Wolfgang Frey (Editor)

Syllabus of Plant Families

13th ed.

A. Engler's Syllabus der Pflanzenfamilien

1/2 Ascomycota

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Syllabus of Plant Families

Adolf Engler's Syllabus der Pflanzenfamilien

13th edition by Wolfgang Frey

Part 1/2 Ascomycota

Walter Jaklitsch, Hans-Otto Baral, Robert Lücking, H. Thorsten Lumbsch

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Ascomycota: Introduction, Characterization and systematic arrangement*

* with contributions by H.-O. Baral and W. Jaklitsch

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Non-lichenized Ascomycta p.p.

Taphrinomycotina, **Saccharomycotina**, **Dothideomycetes** (exc. Lichenized Ascomycota: Abrothallales, Racodiaceae, Lichenoconiales, Lichenostigmatales, Lichenotheliales, Monoblastiales, Arthopyreniaceae, Mycoporaceae, Naetrocymbaceae, Strigulales, Trypetheliales, Moriolaceae; Patellariales; **Eurotiomycetes** (exc. Lichenized Ascomycota: Lyrommataceae, Microtheliopsidaceae, Pyrenotrichaceae, Pyrenulales, Verrucariales, Mycocaliciomycetidae); **Laboulbeniomycetes**, **Leotiomycetes** (Erysiphales, Leotiomycetes fam. inc. sed.); **Sordariomycetes**, **Xylonomycetes**, **Pezizomycotina** fam. inc. sed. p.p. (Batistiaceae, Diporothecaceae, Eoterfeziaceae, Hispidicarpomycetaceae, Kathistaceae, Mucomassariaceae, Seuratiaceae); **Pezizomycotina** gen. inc. sed

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Non-lichenized Ascomycota p.p.

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Lichenized Ascomycota

Arthoniomycetes, **Coniocybomycetes**, **Dothideomycetes** (Abrothallales, Racodiaceae, Lichenoconiales, Lichenostigmatales, Lichenotheliales, Monoblastiales, Arthopyreniaceae, Mycoporaceae, Naetrocymbaceae, Strigulales, Trypetheliales, Moriolaceae, Lyrommataceae, Microtheliopsidaceae, Pyrenotrichaceae, Pyrenulales, Verrucariales, Mycocaliciomycetidae), **Lecanoromycetes** (exc. Phaneromycetaceae, Lecanoromycetes gen. inc. sed.), **Lichinomycetes**, **Pezizomycotina** ord. inc. sed., **Pezizomycotina** fam. inc. sed. p p. (Aphanopsidaceae, Dactylosporaceae, Epigloeaceae, Requienellaceae, Strangosporaceae, Xanthopyreniaceae).

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Synopsis of classification of the Ascomycota Caval.-Sm.

DI Dr. Walter Jaklitsch, Prof. Dr. W. Frey. Addresses s.ab.

Preface

Half a century ago, in 1954, the 12th edition (vol. 1, 2) of Adolf Engler's well-known "Syllabus der Pflanzenfamilien" ("Syllabus of Plant Families"), ed. by H. Melchior and E. Werdermann was published. Later, a revision of the mosses (13th ed., Kapitel V,2 Bryophytina), by K. Walther, followed in 1983.

The 13th edition will be published in five parts, started in 2009 with **Part 3** "**Bryophytes and seedless Vascular Plants**" and followed in 2012 by **Part 1/1** "**Blue-green Algae, Myxomycetes and Myxomycete-like organisms, Phytoparasitic protists, Heterotrophic Heterokontobionta and Fungi p.p.**", in 2015 by **Part 2/1** "**Eukaryotic Algae**" **[Glaucobionta, Heterokontobionta** p.p. (Cryptophyta, Dinophyta, Haptophyta, Heterokontophyta), **Chlorarachniophyta, Euglenophyta, Chlorophyta, Streptophyta** p.p. (except Rhodobionta**)**] and **Part 4** "**Pinopsida** (Gymnosperms), **Magnoliopsida** (Angiosperms) p.p.: **Subclass Magnoliidae** [Amborellanae to Magnolianae, Lilianae p.p. (Acorales to Asparagales)]". Now, **Part 1/2** "**Ascomycota**" is published. This volume provides a basic treatise of the world-wide morphological and molecular diversity of the **Ascomycota**.

While the Fungi are not part of the Plant Kingdom, they are formally included within the classic Engler's title "Syllabus der Pflanzenfamilien / Syllabus of Plant Families", which comprised families of blue-green algae, algae, fungi, lichens, ferns, gymnosperms and flowering plants.

Following the tradition of Engler, and incorporating the latest results from molecular phylogenetics and phylogenomics, this completely restructured and revised 13th edition provides an up-to-date evolutionary and systematic overview of the fungal and plant groups. It is a mandatory reference for students, experts and researchers from all fields of biological sciences, particularly botany, phycology, and mycology.

The authors and the editor are grateful to the publisher, Dr. A. Nägele, for realizing this basic and fundamental systematic treatise, the **"Syllabus of Plant Families"**.

Berlin, summer 2015 W. Frey

Contents

Abbreviations

A	anamorphic (in parentheses)
acc.	according to
anam.	anamorph, anamorphic
approx.	approximately
c.	circa, about, approximately
cf.	confer, compare
clthec.	cleistothecial (ascomata that never open)
cosmopol.	cosmopolitan
DBBs	De Bary bubbles
diam.	diameter
e.g.,	exempli gratia, for example
esp.	especially
et al.	et alii“ (masc.) bzw. “et aliae” (fem.): “and others”.
exc.	except
ext.	extending
extratrop.	extratropical
fam.	family, families, familiae, famila
fam. inc. sed.	familia/ae incertae sedis
gen.	genus, genera
gen. inc. sed.	genus/genera incertae sedis
i.e.,	id est, that is
incl.	including
ined.	inedited, not published
inc. sed.	incertae sedis; uncertain systematic position
Ma	million years ago
medit., Medit.	mediterranean, Mediterranean region
N	North, northern
neotrop., Neotrop.	neotropical, Neotropics, Neotropical region
nom. illeg.	nomen illegitimum; validly published name, but not in accordance with one or more rules of nomenclature
nom. inval.	nomen invalidum, not validly published
occ.	occasional, occasionally
ord.	order, orders
ord. inc. sed.	order incertae sedis
orig.	originally, original
pantrop.	pantropical, in all tropical areas
p.p.	pro parte
predom.	predominant, predominantly
prob.	probably
resp.	respectively
SCBs	KOH-soluble (unstable) cytoplasmic bodies
s.l.	sensu lato, in a wide sense
spec., sp.	species
spp.	species (plural)
s.str.	sensu stricto, in a strict sense
subcosmopol.	subcosmopolitan
subtrop.	subtropical, subtropics
syn, syns.	synonym, synonymous, synonyms

synanam.	synanamorph
T	teleomorphic (in parentheses)
teleo-syn., teleo-syns.	teleomorphic synonym(s)
teleom.	teleomorph, teleomorphic
temp.	temperate, in temperate zones
text.	textura
trib.	tribus, tribe
trop., Trop.	tropical, tropics, Tropic (geo)element, Tropics
VB, VBs	(refractive) vacuolar bodies
vs.	versus
WBs	Woronin bodies
?	before a generic name means that placement in the family is uncertain or questionable or genera are provisionally

1 Introduction

The last two and a half decades provided revolutionary new insights into the phylogeny and diversity of organisms on earth. This is particularly true of the Fungi, where phylogenetic revisions have revolutionized the systematic classification of taxa from phylum to species level and a new understanding of fungal evolution and species delimitation has emerged. These new insights are here treated in an integrated context of morphological and molecular data, providing an up-to-date synopsis of this phylum while acknowledging that the systematic classification of this diverse group of Fungi is not yet fully settled.

The present Part 1/2 of the 13th edition of "Engler's Syllabus of Plant Families" gives an up-to-date review of the **Ascomycota** (including lichenized forms) and their relationships down to the family and genus level. While several modern treatments of the Ascomycota systematics exist, this synthesis includes a complete phylogenetic synopsis of all taxa down to genus level together with detailed descriptions for all families, and complete listings of genera per family, with estimates of species numbers at the family or genus level, integrating classical anatomical-morphological characters with modern molecular data, combined with numerous new discoveries made during the last ten years.

While the **Fungi** are not part of the Plant Kingdom, they are formally included within the classic Engler's title "Syllabus der Pflanzenfamilien / Syllabus of Plant Families", which comprised families of blue-green algae, algae, fungi, lichens, ferns, gymnosperms and flowering plants.

Engler's Syllabus is an attempt to give an up-to-date evolutionary and systematic overview of the plant, algal and fungal groups. The Fungi will be treated in 3 parts [Part 1/1 Fungi p.p. (Chytridiomycota, Zygomycota, Glomeromycota; published 2012); Part 1/2 Ascomycota; published now, Part 1/3 Basidiomycota] arranged according to the most recent phylogenetic classification systems. Part 1/3 "Basidiomycota" will follow.

2 Ascomycota

2.1 Introduction

The Ascomycota represent the largest phylum within the kingdom Fungi, with nearly 65,000 known species, corresponding to over 60% of all known fungi (Kirk et al. 2008). Together with Basidiomycota, Ascomycota form the subkingdom Dikarya, and both phyla together with Glomeromycota the informal clade Symbiomycota (Tehler et al. 2003, Hibbett et al. 2007). The Ascomycota are also called the 'sac fungi', as their meiosporangium, the ascus, commonly takes the shape of a sac, and meiospores, called ascospores, are formed within the ascus. For a long time considered a class (Ascomycetes), the Ascomycota were only recently elevated to the level of phylum (Cavalier-Smith 1998).

Biological life styles in the Ascomycota range from chemoorganotrophs to saprotrophs, to parasites on plants and animals, to parasites, hyperparasites and parasymbionts on other fungi and on lichens, to endophytes and endolichenic fungi, carnivores, to mutualistic associations, such as ectomycorrhizae and lichens (Hawksworth 1988, Alexopoulos et al. 2004, Deacon 2005, Hock 2012). Especially lichenized associations with algae and/or cyanobacteria represent a successful lifestyle with over 18,500 known species, whereas ectomycorrhizal fungi in the Ascomycota are not as speciose as in the Basidiomycota (Feuerer & Hawksworth 2007, Hock 2012). Lichenization is considered one of the most derived biological lifestyles in the Ascomycota (Brodo et al. 2001, Nash 2008, Schoch et al. 2009).

Historically, lichens were for a long time considered to be a separate group of organisms, and it was not before DeBary and Schwendener discovered in the 1860s (Schwendener 1867) that lichens are actually symbiotic organisms consisting of a fungal and one or several algal/cyanobacterial partners. Lichen symbioses are found in several classes in Leotiomyceta, but are concentrated in Arthoniomycetes, Dothideomycetes, Eurotiomycetes, Lichinomycetes, and esp. Lecanoromycetes.

2.2 Characterization and systematic arrangement

2.2.1 Characterization

The cell walls in Ascomycota consist of chitin and glucanes and are two-layered. Filamentous species have simple septa which are often surrounded by peroxisome-derived, dense core microbodies, so-called Woronin bodies (WBs) that can block the septal pores (Beckett et al. 1974, Bowman & Free 2006). Most Ascomycota grow as microscopically visible filamentous hyphae, in larger bundles visible as mycelia or 'mold'. Budding is mostly found in yeasts and yeast-like forms, and many of those can develop both budding and hyphal growth (Pöggeler & Wöstemeyer 2011). Vegetative mycelia and cells are typically haploid (exception: Taphrinomycetes) and, usually in specialized structures, undergo fertilization and sexual reproduction. A particular feature of lichen fungi is the formation of a vegetative thallus, often highly differentiated, that is unknown from non-lichenized fungi, and which permits lichens to persist non-cryptically in a wide range of ecosystems (Henssen & Jahns 1974, Sanders 2001).

Sexual reproduction. Fertilization in Ascomycota can happen through gametangiogamy (fusion of male, called antheridia, and female gametangia, called ascogonia), gameto-gametangiogamy (spermatia fuse with ascogonia) or rarely somatogamy (no gametangia are formed). Typically, a long, thin hypha emerges from the ascogonium, which is called trichogyne and functions as a conceptual organ. After fertilization, the two nuclei remain separate for a short dikaryotic phase and eventually fuse to form a diploid nucleus, which soon undergoes meiosis. Fusion and meiosis occur in the ascus, which usually produces eight ascospores internally (as opposed to the usually four externally produced basidiospores in the Basidiomycota); for "pyrenomycetous" taxa in this treatment not further noted. However, the number of ascospores can vary from one to many hundreds within a single ascus, due to either degeneration of spores, omitted mitotic division, or subsequent mitotic divisions before spore wall formation (Alexopoulos et al. 2004, Deacon 2005).

In basal lineages of the Ascomycota, asci are formed on undifferentiated mycelium, whereas in the genus *Neolecta* and in subphylum Pezizomycotina, the asci are produced in fruiting bodies (Pöggeler & Wöstemeyer 2011). These fruiting bodies (ascomata) are variably composed of vegetative (haploid) and generative (dikaryotic) hyphae plus the initially diploid asci and can take many different shapes: apothecia (with the hymenial surface containing the asci and sterile hyphae exposed), perithecia (hymenium covered and opening by a pore), cleistothecia (remaining completely closed; asci randomly arranged), chasmothecia (remaining completely closed; asci arranged in fascicles); hysterothecia or lirellae (elongate with an exposed or slit-like hymenium), and pseudothecia (morphologically similar to perithecia but with different ontogeny and bitunicate asci; perithecioid ascomata called herein), thyriothecia (shield-like), loculi in stromata (lacking a wall, with bitunicate asci) and ascostromata (asci singly immersed in stromatic tissue; see Myriangiales). Within the fruiting body, the asci are either randomly arranged or mostly arranged in a single layer, the hymenium, separated by sterile hyphae called paraphyses or analogous structures (the hamathecium). In most cases, asci develop a particular apical apparatus which aids in the active discharge of the ascospores; this apparatus and the overall structure of the ascus are important systematic characters (Peršoh et al. 2004). In several lineages, mostly in lichenized forms, the asci decompose prematurely and the ascospores remain as a dry mass on the fruiting body (mazaedium), supposedly an adaptation to wind dispersal.

Variation in ascospore shape, size, pigmentation, ornamentation, and internal structure and septation usually provides a valuable set of characters for identification at various levels, from species to genus and sometimes family or even order. The same is true to a certain extent of ascus types. The internal anatomy of sexual and asexual fruiting bodies also provides important characters not only for taxonomy but also to predict phylogenetic relationships (Miller & Huhndorf 2005), whereas the external morphology is often misleading and cases of parallel evolution of functionally similar fruiting bodies are common. Often, the ontogeny of fruiting bodies, the hamathecium, asci, and ascospores shed light on the evolutionary relationships of these structures (Henssen & Jahns 1974).

Asexual reproduction. Besides sexual fruiting bodies or ascomata, most Ascomycota also reproduce asexually by means of conidia, mitotically formed cells that either are produced superficially or in specific asexual fruiting bodies or conidiomata. These often take a shape similar to perithecia and are then called pycnidia, or simple cavities (acervuli), can be asymmetrical and lobe-shaped (campylidia) or produce the conidia at the tip of agglutinate setae (hyphophores) or as extended, superficial cushions (sporodochia). Many Ascomycota are only known to produce conidiomata in so-called anamorphic life cycles. Fungi with superficially formed conidia are characterized as hyphomycetous, whereas those with internally formed conidia are termed coelomycetous, but these terms do not denote natural groups. Anamorphic or sterile Ascomycota were previously classified in the subphylum Deuteromycotina, comprising the form-classes Agonomycetes (Mycelia Sterilia), Coelomycetes (Sutton 1980) and Hyphomycetes (Seifert et al. 2011, Seifert & Gams 2011). However, with the help of DNA sequence data they can now be readily assigned to specific lineages (Cannon & Kirk 2000, Kirk et al. 2008, Hawksworth 2011). Phylogenetic studies have shown that these forms are spread across the Ascomycota (and Basidiomycota). Fungi that produce both asexual conidia (anamorphic) and sexual ascospores (teleomorphic) as distinctive elements of a complex life cycle are called pleomorphic, and the entirety of these forms are called holomorphs. In some lineages, and especially in lichenized fungi, both asexual and sexual reproduction may occur on the same individual, but may also be part of a more complex life cycle that may include synanamorphs or synteleomorphs.

A large number of lichens produce amphigenous diaspores propagating both fungal and algal/cyanobacterial partner simultaneously. The simplest form is fragmentation of the lichen thallus, common in terrestrial fruticose lichens. However, special structures are formed by numerous lichens. Soredia consist of groups of photobionts surrounded by fungal hyphae and occur in cracks of the thallus surface called soralia. Corticate outgrowths of the thallus that break off and thus function as propagules are called isidia; in many cases these become applanate and dorsiventral and then are termed phyllidia. Schizidia are well-defined, corticate, often disc-shaped thallus fragments specifically modified for dispersal.

Ecology and distribution. Ascomycota are found in all terrestrial ecosystems and several lineages are aquatic in freshwater or marine environments. Cosmopolitan distributions are often anthropogenic, whereas most species with natural distribution ranges are restricted to certain geographic regions; parasitic lineages are typically correlated with the distribution of their hosts. Across all biological lifestyles present in the phylum, many widespread 'species' actually represent geographically differentiated species complexes and sometimes not even closely related species at all (Cai et al. 2011, Moncada et al. 2014).

Ascomycota, together with other fungi and microorganisms, fulfil a pivotal role in ecosystem function, particularly as biomass decomposers and controlling host populations as parasites, as well as enhancing plant growth in mutualistic relationships (Alexopoulos et al. 2004, Deacon 2005, Hock 2012). Thus, they directly and indirectly influence ecosystem diversity and species richness, as well as ecosystem productivity. The ascomata and to some extent also the mycelia are important food sources for animals, mostly invertebrates but also mammals. Many Ascomycota live as endophytes, forming sterile hyphae within living plant tissues (Arnold & Lutzoni 2007, Higginbotham et al. 2013). The biological role of these endophytes is not precisely known, but many appear to represent latent forms of saprotrophs that eventually decompose plant parts after these die off. Some Ascomycota form symbioses with insects, such as the bark beetles in the family Curculionidae, which are notorious pests by themselves and by spreading fungal diseases such as Dutch Elm disease (Haugen 1998). In most ecosystems, the most obviously visible Ascomycota are lichenized forms, and in some ecosystems, such as the arctic tundra, coastal maritime Antarctica, coastal deserts in western America and southwestern Africa, and parts of the alpine zone in high mountains, lichens dominate the landscape (Kappen 1988).

Physiologically, Ascomycota have developed the ability to break down a large variety of organic substances, including cellulose, lignin, collagen, and keratin, without the aid of bacteria or other microorganisms, using their own enzymes (Harms et al. 2011). Extreme examples are the fungi *Aureobasidium pullulans* (de Bary & Löwenthal) G. Arnaud (Dothioraceae), a black, yeast-like fungus that decomposes wall paint, and *Amorphotheca resinae* Parbery (Amorphothecacae), which consumes kerosene and fuel components (Chi et al. 2009, Zhang et al. 2010). Some lichens that colonize man-made substrates such as concrete and marble may cause surface damage through the excretion of lichen acids, especially on historical monuments (Aptroot & James 2002, Pinna 2014). Besides playing a pivotal role as decomposers, Ascomycota and other fungi have also attracted the interest of the pharmaceutical industry due to their rich chemical properties (Hofrichter 2011).

Of particular interest among the Ascomycota are those that attack invertebrates and especially arthropods, either as carnivores or as parasites, particularly in the classes Orbiliomycetes, Laboulbeniomycetes, and Sordariomycetes (Alexopoulos et al. 2004, Deacon 2005). Species in Orbiliomycetes produce peculiar traps to capture nematodes and other invertebrates, which are then digested (Nordbring-Hertz et al. 2011). Laboulbeniomycetes are usually non-lethal ectoparasites of insects, most commonly on Coccinellidae beetles, and are usually highly specific not only to their host species but to particular body parts (Weir & Hammond 1997). Perhaps the most conspicuous animal-parasitic lineages in the Ascomycota are the families Cordycipitaceae and Ophiocordycipitaceae in Sordariomycetes (Hypocreales). These typically club-shaped fungi are obligate endoparasites on insects and other arthropods (Xiao-Liang & Yi-Jian 2011). After attacking a host, the fungal mycelium replaces the host tissue and, in some species, the behaviour of the host is chemically affected thus that it climbs to an exposed position, thus facilitating subsequent dispersal of the ascospores or conidia produced by the fungal parasite.

Some Ascomycota, esp. Hypocreales, act as hyperparasites by attacking other fungi via enzymatic breakup of cell walls and by antibiotics. Fungal parasites or parasymbionts are also common on lichens and can usually be categorized into two groups: parasites that attach to the lichen mycobiont, often damage the lichen, and are phylogenetically related to non-lichenized fungi, and parasymbionts that associate with the lichen photobiont, generally to not harm the host thallus, and are phylogenetically close to lichenized lineages (Grube & Lücking 2002).

Evolution. The age of the Ascomycota has been estimated as between several hundred million and up to 1.5 billion years (Berbee & Taylor 1993, 2007; Taylor & Berbee 2006; Prieto & Wedin 2013; Taylor et al. 2014). Unfortunately, the fossil evidence is scarce (Taylor et al. 2014). Revised molecular clock studies indicate that the split between Ascomycota and Basidiomycota occurred between 500 and 600 Ma (Lücking et al. 2009a, Berbee & Taylor 2010), although a recent study using internal (mostly terminal) fossil calibrations only suggests a more ancient split (Beimforde et al. 2014). However, internal and especially terminal calibrations do not take into account the effect of decreasing evolutionary rates over time and hence can considerably overestimate basal node ages through extrapolation. The estimate of the early diversification of the Ascomycota at around 500 Ma is comparatively well in line with the transition of plants to land and the early evolution of land plant lineages (Lücking et al. 2009a), which supports the notion that higher fungi generally show close ecological associations with terrestrial ecosystems (Alexopoulos et al. 2004, Deacon 2005, Hock 2012). On the other hand, estimates for a more ancient origin of the Ascomycota would support the alternative hypothesis that Ascomycota originated earlier than land plants and initially existed as lichen-like associations, the so-called 'protolichens' (Eriksson 2005).

Although about 65,000 species of Ascomycota are currently recognized, predictions estimate a much higher number, between 1.5 and 3 million for all fungi and somewhere between 1 and 2 million Ascomycota (Hawksworth 2001). That such numbers are perhaps not far from reality is shown by the example of the recently described class Archaeorhizomycetes (Rosling et al. 2011, Menkis et al. 2014). This class currently contains two described species in a single genus, *Archaeorhizomyces*, but about 500 species have been predicted based on rarefaction analysis and many more species are found when analyzing environmental sequence data from next-generation sequencing techniques (Smith & Lücking, unpubl. data). Correct estimations of species richness in Ascomycota is also dependent on the application of species concepts to known data, and *Neurospora* (class Sordariomycetes) has long been used as a model organism to understand the mechanisms of speciation, integrating biological, morphological and phylogenetic species concepts as well as genomics (Metzenberg & Glass 1990, Glass & Smith 1994, Ellison et al. 2011, Turner et al. 2011).

The most detailed predictions of undiscovered species richness have been made for lichenized Ascomycota. Currently almost 18,500 lichenized Ascomycota are accepted worldwide (Feuerer & Hawksworth 2007), but a total of 28,000 spp. has been predicted (Lücking et al. 2009b). The family Graphidaceae alone is estimated to contain over 1,800 undiscovered species (Lücking et al. 2014). Until most recently, it was widely accepted that undiscovered species would be found mostly in little-studied microlichens, but findings from presumably well-known macrolichen families such as Lobariaceae and Parmeliaceae (Crespo & Lumbsch 2010, Lumbsch & Leavitt 2011, Moncada et al. 2014) have challenged this view.

Importance and uses Ascomycota are of great importance for humans in both positive and negative terms, to the point that these fungi are practically present in our daily lives without us noticing them (Deising 2009, Hock 2012). Mushroom-like Ascomycota in the Pezizomycetes are considered delicacies, such as the highly prized morels (*Morchella* spp.) and truffles (*Tuber* spp.) and the Lobster Mushroom [*Hypomyces lactifluorum* (Schwein.) Tul. & C. Tul.]. Some lichens are also eaten by humans, such as the manna lichens (*Circinaria* spp.) and *Umbilicaria esculenta*, known in Japan as Iwatake. Molds of the genus *Penicillium* are important in the food industry, specifically in the production of strongly flavored cheeses such as Blue Cheese, Gorgonzola, Roquefort, and Camembert. Yeasts (*Saccharomyces* spp., especially *S. cerevisiae* Meyen) are widely used in the baking and beverage industry for their carbon dioxide and alcohol fermentation (Hofrichter 2011). Fungi are applied as biological control agents (Butt et al. 2001, Mahr et al. 2008) and several representatives of the Hypocreales are used in agriculture for biocontrol of insects [e.g., *Beauveria bassiana* (Bals.-Criv.) Vuill.] and phytopathogenic fungi (e.g., *Trichoderma* spp.), and also for increasing of plant health by protective action (*Trichoderma* spp.).

Many lineages of Ascomycota are chemically rich and contain pharmaceutically important secondary compounds, especially in the classes Eurotiomycetes, Dothideomycetes, Sordariomycetes, and Lecanoromycetes (Huneck & Yoshimura 1996, Hanson 2008, Stocker-Wörgötter 2008). The first known antibiotic known was penicillin, a group of closely related substances isolated from species of *Penicillium* in the Eurotiomycetes (Eurotiales, Aspergillaceae). Apart from antibiotics, large-scale industrial production involves citric acid (by *Aspergillus niger* Tiegh.) and enzymes, e.g., cellulases and pectinases by *Trichoderma* spp., used in the detergent, food and other industries (Hofrichter 2011). Species of the genus *Elsinoë* (Elsinoaceae) produce the powerful antioxidant Elsinochrome A (Liao & Chung 2008), which recently has also been detected in cultures of the lichen fungus *Graphis elongata* Zenker (Graphidaceae). The important immunosuppressant cyclosporin, used for instance during organ transplantation, was originally isolated from the non-lichenized fungus *Tolypocladium niveum* (O. Rostr.) Bissett (Ophiocordycipitaceae). Due to their rich secondary chemistry, lichens have long been used in traditional and homeopathic medicine, such as species of the genera *Cetraria*, *Lobaria*, and *Usnea* (Brodo et al. 2001, Boustie & Grube 2005, Malhotra et al. 2007, Zambare & Christopher 2012).

As much as Ascomycota have a positive impact on our lives, there are many harmful species acting as parasites or diseases on agricultural products or on humans directly. Dutch Elm Disease, which is caused by species of *Ophiostoma* (Ophiostomataceae), killed large numbers of elms in the Northern Hemisphere (Haugen 1998), and the Asian fungus *Cryphonectria parasitica* (Murrill) ~~M.E. Barr~~ (Cryphonectriaceae) attacks sweet chestnuts and is responsible for eliminating the American Chestnut. Powdery mildew disease of grapevines is caused by *Uncinula necator* (Schwein.) Burrill (Erysiphaceae). Ergot [*Claviceps purpurea* (Fr.) Tul.] attacks rye or barley, producing dark grain kernels that contain toxic and carcinogenic alkaloids that, when consumed, cause hallucinations and burning sensations in the limbs, also called ergotism or 'Saint Anthony's Fire'. These symptoms are also considered a medical explanation for 'bewitchment' (Matossian 1982). Lysergic acid diethylamide (LSD), which is used as a recreational drug has been isolated from the ergot fungus. Ascomycota molds of different systematic affiliations commonly destroy food items, among them the genera *Alternaria*, *Aspergillus*, *Cladosporium*, *Fusarium*, *Penicillium*, and *Trichoderma*. Many molds produce harmful mycotoxins. As an example, *Aspergillus flavus* Link, found on grains, legumes, and nuts, generates aflatoxin, a carcinogenic substance which also damages the liver. Grains infected with *Fusarium graminearum* Schwabe may contain the mycotoxin deoxynivalenol, causing mucous membrane lesions.

Many Ascomycota are human pathogens as agents of mycotoxicoses or mycoses, although compared to bacteria and viruses, the impact of fungal diseases on human health is minor. The best known fungal pathogen is the yeast *Candida albicans* (C.P. Robin) Boekhout, which attacks the mucous membranes, infecting the mouth or vagina (candidiasis). Common skin diseases such as athlete's foot and other forms of tinea are caused by Ascomycota, specifically the genera *Epidermophyton*, *Microsporum*, and *Trichophyton* (Eurotiomycetes, Onygenales, Arthrodermataceae). Immuno-compromised patients can develop severe lung infections through the fungus *Pneumocystis jiroveci* Frenkel and several disorders and even fatal infections by certain species of *Trichoderma*. Last but not least, conidia of several mold genera (e.g., *Alternaria*, *Aspergillus*, *Cladosporium*) cause allergies.

Several species of Ascomycota are important biological model organisms, such as *Saccharomyces cerevisiae* Meyen, *Schizosaccharomyces pombe* Lindner, and *Neurospora crassa* Shear & B.O. Dodge, including novel approaches to genome sequencing and gene expression (Davis & Perkins 2002, Fosburg 2005, Ruderfer et al. 2006).

2.2.2 Systematic arrangement of taxa

The systematic classification of the Ascomycota has undergone many changes in the past decades, reflecting methodological progress in recognizing systematically important characters such as ascoma morphology, ascoma development, ascus type, secondary chemistry, and cellular ultrastructure. However, by far the largest numbers of taxonomical changes at higher level within the Ascomycota have been made within the last 25 years based on DNA sequence data. While the first studies employed single locus data sets, mostly of the ribosomal DNA repeat, the number of multi-gene studies has increased dramatically within the last years and the availability of fungal-specific primers for a number of protein-coding genes allowed for inclusion of non-ribosomal loci in routine phylogenetic studies of the Ascomycota (Lutzoni et al. 2004, Lumbsch & Huhndorf 2010, Schoch et al. 2009).

The systematics of the Ascomycota has changed dramatically from textbook classifications published until a decade ago. The phylum now contains three subphyla, the Saccharomycotina, the Taphrinomycotina, and the Pezizomycotina. The latter includes all Ascomycota that produce fruiting bodies, except for the genus *Neolecta* in the Taphrinomycotina, which is otherwise a heterogeneous group that includes the fission yeasts and the recently discovered class Archaeorhizomycetes. The Saccharomycotina contain mostly the true yeasts. The three subphyla contain a total of 18 formally recognized classes, by far most of them in the Pezizomycotina (12), followed by the Taphrinomycotina (5). As the phylogenetic framework is still incomplete due to the lack of molecular data in several groups, in cases of uncertainty, the systematic arrangement given here is a pragmatic compromise between a conventional, morphology-based system and phylogenetic system based on molecular data, with emphasis on the latter.

Following a decision in the nomenclature sessions of the XVIII International Botanical Congress in Melbourne, Art. 59 of the International Code of Nomenclature for Algae, Fungi, and Plants now stipulates that only one name is to be used for each pleomorphic fungus based on priority or protected status, irrespective of its morph (anamorph, teleomorph), a rule that had already been in use for lichenized fungi prior to this change. Since this modification has many taxonomic implications and because many claimed anamorph/teleomorph relationships have not been assessed experimentally through culturing or by means of molecular data, nomenclatural changes have only been considered here for some taxa for which a sound consolidation has been achieved.

Species numbers (either exact or best estimates) are given for families and in many cases also for genera, except for some groups of non-lichenized Ascomycota due to tremendously rapid changes in the circumscription and scope of genera and determination of DNA data often for a small number of species within a genus, making estimations of generic affiliations of described species difficult. Established species delimitations have been challenged by recent studies, suggesting that the actual number of species in many groups is much higher than previously assumed. Many lineages have just begun to be studied in any detail, so the synopsis presented here is by no means final but rather represents a snapshot of the current state of knowledge.

In this Syllabus, classes and subclasses are arranged in systematic order and within each class or subclass, orders, suborders, and families are presented in alphabetical order, with the families in some cases divided into subfamilies. Higher taxa mostly are considered until the end of 2014, but a few selected publications in 2015 were included as well. The total number of families of Ascomycota recognized here is 406 (plus an additional ten lineages that might represent separate families but have not been formally named), the total number of genera approx. 6100 (of which nearly 4000 are explicitly listed in this treatment), and the total number of species approx. 57000. The three most species-rich classes of Ascomycota are Dothideomycetes (according to Kirk et al. 2008; no exact figures are currently available for this class due to constantly shifting taxonomic concepts and the unknown affinities of many anamorphic lineages), Lecanoromycetes (approx. 14900), and Sordariomycetes (approx. 11500), followed by Leotiomycetes (4100), Eurotiomycetes (2800), Laboulbeniomycetes (2100), Pezizomycetes (1600), Arthoniomycetes (1500), Saccharomycetes (700), Orbiliomycetes (460), Lichinomycetes (380), and Taphrinomycetes (120). The remaining six classes have less than 100 species each. The ten most species-rich families are Mycosphaerellaceae (possibly about 3300), Parmeliaceae (2760), Graphidaceae (2100), Meliolaceae (2000), Laboulbeniaceae (1930), Botryosphaeriaceae (1500), Xylariaceae (1300), Phyllachoraceae (1175), Verrucariaceae (870), and Ramalinaceae (825), together accounting for almost one third of all Ascomycota, although representing only 2.5% of all families.

The classification of the Ascomycota is periodically summarized in the Outline of the Ascomycota as part of Myconet at [http://www.fieldmuseum.org/ explore/myconet] and nomenclatural information can be obtained from Index Fungorum at [http://www.indexfungorum.org] and from MycoBank at [http://www.mycobank.org].

Part Hans-Otto Baral: Reliable taxonomic concepts until March 2015. Species numbers are provisional.

Part Walter Jaklitsch: Reliable taxonomic concepts until January 2014 under considerations of selected additional publications of 2014 and 2015. Species numbers are only given for a small number of taxa, due to uncertainties after splitting of genera, lacking revision.

Part Thorsten Lumbsch/Robert Lücking: Reliable taxonomic concepts until March 2015. Species numbers are provisional or estimated from recent revisions where available.

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3 Synopsis of classification of the Ascomycota Caval.-Sm.

1. Subphylum Taphrinomycotina O.E.Erikss. & Winka

Class **Archaeorhizomycetes** Rosling & T.Y.James
Order **Archaeorhizomycetales** Rosling & T.Y.James
Archaeorhizomycetaceae Rosling & T.Y.James
Class **Neolectomycetes** O.E.Erikss. & Winka
Order **Neolectales** Landvik, O.E.Erikss., Gargas & al.
Neolectaceae Redhead
Class **Pneumocystidomycetes** O.E.Erikss. & Winka
Order **Pneumocystidales** O.E.Erikss.
Pneumocystidaceae O.E.Erikss.
Class **Schizosaccharomycetes** O.E.Erikss. & Winka
Order **Schizosaccharomycetales** O.E.Erikss., Svedskog & Landvik
Schizosaccharomycetaceae Beij. ex Klöcker
Class **Taphrinomycetes** O.E.Erikss. & Winka
Order **Taphrinales** Gäum. & C.W.Dodge
Protomycetaceae Gray
Taphrinaceae Gäum. in Gäum. & C.W.Dodge

2. Subphylum Saccharomycotina O.E.Erikss. & Winka

Class **Saccharomycetes** O.E.Erikss. & Winka
Order **Saccharomycetales** Kudrjanzev
Alloascoideaceae Kurtzman & C.J.Robnett
Ascoideaceae J.Schröt.
Cephaloascaceae L.R.Batra
Debaryomycetaceae Kurtzman & M.Suzuki
Dipodascaceae Engl. & E.Gilg
Endomycetaceae J.Schröt.
Lipomycetaceae E.K.Novák & Zsolt
Metschnikowiaceae T.Kamieński
Phaffomycetaceae Y.Yamada, H.Kawas., Nagats. & al.
Pichiaceae Zender
Saccharomycetaceae G.Winter

Saccharomycodaceae Kudrjanzev
Saccharomycopsidaceae Arx & Van der Walt
Trichomonascaceae Kurtzman & Robnett
Trigonopsidaceae Lachance & Kurtzman
Saccharomycetales, gen. inc. sed.

3. Subphylum Pezizomycotina O.E.Erikss. & Winka

Class **Arthoniomycetes** O.E.Erikss. & Winka
Order **Arthoniales** Henssen ex D.Hawksw. & O.E.Erikss.
Arthoniaceae Rchb. ex Rchb.
Chrysotrichaceae Zahlbr.
Lecanographaceae Ertz, Tehler, G.Thor & al.
Opegraphaceae Körb. ex Stizenb.
Roccellaceae Chevall.
Rocellographaceae Ertz & Tehler
Arthoniales, gen. inc. sed.
Class **Coniocybomycetes** M.Prieto & Wedin
Order **Coniocybales** M.Prieto & Wedin
Coniocybaceae Rchb.
Class **Dothideomycetes** sensu O.E.Erikss. & Winka
Order **Abrothallales** Pérez-Ortega & Suija
Abrothallaceae Pérez-Ortega & Suija
Order **Acrospermales** Minter, Peredo & A.T.Watson
Acrospermaceae Fuckel
Order **Asterinales** M.E.Barr ex D.Hawksw. & O.E.Erikss.
Asterinaceae Hansf.
Order **Botryosphaeriales** Schoch, Crous & Shoemaker
Aplosporellaceae Slippers, Boissin & Crous
Botryosphaeriaceae Theiss. & H.Syd.
Melanopsaceae Phillips, Slippers, Boissin & al.
Phyllostictaceae Fr.
Planistromellaceae M.E.Barr
Saccharataceae Slippers, Boissin & Crous
Order **Capnodiales** Woron.
Antennulariellaceae Woron.
Capnodiaceae (Sacc.) Höhn. ex Theiss.
Cladosporiaceae Nannizi
Dissoconiaceae Crous & de Hoog
Euantennariaceae S.Hughes & Corlett
Metacapnodiaceae S.Hughes & Corlett
Mycosphaerellaceae Lindau
Piedraiaceae Viégas ex Cif., Bat. & Campos
Racodiaceae Link

Schizothyriaceae Höhn. ex Trotter, Sacc., D.Sacc. & al.
Teratosphaeriaceae Crous & U.Braun
Order **Dothideales** Lindau
Dothideaceae Chevall.
Dothioraceae Theiss. & H.Syd.
Order **Dyfrolomycetales** K.L.Pang, K.D.Hyde & E.B.G.Jones
Dyfrolomycetaceae K.L.Pang, K.D.Hyde & E.B.G.Jones
Order **Eremithallales** Lücking & Lumbsch
Melaspileaceae Walt.Watson
Order **Hysteriales** Lindau
Hysteriaceae Chevall.
Order **Jahnulales** Pang, Abdel-Wahab, El-Sharouney & al.
Aliquandostipitaceae Inderb.
Manglicolaceae Suetrong & E.B.G.Jones
Order **Lichenoconiales** Diederich, Lawrey & K.D.Hyde
Lichenoconiaceae Diederich & Lawrey
Order **Lichenostigmatales** Ertz, Diederich & Lawrey
Phaeococcomycetaceae McGinnis & Schell
Order **Lichenotheliales** K.Knudsen, Muggia & K.D.Hyde
Lichenotheliaceae Henssen
Order **Microthyriales** G.Arnaud
Microthyriaceae Sacc.
Order **Monoblastiales** Lücking, M.P.Nelsen & K.D.Hyde
Monoblastiaceae Walt.Watson
Order **Myriangiales** Starbäck
Cookellaceae Höhn. ex Sacc. & Trotter
Elsinoaceae Höhn. ex Sacc. & Trotter
Myriangiaceae Nyl.
Order **Mytilinidiales** Boehm, C.L.Schoch & Spatafora
Gloniaceae Boehm, C.L.Schoch & Spatafora
Mytilinidiaceae Kirschst.
Order **Natipusillales** Raja, Shearer, A.N.Mill. & al.
Natipusillaceae Raja, Shearer & A.N. Mill.
Order **Patellariales** D.Hawksw. & O.E.Erikss.
Patellariaceae Corda
Order **Phaeotrichales** Ariyawansa, J.K.Liu & K.D.Hyde
Phaeotrichaceae Cain
Order **Pleosporales** Luttrell ex M.E.Barr
Aigialaceae Suetrong, Sakay., E.B.G.Jones & al.
Amniculicolaceae Y.Zhang ter, C.L.Schoch, J.Fourn. & al.
Anteagloniaceae K.D.Hyde, J.K.Liu & A.Mapook
Arthopyreniaceae W.Watson
Bambusicolaceae D.Q.Dai & K.D.Hyde
Biatriosporaceae K.D.Hyde
Coniothyriaceae W.B.Cooke

Cucurbitariaceae G.Winter
Delitschiaceae M.E.Barr
Diademaceae Shoemaker & C.E.Babc.
Didymellaceae Gruyter, Aveskamp & Verkley
Didymosphaeriaceae Munk
Dothidotthiaceae Crous & A.J.L.Phillips
Fenestellaceae M.E.Barr
Halojulellaceae Suetrong, Ariyawansa, K.D.Hyde & al.
Halotthiaceae Y.Zhang, J.Fourn. & K.D.Hyde
Hypsostromataceae Huhndorf
Lentitheciaceae Yin.Zhang, C.L.Schoch, J.Fourn. & al.
Leptosphaeriaceae M.E.Barr
Lindgomycetaceae K.Hiray., Kaz.Tanaka & Shearer
Lophiostomataceae Sacc.
Lophiotremataceae K.Hiray. & Kaz.Tanaka
Massariaceae Nitschke
Massarinaceae Munk
Melanommataceae G.Winter
Montagnulaceae M.E.Barr
Morosphaeriaceae Suetrong, Sakay., E.B.G.Jones & al.
Mycoporaceae Zahlbr.
Naetrocymbaceae Höhnel ex R.C.Harris
Phaeosphaeriaceae M.E.Barr
Platystomaceae J.Schröt.
Pleomassariaceae M.E.Barr
Pleosporaceae Nitschke
Roussoëllaceae J.K.Liu, R. Phookamsak, D.Q.Dai & al.
Salsugineaceae K.D.Hyde & S.Tibpromma
Shiraiaceae Y.X.Liu, Z.Y.Liu & K.D.Hyde
Sporormiaceae Munk
Teichosporaceae M.E.Barr
Testudinaceae Arx
Tetraplosphaeriaceae Kaz.Tanaka & K.Hiray.
Thyridariaceae Q.Tian & K.D.Hyde
Trematosphaeriaceae Suetrong, C.L.Schoch, Spatafora & al.
Zopfiaceae G.Arnaud ex D.Hawksw.
Order **Strigulales** Lücking, M.P.Nelsen & K.D.Hyde
Strigulaceae Zahlbr.
Order **Trypetheliales** Lücking, Aptroot & Sipman
Trypetheliaceae Zenker
Order **Tubeufiales** S.Boonmee, A.Y.Rossman & K.D.Hyde
Tubeufiaceae M.E.Barr
Order **Venturiales** Yin.Zhang, C.L.Schoch & K.D.Hyde
Sympoventuriaceae Yin.Zhang, C.L.Schoch & K.D.Hyde
Venturiaceae E.Müll. & Arx ex M.E.Barr

Dothideomycetes, fam. inc. sed.
Argynnaceae Shearer & J.L.Crane
Ascoporiaceae Kutorga & D. Hawksw.
Aulographaceae Luttr. ex P.M.Kirk, P.F.Cannon & J.C.David
Brefeldiellaceae E.Müll. & Arx
Coccoideaceae P.Henn. ex Sacc. & D.Sacc.
Corynesporascaceae Sivan.
Dacampiaceae Körb.
Englerulaceae Henn.
Eremomycetaceae Malloch & Cain
Kirschsteiniotheliaceae Boonmee & K.D.Hyde
Leptopeltidaceae Höhn. ex Trotter
Meliolinaceae S.Hughes
Mesnieraceae Arx & E.Müll.
Micropeltidaceae Clem. & Shear
Moriolaceae Zahlbr.
Parmulariaceae E.Müll. & Arx ex M.E.Barr
Parodiellaceae Theiss. & H.Syd. ex M.E.Barr
Parodiopsidaceae G.Arnaud ex Toro
Polystomellaceae Theiss. & P.Syd.
Protoscyphaceae Kutorga & D.Hawksw.
Pseudoperisporiaceae Toro
Saccardiaceae Höhn.
Seynesiopeltidaceae K.D.Hyde
Trichothyriaceae Theiss.
Vizellaceae H.J.Swart
Wiesneriomycetaceae Suetrong, Rungjindamai, Somrithipol. & al.
Dothideomycetes, gen. inc. sed.
Catinella lineage
Class **Eurotiomycetes** O.E.Erikss. & Winka
Subclass **Chaetothyriomycetidae** Dowell
Order **Chaetothyriales** M.E.Barr
Chaetothyriaceae Hansf. ex M.E.Barr
Coccodiniaceae Höhn. ex O.E.Erikss.
Cyphellophoraceae Réblová & Unter.
Herpotrichiellaceae Munk
Lyrommataceae Lücking
Microtheliopsidaceae O.E.Erikss.
Pyrenotrichaceae Zahlbr.
Trichomeriaceae Chomnunti & K.D.Hyde
Order **Pyrenulales** Fink ex D.Hawksw. & O.E.Erikss.
Celotheliaceae Lücking, Aptroot & Sipman
Pyrenulaceae Rabenh.
Pyrenulales, gen. inc. sed.

Order **Verrucariales** Mattick ex D.Hawksw. & O.E.Erikss.
Adelococcaceae Triebel
Verrucariaceae Zenker
Verrucariales, gen. inc. sed.
Chaetothyriomycetidae, fam. inc. sed.
Rhynchostomataceae Winka & O.E.Erikss.
Subclass **Eurotiomycetidae**
Order **Arachnomycetales** Gibas, Sigler & Currah
Arachnomycetaceae Gibas, Sigler & Currah
Order **Coryneliales** Seaver & Chardon
Coryneliaceae Sacc. ex Berl. & Voglino
Order **Eurotiales** G.W.Martin ex Benny & Kimbr.
Aspergillaceae Link
Elaphomycetaceae Tul. ex Paol.
Thermoascaceae Apinis
Trichocomaceae E.Fisch.
Order **Onygenales** Cif. ex Benny & Kimbr.
Ajellomycetaceae Unter., J.A.Scott & Sigler
Arthrodermataceae Locq. ex Currah
Ascosphaeraceae L.S.Olive & Spiltoir
Eremascaceae Engl. & E.Gilg
Gymnoascaceae Baran.
Nannizziopsidaceae Guarro, Stchigel, D.A.Sutton & al.
Onygenaceae Berk.
Eurotiomycetidae, gen. inc. sed.
Subclass **Mycocaliciomycetidae** Tibell
Order **Mycocaliciales** Tibell & Wedin
Sphinctrinaceae M.Choisy
Class **Laboulbeniomycetes** Engl.
Order **Laboulbeniales** Engl.
Ceratomycetaceae S.Colla
Euceratomycetaceae I.I.Tav.
Herpomycetaceae I.I.Tav.
Laboulbeniaceae G.Winter
Order **Pyxidiophorales** P.F.Cannon
Pyxidiophoraceae G.R.W.Arnold
Class **Lecanoromycetes** O.E.Erikss. & Winka
Subclass **Acarosporomycetidae** Reeb, Lutzoni & Cl.Roux
Order **Acarosporales** Reeb, Lutzoni & Cl.Roux
Acarosporaceae Zahlbr.
Subclass **Candelariomycetidae** (ined.)
Order **Candelariales** Miadl., Lutzoni & Lumbsch
Candelariaceae Hakul.
Pycnoraceae Bendiksby & Timdal