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SYSTEMATICS OF DIVISION BASIDIOMYCOTA 3

Gasteromycetes are an unnatural assemblage of basidiomycetes sharing the common negative character that the basidiospores are not discharged violently from their basidia. Instead of the ballistosporic basidiospores of other basidiomycetes which are asymmetric in side view, those of the gasteromycetes are usually symmetrically poised on their sterigmata or are sessile and such basidiospores statismospores. Commonly the basidia open into cavities within a fruit body, and the basidiospores are released into these cavities as the tissue between them breaks down or dries out. A recognizable fertile layer (hymenium) may be present or absent. The internal production of basidiospores has given the gasteromycetes their name (gaster: stomach). The gasteromycete fruit body is termed the gasterocarp, and the spore mass enclosed by the gasterocarp wall (peridium) is the gleba. Sometimes, as in *Lycoperdon* or *Geastrum*, the gasterocarp opens by a pore through which the spores escape, but in forms with subterranean (hypogeous) fruit bodies there is no special opening, and it is possible that the spores are dispersed by rodents and other burrowing animals. In *Phallus* and its allies, the basidiospores are exhibited in a sticky mass attractive to insects, whilst in *Cyathus* and *Sphaerobolus* the spores are enclosed in separate glebal masses or peridioles which are dispersed as units. In spite of these variations in gasterocarp morphology, the life cycles of most gasteromycetes follow the general Homobasidiomycete pattern. Most species for which details are known appear to be heterothallic, with a basidiospore germinating to give a monokaryotic primary mycelium. Following fusion of compatible primary mycelia, a dikaryotic secondary mycelium is established, and this produces gasterocarps in which karyogamy and meiosis occur, and haploid basidiospores are formed. Dikaryotic asexual propagules are also known in some gasteromycetes.

Most members of the group are saprotrophic and grow on soil, rotting wood and other vegetation, or dung. Mycelial cords or rhizomorphs are often formed. *Rhizopogon* which produces hypogeous gasterocarps, and *Scleroderma* and *Pisolithus* with epigeous fruit bodies, are important ectomycorrhizal associates of forest trees. There are also two genera of aquatic gasteromycetes. *Nia vibrissa* grows on driftwood in the sea, forming globose, yellowish gasterocarps a few millimetres in diameter. Its basidiospores bear 4-5 radiating appendages. Such appendages are a typical adaptation to the aquatic habitat. *Limnoperdon* forms small, floating fruit bodies in freshwater swamps and marshes.

GASTEROID FUNGI IN THE EUAGARICS CLADE

The euagarics clade contains some 10 000 fungi in 26 families. Hymenia may be produced on the gills, pores and ridges of mushrooms and on the surface of coral-shaped fruit bodies, or basidia may be enclosed in gasterocarps. Among the gasteromycetes found within the euagarics, the important family is *Agaricaceae*.

AGARICACEAE (PUFFBALLS)

Puffballs such as Lycoperdoid *Agaricaceae*, *Vascellum* and *Calvatia* form a phylogenetically well-defined group which seems to be closely related to the genus *Macrolepiota* both on the basis of DNA sequence analyses and because of similarities in the ontogeny and architecture of rhizomorphs. Lycoperdoid *Agaricaceae* contains 18 genera and 158 species of gasteromycetes with epigeous fruit bodies. The mature gasterocarp is thinwalled and either forms an apical pore or disintegrates from the apex downwards (*Calvatia*, *Vascellum*, *Bovista*). Basidiospores are brown in colour and have warty or spiny walls, with the distal part of the basidial sterigma often remaining attached to mature spores. Most species are saprotrophic on soil and humus.

Genus: *Limnoperdon*

About 50 species are known, producing fruit bodies which are pear-shaped or top-shaped.

Most species grow on the ground. *Lycoperdon pyriforme* is unusual in growing directly on old stumps, rotting wood and sawdust heaps.

Genus: *Calvatia*

Gasterocarps about the size of a rugby football are produced by *Calvatia* (*Langermannia*) *gigantea* growing on grassland and on disturbed ground. There is no definite pore; the peridium breaks away to expose a brown spore mass.

AGARICACEAE (BIRD'S NEST FUNGI)

Gasterocarps are funnel-shaped, and the gleba is differentiated into lens-shaped peridioles (glebal masses) which contain the basidiospores. Some 50 species in 4 genera are known, of which the most common examples are *Cyathus* and *Crucibulum*. Members of this family are saprotrophic and are capable of degrading lignin.

Genus: *Cyathus*

The fruit bodies of *C. olla* can be found in autumn growing amongst cereal stubble. *Cyathus striatus*, recognized by the furrowed inner wall of its cups, grows on old stumps and twigs whilst *C. stercoreus* grows on old dung patches. This last species can be made to fruit readily if mycelium.

GASTEROMYCETES IN THE BOLETOID CLADE

The boletoid clade, as defined by molecular phylogeny, contains fungi with a wide range of fruit body types, including lamellate (e.g. *Paxillus*), boletoid (e.g. *Boletus*, *Leccinum*, *Suillus*, *Xerocomus*) and resupinate forms (e.g. *Coniophora*, *Serpula*). These have been described previously. Gasteromycete fungi have arisen from boletoid ancestors on several occasions, with the family Sclerodermataceae having an affinity with *Gyroporus* in a 'boletoid' branch, and the Rhizopogonaceae with *Suillus*. Both families contain mainly

ectomycorrhizal fungi. Features of their association with tree roots are typical of members of the boletoid clade in that there is a large amount of fungal biomass extending from the mantle into the soil by means of mycelial cords or rhizomorphs which may be several metres long. This type of ectomycorrhiza appears to be particularly effective in exploiting a large volume of soil for nutrients, and it is also credited with improving the water status and thus the performance of the tree host under conditions of drought. The ability to form an extensive rhizomorph system may explain why mycorrhizal gasteromycetes belonging to the boletoid clade are particularly prominent in dry habitats. It is probable that long-distance transport processes in rhizomorphs are facilitated by peristaltic movement through a system of tubular vacuoles. Certain ectomycorrhizal fungi such as *Rhizopogon*, *Scleroderma* and *Pisolithus* can be grown in pure culture, and basidiospore inoculum from their relatively large fruit bodies is also easily collected and stored. Hence, these species are suitable for laboratory-based research as well as inoculation of trees prior to outplanting into forestry situations.

In addition to the morphology of ectomycorrhiza, there are several further features betraying an affinity of the *Sclerodermataceae* and *Rhizopogonaceae* with the boletoid clade. For instance, pulvinic acid-type pigments typical of *Boletus*, *Suillus* and *Xerocomus* are also found in their gasteromycete relatives, either in a pure form or as derivatives. Further, the mycoparasitic mould *Apiocrea chrysosperma* (anamorph *Sepedonium chrysospermum*), which frequently forms a golden yellow conidial crust on fruit bodies of *Boletus*, *Suillus*, *Xerocomus* and *Paxillus*, also infects gasteromycetes such as *Scleroderma* and *Rhizopogon*

Family: *Sclerodermataceae*

This family comprises some 50 species in 7 genera, including the earth ball *Scleroderma*, the stalked puffball *Calostoma*, the dye ball *Pisolithus*, and the barometer earth star *Astraeus*. All members seem to be ectomycorrhizal with trees. Here we shall consider the two most important genera, *Pisolithus* and *Scleroderma*.

Family: *Rhizopogonaceae*

This family comprises some 150 species in 4 genera. By far the most important genus is *Rhizopogon*, which is mycorrhizal mostly with coniferous trees.

GASTEROID FUNGI IN THE GOMPHOID-PHALLOID CLADE

The gomphoid-phalloid clade contains some 350 species of morphologically diverse fungi. Most of the species with active basidiospore discharge form coral- or club-shaped basidiocarps, e.g. *Ramaria*, *Clavariadelphus* and *Gomphus*.

Family: *Phallaceae*

An original solution to the problem posed by the loss of active basidiospore discharge has been developed also by members of the Phallaceae which attract insects, especially cadaverfeeding flies such as bluebottles, to visit their gasterocarps. Attraction may be by the emission of a cadaverous smell or by colour, with gasterocarps of species like *Clathrus ruber* and *C. archeri* appearing dark red due to the accumulation of carotenoids, chiefly lycopene. There may be a synergism of attractions because species with brightly coloured gasterocarps tend to emit less evil smells than dull-coloured ones.

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