
Family: Pezizaceae
Genus: Peziza

Division Amastigomycota is characterized by having absorptive type of nutrition and absence of motile spores in its memberspecies. Fungi in class Ascomycetes have septate hyphae, specialized spores (called ascospores) produced endogenously in specialized sporangium, known as ascus. Typically eight ascospores are formed by free cell formation after karyogamy and subsequent meiosis. In contrast to Basidiomycetes, where spores are produced exogenously, in Ascomycetes they are produced endogenously. Ainsworth (1973) raised already recognized class Ascomycetes to subdivision category as Ascomycotina and subsequently recognized six classes within this subdivision, with Discomycetes one of them. Discomycetes containing genus Peziza, constitutes the group of fungi having apothecium as ascocarp (fructifying body). Apothecial ascocarps produced have an exposed hymenium at maturity. Pezizales (Alexopoulos et al., 1996) is a large order that contains the
species commonly called operculate Discomycetes as well as derived hypogeous forms that have evanescent asci with ascospores spread by mycophagy. Apothecia may be either eugymnohymenial or paragymnohymenial or cleistohymenial. The apothecium may have an apical operculum or slit at the apex or it may have an operculum just below the apex.

Family Pezizaceae (Alexopoulos et al., 1996) is characterized by having fleshy or brittle, sessile or feebly stalked and usually cup or disc-shaped apothecia. They may be minute to very large; bright coloured to dark brown; and smooth, velvety, hairy or bristly. The family Pezizaceae can be segregated from related families like Sarcoscyphaceae and Sarcosomataceae by having operculum generally placed at the apex of the ascus. Further Pezizaceae is characterized by asci that turn blue in Melzer’s reagent. The location and intensity of the blueing reaction varies and it is indicative of evolutionary lineages within the family (Hansen et al., 2005). Ascospores in Pezizaceae generally are thin-walled, hyaline or brown, rarely greenish-yellow and always uninucleate. The constituent species usually use dung, soil and wood as substrate. Field characteristics of the family are variable and fruit bodies are so similar in size, shape and colour that final identification of the species must be made with the microscope.

*Peziza* is the largest genus in the order Pezizales. The genus *Peziza* includes the fungal species where asci line is the inner or upper surface of a cup-shaped fruiting body. The ascus opens at maturity and discharges its spores into the air. Most members of the genus *Peziza* are difficult to identify as they look outwardly similar. So identification and verification
of microscopic features is usually required for identification. The spore ornamentation, which is visible when stained with cotton blue, is used in the identification of species. In common with other Ascomycetes the upper surface of the fungus has a layer of cylindrical spore producing cells called asci from which the ascospores are forcibly discharged. Like a mushroom (Division Basidiomycota), *Peziza* produces above-ground heterokaryotic reproductive structures that come from an underground mycelium. One way that *Peziza* differs from mushrooms is that it produces spores on top of its cup, not underneath like a mushroom. Like species delimitation inter-generic and infra-generic relationships of *Peziza* are debatable. Recent molecular analysis of rDNA (Hansen *et al.*, 2002) and multiple genes (Hansen *et al.*, 2005) suggest that the genus is paraphyletic. Preliminary analyses, based on nuclear LSU rDNA sequences from a broad sampling of taxa within *Peziza*, as well as from related genera suggest that all other genera in the Pezizaceae are nested within *Peziza*. Some species of *Peziza* appear to be more closely related to the species in other genera within the family than they are to some other species within genus *Peziza* (Hansen *et al.*, 2002 and 2005). This infers that either more species would need to be drawn into *Peziza*, or *Peziza* will need to be broken up into a number of genera. The morphologically deviating *P. gerardii* appears to be the basal lineage in the Pezizaceae. The lineages broadly correlate with spore morphology and pigmentation. Morphological characters previously used to delimit species within the *Peziza* species complex, such as colour variation of the apothecia, presence or absence of a stipe, stratified or non-stratified medullary exciple (or thickness of the excipular layers), cell types in the outermost exciple and moniliform versus filiform paraphyses are
not correlated with the subgroups supported by ITS analyses and appear to be plastic (Hansen et al., 2002). Further the substrate and habitat have been much emphasized in the taxonomy of Peziza, but the populations on a diverse array of substrates may be closely related, or indeed, conspecific (Hansen et al., 2002). Still certain morphological characters are used to distinguish different species. For example *P. praetervisa* is recognized by its flattened purple, cup-like fruiting bodies. A combination of characters makes *P. vesiculosa* relatively easy to identify. Most obvious is its preference for fruiting in clusters on horse dung or decayed straw. *Peziza vesiculosa* is additionally distinguished by an urn-shaped cup with a margin incurved even at maturity, a wrinkled yellowish-brown hymenial inner surface and a pale outer surface with minute pustules. Fruiting body in *P. vesiculosa* is 2-5 cm broad, sessile, often contorted when clustered; margin incurved, remaining so with age, at times erodes or cracks with age. The hymenium (inner surface) is light-brown, pale yellow-brown to medium brown in colour, frequently convoluted or wrinkled. The outer surface of hymenium is granulose to furfuraceous, sometimes indistinctly so when weathered, tan, pale-buff, to nearly white. *P. domiciliana* is a brownish cup fungus while *P. cerea* is a yellow grey to beige fungus internally, less than 5 cm across with a granular or brittle flesh. The spores in *P. cerea* are smooth, elliptical, white-coloured or creamy or yellowish. The cup exterior is white in colour. Its upper surface (at maturity) is usually somewhat wrinkled near the centre; a whitish and minutely fuzzy under surface; round, cup-like shape when young, and a flattened-irregular shape when mature. *Peziza repanda* can be identified by its growth on rotted wood or wood chips, its brown upper surface (at maturity) that is usually
somewhat wrinkled near the centre; a whitish and minutely fuzzy under surface; a round, cup-like shape when young, and a flattened irregular shape when mature; elliptical spores that lack oil droplets. *Peziza depressa* has fruiting body about 20-40 mm, irregularly cup- to saucer-shaped. The fruiting body has short stipe and its inner surface is smooth, purple to chestnut- brown. The outer surface is almost smooth, brighter than the inner surface. The fruiting body exuding a watery juice when cut. *P. domiciliana* is a brownish cup fungus. It is often found to grow through cracks in concrete. It is also found in sandstone and in crumbling building remains, as well as in carpets, plasters, shower stalls, and so on. It is not only the species that could conceivably grow in such settings, but it is the species that is usually found indoors or in concrete. The closely related *P. praetervisa* is also violet coloured and prefers growing on burned ground. In general *P. praetervisa* is more purple rather than violet coloured like *P. violacea*. However, fruiting body colour can vary depending on humidity and other factors, so they are more reliably distinguished microscopically. *P. praetervisa* has rough, not smooth spores with two polar oil drops. Fruiting bodies in *P. praetervisa* resemble flattened cups with diameter of up to 3 cm. The inner spore bearing surface, the hymenium is purple- brown, but lightens to brown with age. The exterior surface is pale purple and scurfy. This species is sessile and does not have a stipe. The flesh is thin and mauve coloured. The pores in *P. praetervisa* are elliptical, hyaline, with small fine warts on the surface, and have dimensions of 12-14 x 7-8 micrometers. They are biguttulate, containing two oil drops at either end of the spore. The asci are 250-300 x 10-12 µm.
Peziza badioconfusa has cups up 3-10 cm across, deeply cup-shaped, becoming irregular; inner surface dull reddish brown, outer surface similar but roughened or unpolished. There is no stipe in this species. The asci are about 140 x 12µ in size. The spores are ellipsoid, finely warted, containing two oil drops of 17-21 x 8-10µ size.

**Structure**

The mycelium is frequently perennial and consists of a dense network of branched, septate hyphae. The cells are uninucleate. The hyphae ramify within the substratum and form a complex system which extracts nutrients from the substratum. The apothecia (sporocarps) are aerial extensions of the subterranean mycelial network. They are semi-immersed in *P. ammophila* while in certain species they are flattened (cupulate). The size of apothecium varies from one to several centimeters. Similarly they vary in colour, e.g., they are bright orange in *P. aurantia*. The exposed hymenium which lines the interior of the apothecium consists elongated (exhibiting various stages of development) and paraphyses. Both the asci and paraphyses are phototropic and their tips are always bent towards incident light. In apothecia receiving light from the asci at the base of the cup are straight while those on the sides are curved.

The primary wall in ascospores is devoid of chitin and is composed of $\beta$-1,3 glucans. Barium permanganate treatment does not indicate appreciable amount of protein and lipids in it. Ultra-structural data confirm light microscopic studies that show an expansion of the investing membrane within which further wall deposition occurs (Dyby and Kimbrough, 1987). The
coalescing of cytoplasmic vesicles with the investing membrane creates a large vacuole, the perisporic sac, around the spore. Simultaneous with the formation of the perisporic sac, osmiophilic lumps are deposited on the primary spore wall. The osmiophilic lumps increase, coalesce, and form the initial epispore. The epispore consists of zones or bands of varying electron opacity whose staining properties indicate complex carbohydrates. Further deposition of material from the perisporic area results in the formation of spore ornaments made up of fibrillar strands. The staining reactions indicate that spore ornaments consist of a matrix of lipids, protein, glyco- proteins and chitin.

**Reproduction**

**Asexual Reproduction**

Asexual reproduction is absent in most of the species of *Peziza*. But a few species (e.g. *P. fuckeliana*, *P. ostracoderma*, *P. repanda* and *P. vesiculosa*) produce conidia and chlamydospores.

**Conidia:** At the time of formation of conidia, some hyphae grow upwards and act as conidiophores. The conidiophores are long, cylindrical, erect and septate. The tip of the conidiophores swells to form a vesicle. Conidia are formed on the surface of the vesicle. They are hyaline or light coloured, elliptical and thin walled structures. They germinate on the suitable substratum and produce new mycelia.

**Chlamydospores:** Chlamydospores are thick walled resting cells which are formed in intercalary positions on the hyphae, either singly or in chains. In favourable conditions they germinate and form germ tubes which eventually grow into new mycelia.
**Sexual Reproduction**

Definite sex organs, i.e., antheridium and ascogonium, are not formed in *Peziza*. Sexual reproduction takes place by somatogamous copulation. The hyphae grow in all directions and form a psuedoparenchymatous mass. Some hyphal branches in this parenchymatous mass have dense protoplasmic contents and their cells are uni- or multinucleate. Usually two adjacent cells of these hyphae fuse to form a dikaryotic cell, but sometimes two nuclei of the same cell form a dikaryon. The latter process is known as autogamous pairing. Each dikaryotic cell gives rise to an ascogenous hypha. The terminal cell of the ascogenous hypha usually functions as ascus mother cell. But in *P. vesiculosa* the dikaryotic cell directly acts as ascus mother cell and it elongates and forms a cylindrical or club-shaped ascus. The diploid nucleus undergoes a reduction division, followed by a mitotic division, resulting in eight haploid nuclei. Each of these nuclei secretes a wall and organizes into an ascospore. In this way, eight ascospores are formed in an ascus. The uninucleate ascospores are hyaline, oval or elliptical and have smooth or coarsely reticulate wall. The ascospores are placed obliquely in a row in the ascus. During the development of an ascus, the surrounding mono- karyotic hyphae organize a thick protective coat around the developing ascus, collectively called ascocarp. The ascocarps are apothecium type i.e., they are cup- shaped bearing exposed hymenium.

The mature apothecium is a cup shaped, sessile or sub-sessile structure, 1-10 cm in diameter. They may be whitish yellow (*P. aurentia*) or bright red or grey in colour (*P. vesiculosus*). In *P. arverensis* they are solitary sessile,
cupulate, extremely whitish and nearly smooth. Their margins are slightly wavy, 3-10 cm in diameter and often irregular in outline but eventually spreading. The hymenium is concave, even wrinkled or furrowed, glabrous, light brown to chestnut-brown in *P. arverensis*. The exterior surface is white to ash-grey, finely tomentose. The asci are arranged in parallel rows within the apothecium. In apothecia receiving light from above the asci at the base of the cup are straight while those on the sides are curved towards the light. This orientation of the asci ensures smooth upward discharge of ascospores. The asci have a distinct amyloid ring at their apex which stains blue with iodine. Ascospores are large, elliptical, and are discharged violently and in one lot. On the basis of ascospore characteristics the species of *Peziza* fall into two series; (1) those producing smooth-walled spores without oil drops and (2) those producing spores ornamented by warts or ridges and usually containing two large oil drops. Some species of the second series yield a coloured fluid from the flesh of their ascocarp. The ascospores on germination at the suitable substratum, give rise to a haploid mycelium of uninucleate cells. A longitudinal section of the apothecium shows the following regions.

(a) **Hymenium:** It is the innermost region of the apothecium and contains asci, ascospores and paraphyses. Paraphyses are sterile cells often with swollen tips and are at high turgor pressure and are placed at right angle to the surface of the apothecium. Tips of the paraphyses are very tightly together at the surface of the hymenium and create a barrier, the epithelium. The exposed hymenium which lines the interior of the cup consists of elongated asci (exhibiting vari-
ous stages of development) and paraphyses. Both the asci and paraphyses are phototropic and their tips are always bent towards incident light. To disperse spores asci push between the paraphyses from below, shoot off their spore than collapse.

(b) **Sub- hymenium:** The middle region of apothecium is known as sub- hymenium or hypothecium. It is composed of thin walled and light- coloured hyphae, which run parallel to the surface of the hymenium. The asci and paraphyses arise from these hyphae.

(c) **Excipulum:** It is the outermost region of the apothecium, composed of sterile hyphae.

Ascospores are released from the apothecium generally in moist environmental conditions. On germination, the ascospores give rise to a germ tube which develops into a new mycelium.

**Economic Importance**

In general species of Peziza are with no apparent use and there is no concrete evidence about their edibility. However, the species found growing on soil have tendency to increase soil fertility. The species growing on wood logs leads to deterioration of quality of timber. The species growing indoors are potential pollutants. A unique hemaggulating lectin has been isolated from *P. arverensis*. This lectin determined to be a single- chain protein and is biotechnological importance. A largely harmless association have been found between *Peziza repanda* and *Delphinium* spp.
Life cycle

The mycelium is initiated with the germination of an ascospore, or conidium. Many crops of conidia are produced during the growing season, and it is the conidia that are responsible for propagation of the fungus in the species which are reproduced by conidia. Definite sex organs, i.e., antheridium and ascogonium, are not formed and sexual reproduction takes place by somatogamous copulation. The hyphae grow in all directions and form a psuedoparenchymatous mass. Some hyphal branches in this mass of hyphae bear dense protoplasmic contents and their cells are uni- or multinucleate. In general two adjacent cells of these hyphae fuse to form a dikaryotic cell. However, in certain cases two nuclei of the same cell form a dikaryon. This process is known as autogamous pairing. Cell division in the dikaryotic cell occurs in such a way that the resulting cells are dikaryotic and form an ascogenous hypha. The dikaryotic hyphae grow together to form a reproductive structure called an ‘ascocarp’. The two nuclei in the terminal cell (ascus) of the dikaryotic hyphae, fuse ‘karyogamy’ and become a diploid nucleus. The ascus then elongates and the diploid nucleus by meiosis forming four haploid nuclei. Each haploid nucleus divides again by mitosis, resulting in a total of eight haploid nuclei. These haploid nuclei are then cut off in segments of the cytoplasm to form ‘ascospores’. Haploid ascospores germinate to form the primary mycelia, which can produce microscopic hyphal mass. It represents the haploid phase of the fungus. Thus in the lifecycle of *Peziza* there is a long haploid phase, followed by short dikaryotic phase and a transitory diploid phase.