

Wolfgang Frey (Editor)

# Syllabus of Plant Families

13<sup>th</sup> ed.

A. Engler's Syllabus der Pflanzenfamilien

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## 1/3 Basidiomycota and Entorrhizomycota



**Borntraeger**



# Syllabus of Plant Families

## Adolf Engler's Syllabus der Pflanzenfamilien

13<sup>th</sup> edition by Wolfgang Frey

### Part 1/3      Basidiomycota and Entorrhizomycota

Dominik Begerow, Alistair McTaggart, Reinhard Agerer



**Borntraeger Science Publishers 2018**

Engler's Syllabus of Plant Families, 13. Edition, Part 1/3

Address of editor: Prof. Dr. Wolfgang Frey, Ortlerweg 39d, 12207 Berlin, Germany

13. edition 2009, 2012, 2015, 2016, 2017, 2018 (English)	8. edition 1919 (German)	3. edition 1903 (German)
12. edition 1954 (German)	7. edition 1912 (German)	2. edition 1898 (German)
11. edition 1936 (German)	6. edition 1909 (German)	1. edition 1892 (German)
9./10. edition 1924 (German)	5. edition 1907 (German)	
	4. edition 1904 (German)	

Cover: From the top left to bottom right.

*Uromyces scaevolae* (Pucciniaceae). Telia. Image taken by A. McTaggart, used with permission from the "Rust Fungi of Australia Lucid Key" (Shivas et al. 2014).

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*Cintractia amazonica* on *Rhynchospora exserta* (Anthracoideaceae). Sori. Image taken by A. McTaggart, used with permission from the "Rust Fungi of Australia Lucid Key" (Shivas et al. 2014).

*Entyloma ficariae* on *Ficaria verna* (Entylomataceae). Phenotypic appearance. Orig., phot. D. Begerow.

*Phragmidium mucronatum* (Phragmidiaceae). Teliospores. Image taken by A. McTaggart, used with permission from the "Rust Fungi of Australia Lucid Key" (Shivas et al. 2014).

Septal pores of Basidiomycota. Doliporus with 2 cisternal parentheses (arrows) of *Tulasnella* sp. (Tulasnellaceae). (Courtesy of R. Bauer).

*Bibulocystis pulcherrima* (Raveneliaceae). Teliospores. Image taken by A. McTaggart, used with permission from the "Rust Fungi of Australia Lucid Key" (Shivas et al. 2014).

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SHIVAS, R.G., BEASLEY, D.R., McTAGGART, A.R. 2014: Online identification guides for Australian smut fungi (Ustilaginomycotina) and rust fungi (Pucciniales). – IMA Fungus pp. 195–202.

ISBN ebook (pdf) 978-3-443-01131-4

ISBN 978-3-443-01060-7 (Complete work)

ISBN 978-3-443-01098-0 (Part 1/3)

Information on this title: [www.borntraeger-cramer.com/9783443010980](http://www.borntraeger-cramer.com/9783443010980)

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Publisher: Gebr. Borntraeger Verlagsbuchhandlung

Johannesstraße 3A, 70176 Stuttgart, Germany

[www.borntraeger-cramer.de](http://www.borntraeger-cramer.de)

[mail@borntraeger-cramer.de](mailto:mail@borntraeger-cramer.de)

∞ Printed on permanent paper conforming to ISO 9706-1994

Typesetting: Satzpunkt Ursula Ewert GmbH, Bayreuth

Printed in Germany by Strauss GmbH, Mörlenbach

# Scientific parts and addresses of authors

## Scientific parts

### Basidiomycota

D. Begerow, R. Agerer & A.R. McTaggart

### Synopsis

D. Begerow, A.R. McTaggart & R. Agerer

### Pucciniomycotina (excl. Pucciniales)

D. Begerow & A.R. McTaggart

### Pucciniales

A.R. McTaggart & D. Begerow

### Ustilaginomycotina

D. Begerow & A.R. McTaggart

### Entorrhizomycota

D. Begerow & A.R. McTaggart

### Agaricomycotina

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# Preface

Half a century ago, in 1954, the 12<sup>th</sup> 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 (13<sup>th</sup> 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)]**, in 2015 by **Part 4 "Pinopsida (Gymnosperms), Magnoliopsida (Angiosperms) p.p.: Subclass Magnoliidae [Amborellanae to Magnolianae, Lilliana p.p. (Acorales to Asparagales)]"**, in 2016 by **Part 1/2 "Ascomycota"** and in 2017 by **Part 2/2 Phototrophic eukaryotic Algae Rhodophyta**. Now **Part 1/3 Basidiomycota and Entorrhizomycota** is published.

**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.**

This volume provides a basic treatise of the world-wide morphological and molecular diversity of the **Basidiomycota** and **Entorrhizomycota**. The Basidiomycota (Pucciniomycotina, Ustilaginomycotina, Agaricomycotina) are an extremely diverse group of the fungi with c. 36 000 species, with a fascinating range of morphological and biological variation, distributed from the Antarctic, arctic tundra to tropical rainforests, and of high economic value. Many species of Agaricomycotina play a role in human food, most important and of greatest economic interest are the plant parasitic Pucciniomycotina and Ustilaginomycotina. The Entorrhizomycota consist of plant root inhabiting fungi, which diverged from other dikaryotic phyla very early in evolution.

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, May 2018

W. Frey



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# Abbreviations, Symbols

acc.	according to
Afr.	Africa
alp.	alpine, alpine (geo)element
Am.	America
appr.	approximately
arct.	arctic
Austr.	Australia
BP	Bootstrap percentage
C.	Central, central
c.	circa, about, approximately
circ.-pol.	circumpolar
class.	classes
comp.	compare
cosmopol.	cosmopolitan
CYTB	gene coding for cytochrome B
diam.	diameter
E.	East
ed., eds.	editor, editors
e.g.,	for example, <i>exempli gratia</i>
emend.	emendavit, emendation, amentment
et al., & al.	et alia, and others
Eur.	Europe
exc.	exceptionally
fam.	family, families, familia, -ae
fig., figs	figure, figures
gen.	genus, genera
h	haustorial apex
I., Is., i., is.	island, isle; islands, isles
i.e.,	that is, <i>id est</i>
inc. sed.	incertae sedis, uncertain systematic position
incl.	including
ITS rRNA	internal transcribed spacer of ribosomal RNA
LSU rRNA	gene coding for large subunit of ribosomal RNA
Ma	million of years ago
max.	maximal, maximally
medit., <i>Medit.</i>	mediterranean, Mediterranean region
µm	micrometer
N.	North
neotrop., <i>Neotrop.</i>	neotropical, Neotropics, Neotropical region
nom. cons.	nomen conservandum, conserved name
nom. nov.	nomen novum
NSW	New South Wales (Australia)

ord.	order, orders
Orig., orig.	original, originally
p.p.	pro parte
p., Pp.	page, pages
pantrop.	pantropical, in all tropical areas
PDA	potato dextrose agar
phot.	photograph
p.p.	pro parte
PP	Bayesian posterior probabilities
prob.	probably
R	host response
Rep.	Republic
resp.	respectively
RPB	gene coding for RNA-polymerase II
s.	see
S.	South
SE.	Southeast
sect.	section
SPB	spindle pole body
SSU rRNA	gene coding for small subunit of ribosomal RNA
subclass.	subclasses
subfam.	subfamily
subgen.	subgenus
s. l.	sensu lato
spec., sp.	species
spp.	species (plural)
s. str.	sensu stricto
subfam.	subfamily, subfamilies
subgen., subg.	subgenus, subgenera
subord.	suborder
subtrop.	subtropical, Subtropics
superord.	superorder
SW.	Southwest
syn.	synonym, synonymous
TEF1	gene coding for translation elongation factor EF-1 alpha
temp.	temperate
trop., Trop.	tropical, Tropics
Vic	Victoria (Australia)
vs.	versus
W.	West
&	and
& al.	et alia, and others
(5)	number of species

# 1 Introduction

As noted in Part 1/2 “Ascomycota” and repeated here, the last three decades provided revolutionary new insights into the phylogeny and diversity of organisms on earth. This is particularly true for 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, anatomical 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 1/3 of the 13<sup>th</sup> edition of “Engler’s Syllabus of Plant Families” gives an up-to-date review of the **Basidiomycota** and **Entorrhizomycota** and their relationships down to the family and genus level, integrating morphological-anatomical and molecular data. 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, combined with numerous new discoveries and systematic novelties 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 are treated in 3 parts [Part 1/1 Fungi p.p. (Chytridiomycota, Zygomycota, Glomeromycota; published in 2012); Part 1/2 Ascomycota (2016), and Part 1/3 **Basidiomycota** and **Entorrhizomycota**, published now] arranged according to the most recent phylogenetic classification systems.

## **2 Phyla Basidiomycota R.T. Moore and Entorrhizomycota R. Bauer, Garnica, Oberw. & al.**

### **Characterization and systematic relationships**

The Basidiomycota R.T. Moore together with the Ascomycota (Berk.) Caval.-Sm. and Entorrhizomycota R. Bauer, Garnica, Oberw. & al. represent the Dikarya Hibbett. The dikaryotic phase of the Ascomycota is limited to a short period during early development of the ascus, whereas this phase continues for an extended period in the Basidiomycota, typically only suspended during sporogenesis. Interestingly, the vegetative hyphae of Entorrhizomycota are also dikaryotic, and therefore a short dikaryotic phase in ascomycetous fungi might be a derived state (Bauer et al. 2015). In contrast to the Ascomycota, where spores are produced inside asci, basidia of the Basidiomycota produce external spores. In total, basidia comprise four functions: karyogamy, meiosis, spore development and spore dispersal. Thus, the basidium represents the meiosporangium of the Basidiomycota and is the defining character of the phylum (Oberwinkler 1978). Affiliation of a taxon to the Basidiomycota was based on recognition of the basidia before the invention of additional markers like anatomy, ultrastructure, cell-wall biochemistry or molecular phylogenetic methods (Gottschalk & Blanz 1985; Oberwinkler 1977, 1985; Prillinger et al. 1993; Swann & Taylor 1993). Glomeromycota, Ascomycota, Basidiomycota and Entorrhizomycota harbour many taxa interacting with living plants, which suggest their early radiation to be related to early land plants. Thereby, Entorrhizomycota links Ascomycota and Basidiomycota with intermediate characters and might be seen as living fossil, because only very few species have survived up to the present.

Implementation of molecular phylogenetic tools revolutionized views on the evolution of fungi and several links between taxa have been recognized only by the use of molecular techniques. Especially, many anamorph-teleomorph connections could only be identified using these characters. However, several previous hypotheses on the evolution of Basidiomycota based on excellent, detailed morphological and especially anatomical studies, were since supported by molecular data (Bauer et al. 1997, 2006; Oberwinkler 1982, 1985, 2017). Finally, the use of phylogenetic trees based on molecular data allows the identification of meaningful characters in specific lineages. Unfortunately, only a small percentage of species has been used in molecular phylogenies and the challenge to affiliate taxa, where sequences are not yet available, remains for the majority of species. Therefore, we want to highlight a few aspects before we present our most updated view on the classification of Basidiomycota.

## Morphological characteristics and life-cycle

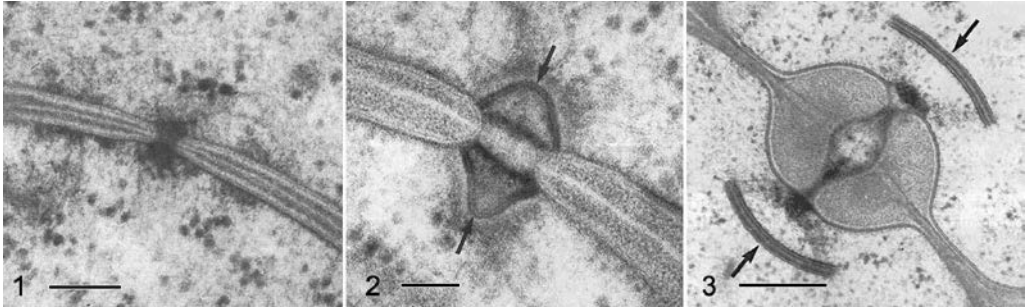
Morphologically, Basidiomycota are very diverse and include the largest known living organism on earth, *Armillaria bulbosa* (Barla) Kile & Watling (Smith et al. 1992), but many single celled yeast species are known from the phylum as well. Yeasts, which are single celled, lack characters useful for morphological classification in a larger context. On the other hand, members of Agaricomycotina Doweld, such as the mushrooms, are very rich in morphological and anatomical characters and can easily be separated in many lineages on macroscopic and microscopic traits. It remains difficult to characterize the entire phylum by morphology, and the most important structure, the basidium, can have very diverse morphologies in different lineages. Overall, the shape of basidia appears highly diverse and has been overlooked in many groups for a long time. The common unicellular holobasidia has four apical spores developing on sterigmata and an active discharge mechanism (Fig. 4-25.6), and this simple structure of a basidium has repeatedly converged in several lineages. Another simple morphology of basidia, phragmobasidia, have longitudinal (Fig. 4-25.5) or transversal septa (Fig. 4-25.4) and often germinate from a resting spore (Figs 4-21.1, 2, 4-6, 22.3, 4). Most of the known basidia can be attributed to one of these general types, despite complex diversity of this structure within the phylum. Similarly, the presence of clamps is indicative for the phylum, as it has been never observed outside the Basidiomycota. The characteristic structure of clamps appears similar to the hook formation of generative hyphae in Pezizomycotina O.E. Erikss. & Winka and is therefore interpreted as direct link to the dikaryotic situation (Iwasa et al. 1998). However, the lack of clamps does not necessarily exclude taxa from Basidiomycota.

Interestingly, the morphology and anatomy of Basidiomycota is more unique at the ultrastructural level and cellular organisation. The cell walls of the Basidiomycota are characterized by a multi-layered composition of differently stained layers, i.e., dark-light-dark (Bauer et al. 2006), while Ascomycota often show only two layers. Similarly, the organization of nuclear division seems more uniform on phylum level, as the organization of spindle pole bodies (SPB) seems to be conserved. I.e., the duplication of the SPB occurs during interphase by *de-novo* formation in Basidiomycota, although some variation can be subdivision specific, and before nuclear division by cleavage in Ascomycota (Oberwinkler & Bauer 1990).

In contrast, other characters like septal pore structure, and, where present, differently shaped and sometimes associated cisternae (called parenthesomes) or additional cellular organelles are excellent to characterize monophyletic lineages within the Basidiomycota (Figs 2-1.1-3, 4-25.1-3). Therefore, these respective ultrastructural characters are highlighted at the taxonomic level when they support the monophyly of specific lineages. In addition, we use physiological characteristics mainly of yeast lineages where appropriate to delimitate taxa (Kurtzman et al. 2011).

The typical life cycle of Basidiomycota appears to be simple, with a mainly dikaryotic stage resulting in the formation of a basidiocarp with hymenium and basidia or sorus-like fructifications with meiotically formed haploid, monokaryotic spores germinating with hyphae or by repetition (ballistospores or yeasts). Sometimes the end of the dikaryotic phase is characterized by special types of resting spores before a basidium is finally formed from it. As mentioned above, the basidium represents the meiosporangium and comprises four functions from karyogamy to spore dispersal. However, like in Ascomycota many species are known from their anamorphic stage only. The most complex life-cycle of Basidiomycota is





**Fig. 2-1. Septal pores of Basidiomycota.** 1. Simple septal pore apparatus of *Ustilentyloma fluitans* (Microbotryales, Pucciniomycotina). 2. Septal pore apparatus with 2 outer membrane caps (arrows) and 2 inner discs of *Ustacystis waldsteiniae* (Urocystidales, Ustilaginomycotina). 3. Doliporus with 2 cisternal parentosomes (arrows) of *Tulasnella* sp. (Tulasnellales, Agaricomycotina). (Courtesy by R. Bauer) (Scale bar 1–3: 0.1  $\mu\text{m}$ ).

probably that of rust fungi (Pucciniales T. Caruel) bearing up to five different spore generations each with their own ecological function (Fig. 4-8). Since the link of several spore generations to a single taxon was often difficult without molecular tools, two nomenclatural systems of anamorphic (asexual state) and teleomorphic (sexual state) names developed. The introduction of the ‘one name = one species’ concept to unify the two nomenclatural systems resulted in many new combinations and on-going renaming procedures. We tried to incorporate this knowledge whenever possible, but several lineages have not been finally studied in this respect and therefore we comment on that situation where possible or needed.

### Ecology and distribution

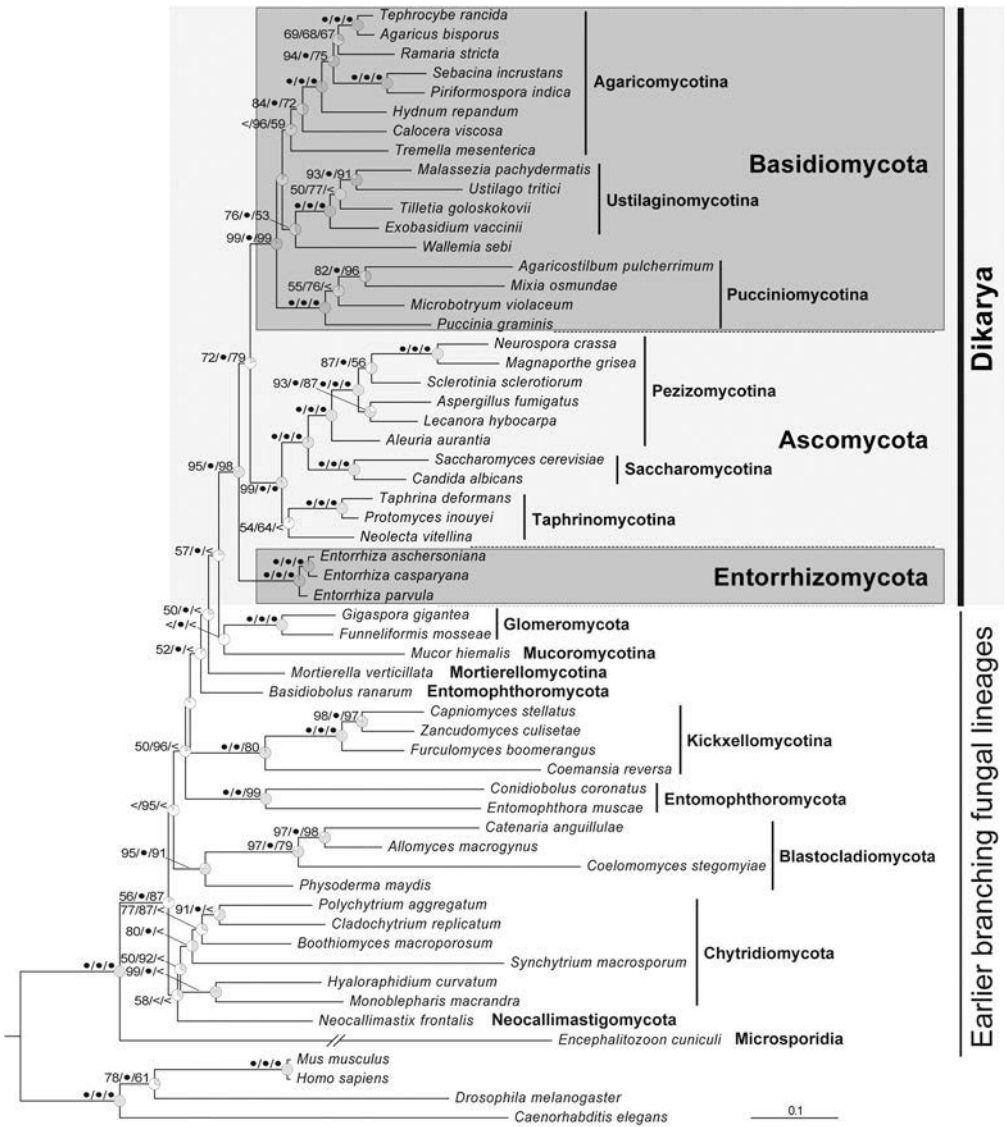
The ecology of Basidiomycota is as diverse as the group itself. It seems that their major radiations are associated with radiations of plants. Symbiotic plant interactions are abundant in all lineages, but they also occur as parasites of animals and humans, as well as in aquatic environments or as saprotrophs (e.g., Manohar & Raghukumar 2013, Peršoh 2015). Interestingly, many lineages have retained a degree of saprotrophic life-style strategies and only a few lineages, like the Pucciniales, are obligate parasites. The saprotrophic life-style often enables cultivation on artificial media, but finding the proper condition for each species is difficult and successful, fertile growth, e.g., basidiocarps, is most often only possible on the original substrate or with living plants. Several species have evolved specific adaptations to certain environments, like appendages on spores or conidia for dispersal via water, or the optimal growth temperature, found in human pathogens (e.g., Ingold 1975, Köhler et al. 2017). Although several studies have discussed the evolutionary trends in terms of life-style within Basidiomycota, an overall picture is still desired, and probably further molecular data and ecological experiments are needed. With respect to the low number of known species relative to the estimated number of fungi, i.e., only 5–10% of the estimated 1.5 million fungi are known (Hawksworth & Rossmann 1997), the lack of knowledge is even more dramatic. However, we provide rough, often generalized information on the ecology of genera, when available.

The distribution of species is even more difficult to assess and evaluate. The majority of taxonomic work is based on European and North American material and for a long time, the available names from the Northern Hemisphere have been applied to material worldwide. Molecular studies have often revealed some species do not show genetic variation in selected genes and seem to represent a global population (e.g., Razaq et al. 2013). However, other species clearly show genetic variation and one morphological species may include several cryptic regional species (e.g., Morgado et al. 2013). In addition to the limitation in anatomical characters to distinguish such regional populations, there is an even larger limitation due to sampling bias. Many areas have not been studied on a broader taxonomic base, and the absence of taxa from species lists may indicate that they have not yet been looked for in an area. As for all fungi, the most prominent structures of Basidiomycota are only visible for a short period of time (i.e., the basidiocarps or sori) and they remain almost invisible for the rest of the year, or even for some years. Molecular tools such as meta-barcoding approaches can sequence all of the organisms in an environmental sample and overcome this lack of fruiting structures. The number of sequenced habitats and regions is still very poor, but most of these studies support the assumption, that diversity in all habitats is higher than measured by basidiocarp observations or isolation by culture.

Finally, knowledge about the distribution of a certain taxon is biased by the location of specialists. This is especially true for the microscopic fungi, which cannot be seen by the naked eye and are therefore overlooked even from most mycologists in the field. Our knowledge of many of these taxa is based on type material only or on a few collections. Therefore, an outreach of taxonomic knowledge about fungi is urgently needed to fill these gaps in the future.

### **Systematic arrangement of taxa**

Historically, mainly basidiocarp or sorus morphology together with anatomy have been used to classify the various taxa in groups and lineages. Many of the genera established on this basis in the 19<sup>th</sup> and 20<sup>th</sup> centuries are still valid and were proven to be monophyletic by molecular phylogenetic analyses. The taxonomy of higher ranks was much more of a debate and corrupted by taxonomic changes, as characters were vague or not known for a certain lineage. Especially, micro-fungi and yeasts have got little attention and detailed studies of the basidium alone allowed a more natural classification in the mid of the last century (see Yang 2011 and references therein). Thus, it is not surprising that several concepts like those of Patouillard, Talbot or Donk were proposed and discussed, as long as additional characters were lacking (see Swann & Taylor 1993 for details). The inclusion of physiological data like the composition of cell wall compounds or the early use of DNA sequence comparisons allowed the recognition of new relationships and paved the ground for modern molecular phylogenetic analyses. The increasing number of articles using molecular phylogenetic data improved our knowledge on the natural system of Basidiomycota in many ways, but we have to remember, that still only about 10–15% of the fungal species are sequenced so far (Begeerow et al. 2010, Schoch et al. 2012). In addition, it became clear, that a single locus like the ITS rRNA gene region is not a panacea to distinguish species in all lineages properly (Stielow et al. 2015).



**Fig. 2-2. Phylogeny of Fungi including systematic position of Entorrhizomycota, Ascomycota and Basidiomycota.** Maximum likelihood tree derived from a combined dataset of rDNA (SSU, 5.8S and LSU) and amino acid (RPB1 and RPB2) sequences. Branch support is given as maximum likelihood bootstrap percentage (1,000 replicates) / Bayesian posterior probability (consensus of 2 independent MCMC processes, each with 4 chains over 5 million generations) / maximum parsimony bootstrap (1,000 replicates). Values of 100% are designated with bullets, values below 50% are omitted or designated by <. (Modified from Bauer et al. 2015, with permission).

Finally, many key taxa are only known from type material and the use of old DNA, from herbarium specimens, has so far only been successfully amplified for a few species.

Given all these challenges, it may be surprising to see how many of the long-standing questions on systematic arrangement in the Basidiomycota are already resolved (Fig. 2-2). The three major lineages, Pucciniomycotina, Ustilaginomycotina and Agaricomycotina, are well supported in many studies (Begerow et al. 1997, Hibbett et al. 2007, Swann et al. 1993). Although, the systematic position of Wallemiomycetes and Entorrhizomycota might not be finalised, major changes to the classification are not expected in the near future, unless completely new lineages are discovered (Bauer et al. 2015, Zalar et al. 2005). The incorporation of morphological, anatomical, ultrastructural and molecular data in a conceptual taxonomy including a hierarchy of characters as exemplified for Ustilaginomycotina (Bauer et al. 1997) and Pucciniomycotina (Bauer et al. 2006) provides the basis for the current systematic arrangement (Hibbett et al. 2007). The comparative analysis of more genes and even genomes supported these findings in principal. However, in addition to phylogenetic support, the latest studies based on whole genome comparisons and phylogenomics allowed the interpretation of gene content and evolution of functional biochemical pathways (Martin et al. 2016, Nagy et al. 2016). Such kinds of studies will provide not only the best possible phylogenetic resolution, but they will also allow recognition of key evolutionary innovations, which supported radiation of a given lineage. We only touched this topic in a few cases, but we hope that our taxonomic survey helps to provide a picture of genera, families and higher ranked taxa and to improve further studies on the systematics and evolution of Basidiomycota. 3 subphyla, 19 class., 65 ord., 232 fam., 1839 gen. (c. 36000)

**Acknowledgements.** Lots of publications are nowadays electronically available, due to financial support by German Research Council (DFG), Universities' engagement, and due to government money. But a great deal of recent publications and of rather old ones are not available electronically or publicly. For obtaining these important contributions, many colleagues helped to get access to their data and hardly accessible publications. The authors' and the companies' permit to reuse line-drawings and black-and-white figures already published in different journals and books (cited in the legends). Special thanks to Cathie Aime, West Lafayette, R. Bauer †, Tübingen, Wilhelm de Beer, Pretoria, Teodor Denchev, Sofia, Martin Kemler, Bochum, Franz Oberwinkler †, Tübingen, Roger Shivas, Toowoomba, and Qi-Ming Wang, Beijing, Andrey Yurkov, Braunschweig, for contributions to Dominik Begerow and Alistair McTaggart for the parts of Pucciniomycotina and Ustilaginomycotina. Additionally, Dr. Thassilo Franke's, München, Helmut Grünert's, München, and Prof. Dr. Ewald Langer's, Kassel, excellent colour photos that have generously been made available for the Agaricomycotina to Reinhard Agerer is highly appreciated.

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# 3 Synopsis of classification of the Basidiomycota R.T.Moore and the Entorrhizomycota R. Bauer, Garnica, Oberw. & al.

## Basidiomycota R.T.Moore

### 1. Subphylum Pucciniomycotina R. Bauer, Begerow, J.P. Samp. & al.

Class **Agaricostilbomycetes** R. Bauer, Begerow, J.P. Samp. & al.

Order **Agaricostilbales** Oberw. & R. Bauer

**Agaricostilbaceae** Oberw. & R. Bauer, **Chionosphaeraceae** Oberw. &

Bandoni, **Kondoaceae** R. Bauer, Begerow, J.P. Samp. & al.,

**Ruineniaceae** Q.M. Wang, F.Y. Bai, M. Groenew. & al.

**Agaricostilbales, gen. inc. sed.**

Class **Atractiellomycetes** R. Bauer, Begerow, J.P. Samp. & al.

Order **Atractiellales** Oberw. & Bandoni

**Hoehnelomycetaceae** Jühlich, **Phleogenaceae** Weese, **Saccoblastiaceae**

Jühlich

**Atractiellomycetes, gen. inc. sed.**

Class **Classiculomycetes** R. Bauer, Begerow, J.P. Samp. & al.

Order **Classiculales** R. Bauer, Begerow, Oberw. & al.

**Classiculaceae** R. Bauer, Begerow, Oberw. & al.

Class **Cryptomycocolacomycetes** R. Bauer, Begerow, J.P. Samp. & al.

Order **Cryptomycocolacales** Oberw. & R. Bauer

**Cryptomycocolacaceae** Oberw. & R. Bauer

Class **Cystobasidiomycetes** R. Bauer, Begerow, J.P. Samp. & al.

Order **Cyphobasidiales** T. Strib. & H. Mayrhofer

**Cyphobasidiaceae** T. Strib. & H. Mayrhofer

Order **Cystobasidiales** R. Bauer, Begerow, J.P. Samp. & al.

**Cystobasidiaceae** Gäum.

Order **Erythrobasidiales** R. Bauer, Begerow, J.P. Samp. & al.

**Erythrobasidiaceae** Denchev

**Erythrobasidiales, gen. inc. sed.**

Order **Naohideales** R. Bauer, Begerow, J.P. Samp. & al.

**Naohideaceae** Denchev

**Cystobasidiomycetes, fam. inc. sed.**

**Buckleyzymaceae** Q.M. Wang, F.Y. Bai, M. Groenew. & al., **Microsporomycetaceae** Q.M. Wang, F.Y. Bai, M. Groenew. & al., **Sakaguchiaceae** Q.M. Wang, F.Y. Bai, M. Groenew. & al., **Symmetrosporaceae** Q.M. Wang, F.Y. Bai, M. Groenew. & al.

Class **Microbotryomycetes** R. Bauer, Begerow, J.P. Samp. & al.

Order **Heterogastridiales** Oberw. & R. Bauer

**Chrysozymaceae** Q.M. Wang, F.Y. Bai, M. Groenew. & al., **Colacogloeaceae** Q.M. Wang, F.Y. Bai, M. Groenew. & al., **Heterogastidiaceae** Oberw. & R. Bauer

**Heterogastridiales, gen. inc. sed.**

Order **Kriegeriales** Toome & Aime

**Camptobasidiaceae** R.T. Moore, **Kriegeriaceae** Toome & Aime

Order **Leucosporidiales** J.P. Samp., M. Weiss & R. Bauer

**Leucosporidiaceae** J.P. Samp., M. Weiss & R. Bauer

Order **Microbotryales** R. Bauer & Oberw.

**Microbotryaceae** R.T. Moore, **Ustilentylomataceae** R. Bauer & Oberw.

Order **Sporidiobolales** Doweld

**Sporidiobolaceae** R.T. Moore

**Microbotryomycetes, gen. inc. sed.**

Class **Mixiomycetes** R. Bauer, Begerow, J.P. Samp. & al.

Order **Mixiales** R. Bauer, Begerow, J.P. Samp. & al.

**Mixiaceae** C.L. Kramer

Class **Pucciniomycetes** R. Bauer, Begerow, J.P. Samp. & al.

Order **Helicobasidiales** R. Bauer, Begerow, J.P. Samp. & al.

**Helicobasidiaceae** P.M. Kirk

Order **Pachnocybales** R. Bauer, Begerow, J.P. Samp. & al.

**Pachnocybaceae** Oberw. & Bauer

Order **Platygliales** R.T. Moore

**Eocronartiaceae** Jülich, **Platyglloeaceae** Racib.

Order **Pucciniales** T. Caruel

Suborder **Melampsorineae** Aime

**Melampsoraceae** Dietel

Suborder **Mikronegeriineae** Aime

**Mikronegeriaceae** Cummins & Y. Hirats.

Suborder **Pucciniineae** Doweld

**Phakopsoraceae** (Arthur) Cummins & Y. Hirats., **Phragmidiaceae** Corda,

**Pileolariaceae** (Arthur) Cummins & Y. Hirats., **Pucciniaceae** Chevall,

**Raveneliaceae** (Arthur) Leppik, **Sphaerophragmiaceae** Cummins &

Y. Hirats., **Uropyxidaceae** (Arthur) Cummins & Y. Hirats.

**Pucciniales, gen. inc. sed. and polyphyletic genera**

Order **Septobasidiales** Couch ex Donk

**Septobasidiaceae** Racib.



- Class **Spiculogloeomycetes** Q.M. Wang, F.Y. Bai, M. Groenew. & al.  
 Order **Spiculogloeales** R. Bauer, Begerow, J.P. Samp. & al.  
     **Spiculogloeaceae** Denchev
- Class **Tritirachiomycetes** Aime & Schell  
 Order **Tritirachiales** Aime & Schell  
     **Tritirachiaceae** Aime & Schell  
     **Pucciniomycotina, gen. inc. sed.**

## 2. Subphylum **Ustilaginomycotina** Doweld

- Class **Exobasidiomycetes** Begerow, M. Stoll & R. Bauer  
 Order **Ceraceosorales** Begerow, M. Stoll & R. Bauer  
     **Ceraceosoraceae** Denchev & R.T. Moore
- Order **Doassansiales** R. Bauer & Oberw.  
     **Doassansiaceae** (Azb. & Karat.) R.T. Moore emend. R. Bauer & al.,  
     **Melaniellaceae** R. Bauer, Vánky, Begerow & al., **Rhamphosporaceae** R. Bauer  
     & Oberw.
- Order **Entylomatales** R. Bauer & Oberw.  
     **Entylomataceae** R. Bauer & Oberw.
- Order **Exobasidiales** P. Henn. emend. R. Bauer & Oberw.  
     **Brachybasidiaceae** Gäum., **Cryptobasidiaceae** Malençon ex Donk,  
     **Exobasidiaceae** P. Henn., **Graphiolaceae** E. Fischer
- Order **Georgefischeriales** R. Bauer, Begerow & Oberw.  
     **Eballistraceae** R. Bauer, Begerow, A. Nagler & al., **Georgefischeriaceae** R.  
     Bauer, Begerow & Oberw., **Gjaerumiaceae** R. Bauer, M. Lutz & Oberw.,  
     **Tilletiariaceae** Moore
- Order **Golubeviales** Q.M. Wang, F.Y. Bai, Begerow & al.  
     **Golubeviaceae** Q.M. Wang, F.Y. Bai, Begerow & al.
- Order **Microstromatales** R. Bauer & Oberw.  
     **Microstromataceae** Jülich, **Quambalariaceae** Z.W. de Beer, Begerow &  
     R. Bauer, **Volvocisporiaceae** Begerow, R. Bauer & Oberw.  
     **Microstromatales, gen. inc. sed.**
- Order **Robbauerales** Boekhout, Begerow, Q.M. Wang & al.  
     **Robbaueraceae** Boekhout, Begerow, Q.M. Wang & al.
- Order **Tilletiales** Kreisel ex R. Bauer & Oberw.  
     **Tilletiaceae** Tul. & C. Tul. emend. R. Bauer & Oberw.
- Class **Malasseziomycetes** Denchev & T. Denchev  
 Order **Malasseziales** Moore emend. Begerow, R. Bauer & Boekhout  
     **Malasseziaceae** Denchev & R.T. Moore
- Class **Monilielliomycetes** Q.M. Wang, F.Y. Bai & Boekhout  
 Order **Moniliellales** Q.M. Wang, F.Y. Bai & Boekhout  
     **Moniliellaceae** Q.M. Wang, F.Y. Bai & Boekhout
- Class **Ustilaginomycetes** R. Bauer, Oberw. & Vánky  
 Order **Urocystidales** R. Bauer & Oberw.

- Doassansiopsidaceae** Begerow, R. Bauer & Oberw., **Fereydouniaceae** S. Nasr, M.R. Soudi, H.D.T. Nguyen & al., **Floromycetaceae** M. Lutz, R. Bauer & Vánky, **Glomosporiaceae** Cifferi emend. Begerow, R. Bauer & Oberw., **Mycosyringaceae** R. Bauer & Oberw., **Urocystidaceae** Begerow, R. Bauer & Oberw.
- Order **Uleiellales** Garnica, K. Riess, M. Schön & al.  
**Uleiellaceae** Vánky
- Order **Ustilaginales** Clinton emend. R. Bauer & Oberw.  
**Anthracoideaceae** Denchev, **Melanotaeniaceae** Begerow, R. Bauer & Oberw., **Ustilaginaceae** Tul. & C. Tul. emend. R. Bauer & Oberw., **Websdaneaceae** Vánky
- Ustilaginales, gen. inc. sed.**  
**Ustilaginomycetes, gen. inc. sed.**
- Order **Violaceomycetales** Albu, Toome & Aime  
**Violaceomycetaceae** Albu, Toome & Aime

### 3. Subphylum **Agaricomycotina** Doweld

- Class **Wallemiomycetes** P. Zalar, G.S. de Hoog & H.-J. Schroers
- Order **Geminibasidiales** H.D.T. Nguyen, N.L. Nickerson & Seifert  
**Geminibasidiaceae** H.D.T. Nguyen, N.L. Nickerson & Seifert
- Order **Wallemiales** Zalar, de Hoog & Schroers  
**Wallemiaceae** R.T. Moore
- Class **Tremellomycetes** Doweld
- Subclass **Tremellomycetidae** Locq. emend. Agerer
- Order **Holtermanniales** Libkind, Wuczkowski, Turchetti & al.  
**Holtermanniaceae** Redhead
- Order **Tremellales** Rea  
**Bulleraceae** X.Z. Liu, F.Y. Bai, M. Groenew. & al., **Bulleribasidiaceae** X.Z. Liu, F.Y. Bai, M. Groenewald & al., **Carcinomycetaceae** Oberw. & Bandoni, **Cryptococcaceae** Kütz. ex Castell. & Chalm., **Cuniculitremaeae** J. P. Sampaio, R. Kirschner & M. Weiss, **Naemateliaceae** X.Z. Liu, F.Y. Bai, M. Groenew. & al., **Phaeotremellaceae** A.M. Yurkov & Boekhout, **Rhynchogastremaceae** Oberw. & Metzler, **Sirobasidiaceae** Lindau, **Tremellaceae** Fr., **Trimorphomycetaceae** X.Z. Liu, F.Y. Bai, M. Groenew. & al.
- Order **Tremellodendropsidales** Vizzini  
**Tremellodendropsidaceae** Jülich
- Order **Trichosporonales** Boekhout & Fell  
**Tetragonomycetaceae** Oberw. & Bandoni, **Trichosporonaceae** Nannf.
- Subclass **Filobasidiomycetidae** Agerer, subclass. nov.
- Order **Cystofilobasidiales** Boekhout & Fell  
**Cystofilobasidiaceae** K. Wells & Bandoni, **Mrakiaceae** X.Z. Liu, F.Y. Bai, M. Groenew. & al.

- Order **Filobasidiales** Jülich  
**Filobasidiaceae** L.S. Olive, **Piskurozymaceae** Liu, Bai, M. Groenew. & al.  
**Tremellomycetes, fam. inc. sed.**  
**Bartheletiaceae** R. Bauer, Scheuer, M. Lutz & al., **Phragmoxenidiaceae**  
Oberw. & R. Bauer  
**Tremellomycetes, gen. inc. sed.**
- Class **Dacrymycetes** Doweld  
Order **Dacrymycetales** Henn.  
**Ceriniacetaceae** Jülich, **Dacrymycetaceae** J. Schröt.  
Order **Unilacrymales** Shirouzu, Tokum. & Oberw.  
**Unilacrymaceae** Shirouzu, Tokum. & Oberw.
- Class **Agaricomycetes** Doweld  
**The phragmobasidial series**  
Order **Sebicinales** M. Weiss, Selosse, A. Rexer & al.  
**Sebacinaceae** K. Wells & Oberw.  
Order **Auriculariales** J. Schroet.  
**Auriculariaceae** Fr., **Hyaloriaceae** Möller  
**Auriculariales, gen. inc. sed.**  
Order **Tulasnellales** Rea  
**Oliveoniaceae** P. Roberts, **Tulasnellaceae** Juel.
- The holobasidial series**  
Subclass **Cantharellomycetidae** Agerer subclass. nov.  
Order **Cantharellales** Gäum.  
**Aphelariaceae** Corner, **Botryobasidiaceae** Jülich, **Cantharellaceae** J. Schröt.  
**Cejpomycetaceae** Jülich, **Clavulinaceae** Donk, **Hydnaceae** Chevall., **Sistotremataceae** Jülich  
**Cantharellales, gen. inc. sed.**
- Subclass **Phallomycetidae** K. Hosaka, Castellano & Spatafora  
Superorder **Gomphanae** Agerer ex Agerer, emend. Agerer  
Order **Gomphales** Jülich  
**Clavariadelphaceae** Corner, **Gomphaceae** Pers., **Lentariaceae** Jülich  
Order **Hysterangiales** K. Hosaka & Castellano  
**Gallaceaceae** Locq. ex P.M. Kirk, **Hysterangiaceae** E. Fisch., **Mesophelliaceae**  
(Cunn.) Jülich, **Phallogastraceae** Locq.  
Order **Geastrales** K. Hosaka & Castellano  
**Geastraceae** Corda, **Pyrenogastraceae** Jülich, **Sclerogastraceae** Locq.,  
**Sphaerobolaceae** J. Schröt.
- Superorder **Phallanae** Agerer superordo nov.  
Order **Phallales** E. Fisch.  
**Clathraceae** Chevall., **Claustulaceae** G. Cunn., **Gastrosporiaceae** Pilát,  
**Lysuraceae** Corda, **Phallaceae** Corda, **Protophallaaceae** Zeller, **Trappeaceae**  
P.M. Kirk  
**Phallales, gen. inc. sed.**
- Subclass **Trechisporomycetidae** Agerer subclass. nov.

- Order **Trechisporales** K.H. Larssen
  - Hydnodontaceae** Jülich
- Subclass **Hymenochaetomycetidae** Agerer subclass. nov.
  - Order **Hymenochaetales** Oberw.
    - Clavariachaetaceae** Jülich, **Hymenochaetaceae** Donk, **Rickenellaceae** Vizzini, **Schizoporaceae** Jülich, **Tubulicrinaceae** Jülich
    - Hymenochaetales, gen. inc. sed.**
  - “Subclass” **Polyporomycetidae**
    - Order **Corticiales** K.H. Larss.
      - Corticaceae** Herter
    - Order **Polyporales** Gäum.
      - Fomitopsidaceae** Jülich, **Fragiliporiaceae** Y.C. Dai, B.K. Cui & C.L. Zhao, **Ganodermataceae** (Donk) Donk, **Meripilaceae** Jülich, **Meruliaceae** P. Karst., **Phanerochaetaceae** Jülich, **Polyporaceae** Corda, **Sparassidaceae** Herter, **Steccherinaceae** Parmasto
      - Polyporales, fam. inc. sed.**
      - Xenasmataceae** Oberw.
      - Polyporales, gen. inc. sed.**
    - Order **Gloeophyllales** Thorn
      - Gloeophyllaceae** Jülich
    - Order **Thelephorales** Corner ex Oberw.
      - Bankeraceae** Donk, **Thelephoraceae** Chevall.
  - Subclass **Agaricomycetidae** Locq.
    - Superorder **Russulanae** Agerer superordo nov.
      - Order **Russulales** Kreisel ex P.M. Kirk, P.F. Cannon & J.C. David
        - Amylostereaceae** Boidin, **Auriscalpiaceae** Maas Geest., **Bondarzewiaceae** Kotlába & Pouzar, **Gloeocystidiellaceae** Jülich, **Hericiaceae** Donk, **Hybogasteraceae** Jülich, **Lachnocladiaceae** D.A. Reid, **Peniophoraceae** Lotsy, **Russulaceae** Lotsy, **Scutigerae** Bondarzew & Singer, **Stereaceae** Pilát, **Wrightoporiaceae** Jülich
        - Russulales, gen. inc. sed.**
    - “Superorder” **Boletanae**
      - Order **Atheliales** Jülich
        - Atheliaceae** Jülich
      - Order **Lepidostromatales** Hodkinson & Lücking
        - Lepidostromataceae** Ertz, Eb. Fischer, Killmann & al.
      - Order **Jaapiales** Manfr. Binder, K.H. Larss. & Hibbett
        - Jaapiaceae** Manfr. Binder, K.H. Larss. & Hibbett
      - Order **Boletales** J.-E. Gilbert
        - Suborder **Tapinellineae** Agerer
          - Tapinellaceae** C. Hahn
        - Suborder **Suillineae** Besl & Bresinsky
          - Gomphidiaceae** Maire ex Jülich, **Suillaceae** Besl & Bresinsky, **Truncocolumellaceae** Locq.

Suborder **Coniophorineae** Agerer & Ch. Hahn

**Serpulaceae** Jarosch & Bresinsky, **Coniophoraceae** Ulbr., **Hygrophoropsidaceae** Kühner

Suborder **Sclerodermatineae** Binder & Bresinsky

**Boletinellaceae** P.M. Kirk, P.F. Cannon & J.C. David, **Calostomaceae** E. Fisch., **Diplocystaceae** Kreisel, **Astraeaceae** Zeller ex Jülich, **Gyroporaceae** Locq., **Pisolithaceae** Maire ex Jülich, **Sclerodermataceae** Corda

**Sclerodermatineae, gen. inc. sed.**

Suborder **Paxillineae** Feltgen

**Gyrodontaceae** Heinem., **Paxillaceae** Maire ex Jülich, **Melanogastraceae** Ulbr.

Suborder **Boletineae** Rea emend. Gilbert

**Boletaceae** Chevall.

**Boletales, fam. inc. sed.**

**Gasterellaceae** Zeller, **Protogastraceae** Zeller

**Boletales, gen. inc. sed.**

Superorder **Agaricanae** Agerer superordo nov.

Order **Amylocorticiales** K.H. Larss., Manfr. Binder & Hibbett

**Amylocorticiaceae** Jülich

Order **Agaricales** Underw.

**Agaricaceae** Chevall., **Amanitaceae** E.-J. Gilbert, **Bolbitiaceae** Singer, **Broomeiaceae** Zeller, **Chromocyphellaceae** Knudsen, **Clavariaceae** Chevall., **Cortinariaceae** R. Heim, **Crepidotaceae** (S. Imai) Singer, **Cyphellaceae** Lotsy, **Cystostereaceae** Jülich, **Entolomataceae** Kotl. & Pouzar, **Fistulinaceae** Lotsy, **Gigaspermaceae** Jülich, **Hemigasteraceae** Gäum. & C.W. Dodge, **Hydnangiaceae** Gäum. & C.W. Dodge, **Hygrophoraceae** Lotsy, **Hymenogastraceae** Vittad., **Limnoperdaceae** G.A. Escoba, **Lyophyllaceae** Jülich, **Marasmiaceae** Roze ex Kühner, **Mycenaceae** Roze, **Niaceae** Jülich, **Omphalotaceae** Bresinsky, **Phelloriniaceae** Ulbr., **Physalacriaceae** Corner, **Pleurotaceae** Kühner, **Pluteaceae** Kotl. & Pouzar, **Psathyrellaceae** Locq., **Pterulaceae** Corner, **Resupinataceae** Jülich, **Schizophyllaceae** Qué. **Stephanosporaceae** Oberw. & Horak, **Stromatoscyphaceae** Jülich, **Strophariaceae** Singer & A.H. Sm., **Tricholomataceae** R. Heim ex Pouzar, **Typhulaceae** Jülich

**Agaricales, gen. inc. sed.**

**Agaricomycetes, gen. inc. sed.**

**Agaricomycotina, gen. inc. sed.**

**Basidiomycota, gen. inc. sed.**

**Entorrhizomycota** R. Bauer, Garnica, Oberw. & al.

Class **Entorrhizomycetes** Begerow, M. Stoll & R. Bauer

Order **Entorrhizales** R. Bauer & Oberw.

**Entorrhizaceae** R. Bauer & Oberw.

Order **Talbotiomycetales** K. Riess, R. Bauer, R. Kellner & al.

**Talbotiomycetaceae** K. Riess, R. Bauer, R. Kellner & al.

## 4 Systematic arrangement of the taxa of the Basidiomycota R.T.Moore

### 4.1 1. Subphylum Pucciniomycotina R. Bauer, Begerow, J.P. Samp. & al.

Members of the Pucciniomycotina are probably the most diverse group of Basidiomycota in terms of morphology and ecology. The subphylum includes saprobic, mycoparasitic, phytoparasitic species and even human parasites or probable mutualists, but all of these life styles seem to have evolved several times independently using different modes of interactions (Aime et al. 2014, Bauer et al. 2006). While the major lineages of the Ustilaginomycotina Doweld and the Agaricomycotina Doweld were clear in their circumscription from the beginning, the Pucciniomycotina were recognized after detailed morphological studies only step by step (Bauer et al. 2006; Oberwinkler 1977, 1987; Oberwinkler & Bauer 1989; Swann & Taylor 1993; Weiss et al. 2004). The largest monophyletic group within the Pucciniomycotina is represented by the *rust fungi* (Pucciniales) and was discussed together with the *smut fungi* (Ustilaginales) because of their plant parasitic nature and the presence of a teliospore representing a resting spore to overcome unfavourable seasonal conditions (Begerow et al. 2014, Talbot 1968). The teliospores were often referred to as probasidia, because nuclear fusion, which is an important character of the meiosporangium in the Basidiomycota, occurs within the teliospore in many species. The concept of heterobasidiomycetes vs. homobasidiomycetes was used for a long time, reflecting the modes of germination of basidiospores (Patouillard 1990). Basidiospores of homobasidiomycetes germinate to produce hyphae, whereas basidiospores of heterobasidiomycetes are more variable and can either bear secondary spores (by repetition), yeast growth (or sporidia), microconidia, or hyphae (Oberwinkler 1982). Thus, the evidence of one or several early branching lineages of basidiomycetes has grown over the years. Studies on the composition of cell wall carbon compounds (Prillinger et al. 1993) and the first sequences of 5S rRNA (Gottschalk & Blanz 1985), supported a monophyletic lineage of Pucciniomycotina. Comprehensive studies using SSU rRNA and LSU rRNA sequences of more species paved the way to further recognize the Pucciniomycotina R. Bauer, Begerow, J.P. Samp. & al. or *Urediniomycetes* at this time (e.g., Begerow et al. 1997, Swann & Taylor 1993, Weiss et al. 2004) as a monophyletic group (Figs 2-2, 4-1). Further detailed studies on the ultrastructure of cell wall layers, septal pore architecture (Figs 4-2.4, 5, 7-8; 4-3.1, 4) spindle pole bodies (Figs 4-2.1, 3; 4-3.3) and additional organelles (Figs 4-2.2, 6; 4-3.5-6) revealed numerous lineages, which were first described by