

Fungal phyla

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40 years ago I learned from my teacher E. GÄUMANN at Zürich, that the fungi represent a monophyletic group of plants which have algal ancestors. The Myxomycetes were excluded from the fungi and grouped with the amoebae.

GÄUMANN (1964) and KREISEL (1969) excluded the Oomycetes from the Mycota and connected them with the golden and brown algae.

One of the first taxonomist to consider the fungi to represent several phyla (divisions with unknown ancestors) was WHITTAKER (1969). He distinguished phyla such as Myxomycota, Chytridiomycota, Zygomycota, Ascomycota and Basidiomycota. He also connected the Oomycota with the Pyrrophyta — Chrysophyta — Phaeophyta. The classification proposed by WHITTAKER in the meanwhile is accepted, e. g. by MÜLLER & LOEFFLER (1982) in the newest edition of their text-book "Mykologie".

The oldest fungal preparation I have seen came from fossil plant material from the Carboniferous Period and was about 300 million years old. The structures could not be identified, and may have been an ascomycete or a basidiomycete. It must have been a parasite, because some deformations had been caused, and it may have been an ancestor of *Taphrina* (Ascomycota) or of *Milesina* (Uredinales, Basidiomycota). Species of these genera now grow on ferns, which also evolved in the Carboniferous Period and which are today the most ancient living larger plants.

Fungi growing on living parts of mosses and ferns are considered to be the most ancient plant parasites. Parasitic fungi on ferns belong to *Synchytrium* (Chytridiomycota, also on mosses), *Taphrina*, several rust genera, e. g. *Milesina* and *Uredinopsis*, and to several ascomycete genera, mainly of the family Parmulariaceae (Dothideales). Ascomycetes with ostiolate ascomata are known to parasitize mosses and are classified mainly in the Dimeriaceae (Dothideales).

SAVILE (1955) regarded *Taphrina* as related to ancient rust fungi, both having been derived from a hypothetical genus *Prototaphrina*. Recently it has been shown that this supposition is not justified. Both *Taphrina* and rust fungi are fundamentally different in the submicroscopical structure of the cell walls, mitosis and chemistry (e. g. von Arx & al., 1982; HEATH & al., 1982). *Taphrina* has ascomycete-like cell walls, in

TEM showing a thin, dark outer and a relatively thick, transparent inner layer. The rust fungi, on the other hand, are basidiomycetous having electron opaque cell walls which become layered due to the formation of new inner walls.

Taphrina species on ferns are rare fungi found in North America. KRAMER (1958) erected a separate genus *Mixia* for a primitive *Taphrina* growing on *Osmunda regalis* and classified it in the Protomycetaceae (Taphrinales). All other members of this family have been found on Apiaceae and Asteraceae, both highly evolved Dicotyledons. The fungus on *Osmunda*, however, may be the ancestor of all Taphrinaceae and Protomycetaceae, but not of other Ascomycetes.

The most ancient, still living Ascomycota are possibly the Endomycetes, e. g. species of *Dipodascus* and *Endomyces*, which grow as saprophytes in mainly liquid media and soil. Nothing is known about their ancestors, but they were probably the precursors of the asciforming yeasts and also the Taphrinales. The hyphal Endomycetes should be distinguished from the Ascomycetes, not only due to the absence of ascospores, but also due to the hyphal septa which are multiporate with micropores (plasmodesmata) or not porate (a closure line in the septum may suggest a central micropore). The septa of the Ascomycetes in TEM show a distinct central pore occluded by electron opaque WORONIN bodies in age. The Endomycetes (including Taphrinales) can also be distinguished from the Ascomycetes by chemical characters (BARTNICKI-GARCIA, 1968; von ARX & al., 1982).

The Parmulariaceae, as delimited by MÜLLER & von ARX (1962), contain rare Ascomycetes parasitic on ferns, conifers and some broad-leaved plants in tropical and subtropical regions of the Southern Hemisphere. They probably evolved on ferns in a precretaceous period in the former southern continent, Gondwanaland, at least 100 million years ago (PIROZYNSKI & WERESUB, 1979). The Parmulariaceae represent the ancestors of the Asterinaceae, Englerulaceae, Perisporiopsidaceae and other bitunicate Ascomycetes with non-ostiolate ascospores. Bitunicate Ascomycetes with ostiolate ascospores, e. g. Dimeriaceae, Venturiaceae and Mycosphaerellaceae probably stem from moss parasites delimited by DÖBBELER (1978). A well known example is *Lizonia emperionia* on the moss *Polytrichum commune*. It has spherical, ostiolate ascospores and bitunicate, paraphysate asci and is usually classified in the Dimeriaceae (MÜLLER & von ARX, 1962).

Rust fungi on ferns are known mainly from the Northern Hemisphere, e. g. species of the genera *Milesina* and *Uredinopsis*. Some of them have conifers as alternate hosts; the haplonts (spermogonia and aecia) of several species parasitize needles of *Abies alba* (GÄUMANN, 1959). They must have evolved simultaneously with their host plants about 200 million years ago (Perm, Trias). In my opinion all heteroe-

cious rust fungi must have evolved simultaneously with their host plants.

Nothing is known about ancestors of other Basidiomycota. They could not have evolved from ancient rust fungi. Ustilaginales and Tilletiales do not occur on mosses, ferns and conifers and must have evolved simultaneously with their monocotyledonous and dicotyledonous host plants from unknown ancestors.

MÜLLER & LOEFFLER (1982) accepted two classes in the Basidiomycota, the Ustomycetes and the Basidiomycetes. The Ustomycetes include the Ustilaginales (parasitic, smut fungi) and the Sporobolomycetales or Sporidiales (saprophytic, red yeasts). Both produce yeast-like haploid states and diploid resting spores germinating with a "promycelium". Distinct basidia are absent and only a few saprophytic species develop hyphae which have septa without dolipores.

MÜLLER & LOEFFLER classified the Tilletiales in the Basidiomycetes and considered them unrelated to the Ustomycetes. The hyphae of the Tilletiales are septate with dolipores. Germinating resting spores form a basidium, usually with one apical whorl of sessile, arcuate or falcate basidiospores. The Exobasidiales, also included in the Basidiomycetes, have rather similar basidia formed on septate hyphae; the basidiospores, however, propagate by budding.

The Uredinales are peculiar within the Basidiomycota having hyphae with septa without dolipores and transversely septate, often arcuate basidia. Anamorphic and spermatial states are commonly found (spermogonia, aecia, uredinia). A separate class Urediniomycetes or Teliomycetes has to be considered (KHAN & KIMBROUGH, 1982; HAWKSWORTH & al., 1983; KREISEL, 1984). The Basidiomycetes (s. str.) would then contain only taxa with aseptate or occasionally longitudinally or cruciately septate basidia, e. g. the Cantharellales, Polyporales, Agaricales, Boletales, Russulales and "Gasteromycetes". Most of the species belonging to these orders do not include anamorphs or the "conidia" are unable to germinate.

The algae are usually considered to be the ancestors of the fungi. Blue, green, golden, brown and red algae are mentioned. All these suppositions are mere suspicion and speculation. Only the Oomycota may be connected with Chrysophyta and Phaeophyta (golden and brown algae). A *Chrysomonas*-like organism may have been a common ancestor. All have motile cells with two types of flagella: of the tinsel- and of the whip lash-type. The Oomycota are also the only fungi with cellulose-containing cell walls.

The Ascomycota have often been derived from the red algae (Rhodophyta). This supposition has been discussed and defended by DEMOULIN (1974). In both endospores are formed in ascus cells, but the caryology, chemistry and submicroscopy are dissimilar. They probably

have common, but unknown ancestors. Rhodophyta and Ascomycota may be very old. Red algal or ascomycete-like fossils are putatively described from the Cambrium. The structures have been found in dolomite from Australia (SCHOPF & BARGHOORN, 1969; TIFFANY & BARGHOORN, 1974). The oldest apparently fungal fossils and the oldest Eucaryotes are found in Southern Africa (Swartkoppie Hornstein, Swaziland) and are described as *Ramsaysphaeria ramses* PFLUG (1976). The age has been determined as 3300 million years (Precambrium). The fossils show hyphal structures covered with protuberant scars and forming blastic cells (conidia) on a rather broad base. PFLUG & von KLOPOTEK (1978) compared the structure with the mycelial yeast *Candida tropicalis*. Some Hyphomycetes, however, have more similar conidiogenous hyphae and protuberant scars. Such fungi, however, are not aquatic. Nevertheless, the discovery of *Ramsaysphaeria ramses* is spectacular and questions all theories of the evolution of eucaryotic life.

WHITTAKER (1969) considered the Zygomycota, Ascomycota and Basidiomycota to have common ancestors, but this cannot be established. In any case the Basidiomycota cannot have been evolved from any known member of the Ascomycota and the latter cannot be descendants of Zygomycota or Chytridiomycota. All represent independent phyla with unknown ancestors, but with a common character in that they are heterotrophic and show absorptive nutrition.

The fungal phyla and their classes are summarized in Fig. 1.

Fig. 1. The higher taxa of the fungi and the number of fungal species (partly from MÜLLER & LOEFFLER, 1982, and from HAWKSWORTH & al., 1983).

phyla (divisions)	classes (number of taxa)
Myxomycota	Myxomycetes (500)
	Acrasiomycetes (20)
	Plasmodiophoromycetes (30)
Oomycota	Oomycetes (600)
	Hyphochytridiomycetes (20)
	Labyrinthulomycetes (20)
Chytridiomycota	Chytridiomycetes (500)
Zygomycota	Zygomycetes (300)
	Endogonomycetes (100)
	Entomophthoromycetes (200)
Ascomycota	Endomycetes (500)
	Ascomycetes (30000)
Basidiomycota	Ustomycetes (400)
	Basidiomycetes (9500)
	Urediniomycetes (5500)
	(Teliomycetes)

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