How understand cryptogams? The development of research methods and their impact on the knowledge of cryptogams

A tribute to Josef Poelt

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Abstract: This article intends to shed light on increasing knowledge of cryptogam biology over 400 years of research. **The progress in biological disciplines involved, is tightly bound to new research methods**. Starting with recognizing algae, mosses, ferns, and fungi in the field, collecting and identifying them was a consequence. It required classifications for handling the rapidly growing number of species. Soon, it became apparent that **lightmicrocopy** was an indispensable method of all kinds of cryptogam studies, especially for elucidating their cellular constructions, an essential basis for studying their functions. **Electron microscopy** broke down the limitations of magnification and resolution in light microscopy. The detection and understanding of subcellular structures revolutionized biology as such, and that of cryptogams in particular. Now, physiological studies with **chemical and physicochemical methods** of earlier days could be coupled more and more with structural characters of cell organelles. Increasing knowledge on metabolisms and applicable products strengthened efforts in **biotechnology** and led to new industrial disciplines. Surprisingly, **sequencing** techniques of nucleic acids were essentially developed in biology and not in chemistry. Their rapidly spreading application to all kinds of organisms, including cryptogams, is unique and marks a most revolutionary period in biology. It covers now developmental, metabolic, ecological, and evolutionary studies, and dominates biological research to a very high percentage. The mass of data produced since then, increasing continously, requires **bioinformatics** as an additional discipline in biology. **Publications** are an essential part of research communication. Methods of publishing scientific results have changed drastically in recent times. Multi-author papers in high impact journals seem to be the clue for young scientists to survive under extreme conditions of competition and to succeed in a scientific career. Even **marketing** strategies for quickly recruiting new data or refreshing cryptic ones are heavily practised, and are made attractive by eyecatcher titles of papers.

Fig. 1: Josef Poelt collecting lichens in the Páramo de Piñango, Venezuela, surrounded by *Espeletia schultzii* and *E. lutescens*, 4200 m. March 16, 1969. (Photo: F. Oberwinkler).

* submitted September 2015

1. Introduction: what are cryptogams?

Why to review the factors determining the progress in crytogam research in a historical context?

First, cryptogams were and are an integral part of plant concepts of various kinds. Second, over a long time, competent individual researchers have covered the whole field of plant biology, including cryptogams. Finally, **this is a tribute to Josef Poelt** (1924–1995), one of the great experts in plant and cryptogam research of the last generation (Fig. 1). His broad and profound knowledge of plant diversity, ecology and systematics was a challenge to many of his students to study cryptogams. Therefore, this article aims to examine causes and reactions for research progress in cryptogamic disciplines under historic viewpoints (Fig. 2).

What are cryptogams?

Traditionally, cryptogams comprise algae, bryophytes, ferns, and fungi, an obviously heterogeneous assembly of plants and plant-like organisms. They have in common cryptic reproductive organs, at least in comparison with angiosperms. However, even those, sometimes have hidden sexual structures, as for example *Ficus*, and were therefore originally grouped within cryptogams (Linné 1735).

In general, cryptogams are much smaller than phanerogams, and many of them are easily to be overlooked. Others, like fungi and small algae, usually are rather ephemeral and therefore require intensive and time consuming fieldwork for sufficient observation and sampling. All together, with certain exceptions, cryptogams do not play a prominent role in the appearance of land vegetation types, however they do very much in terms of functional aspects. Several of these will be discussed in this paper. Light is shed on the fact that integrative biology is not only the application of different methods in a single research object, but is **a challenge for considering habitat conditions of different magnitude as biospheres for organismic interactions under the influence of abiotic parameters**.

2. The begin: collecting and classifying cryptogams

In exploring and cataloguing plants in pre-Linnéan times, cryptogams were only occasionally considered, except of those of medical use in folk medicine (e.g. Fuchs 1543, 1545; Lobelius 1581). In contrast to seed plants, general and regional studies of lower plants tardily came into progress.

The first who tried a **classification of fungi** was Pietro Andrea Mattioli (1501–1577). His fellow countryman Gianbattista della Porta (1539–1615)

considered fungal spores as seeds (1588). The Dutch botanist Carolus Clusius (Charles de L'Écluse, or l'Escluse, 1526–1609) described hungarian mushrooms (Aumüller 1983), based on watercolours, probably painted by his nephew, Esaye le Gillon (Aumüller 1983). The Swiss brothers, physicians and botanists Johann (1541–1612) and Caspar Bauhin (1560–1624) were eminent early contributors for plant and fungal diversity with 5226 species in „Historia plantarum universalis" (Bauhin 1650–51) and approximately 6000 species in „Pinax theatri botanici" (Bauhin 1623).

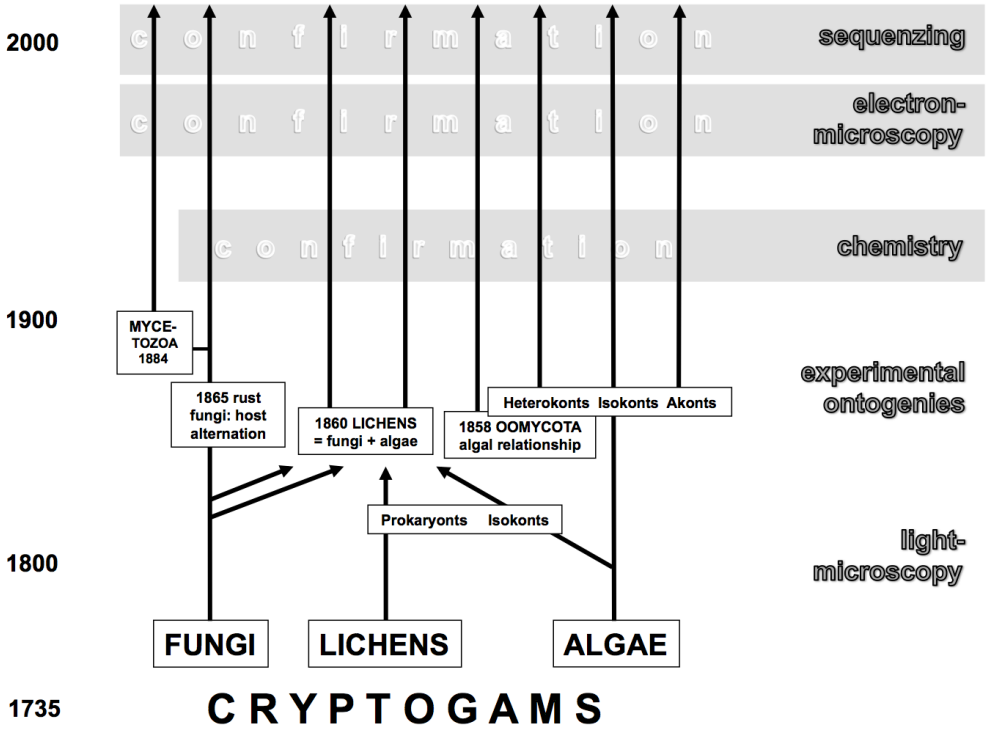


Fig. 2: Simplified scheme of major steps in investigations on fungi, lichens, and algae, depending on the availability of research methods over a period of 300 years. Lichens were identified as organisms composed of fungi and algae, and both partners of diverse origins. Different flagellum types in algae indicated different relationships, later verfied by electron microscopy, biochemical and molecular data. False mildews, Oomycota (Oomycetes) could be matched with heterokontic algae, again subsequently confirmed by ultrastrutural and chemical features. Life cycle characteristics of slime molds were already early indicative of their amoeboid relationship. Infection experiments confirmed the host alternations in many rust fungi. (Graphic: F. Oberwinkler)

A system of **fungi as an independent organismic group**, proposed by Joseph Pitton de Tournefort (1656–1708) in 1700 (Tournefort 1700) was adopted by Johann Jacob Dillen (Dillenius, 1684–1747) and Carl von Linné (1707–1778). Dillen also studied the **reproduction of ferns and bryophytes** (1741). In his flora of Switzerland (1742), Albrecht von Haller (1708–1777)

included also cryptogams. A correspondent of Linné, the Bavarian priest and naturalist Jacob Christian Schaeffer (1718–1790) published four remarkable volumes on fungi of Bavaria, including the Palatinate of those days (Schäffer 1761, 1774). One of Linné's students, Eric Acharius (1757–1819) studied lichens intensively for the first time (Acharius 1789, 1803, 1810, 1814), thus generally known as the **father of lichenology**. – Christian Hendrik Persoon (1761–1836), of Dutch and German origin, was born in the Cape Province, worked in Germany and France, and provided a **classification of fungi** (Persoon 1794, 1801), recognizing the rusts, smuts and gasteromycetes as separate groups. He introduced the term „**mycology**", and adopted the generic name *Puccinia* from Micheli, but used it differently, and proposed *Puccinia graminis* Pers., the scientific name for the **black rust**. Persoon's contemporary, the British allround botanist Samuel Frederick Gray (1766–1828) published a natural arrangement of British plants, including the fungi (Gray 1821), and the German **universal botanist** Christian Gottfried Nees von Esenbeck (1776–1858) treated fresh water algae (Nees 1814), fungal systematics (nees 1816–1817), and European Hepaticae (Nees 1833–1838).

The **habit of mushrooms**, often aesthetically appealing, their ephemeral but mostly habitat predictable appearance, and the curious mixture of edible and poisonous species, always made them rather attractive. **Mushroom illustrations** were early produced as coloured woodblock prints in herbal books and watercolour plates as mentioned above (Clusius 1601). The volumes with coloured copperplate prints, „Icones plantarum et analysis partium..." (Schmidel 1747–1797) of the physician and botanist Casimir Christoph Schmidel (1718–1792) initiated attempts for similar books, e.g. by Schäffer (1762, 1774), Bulliard (1780–1798), Batsch (1783–1789), Bolton (1788–1790), Sowerby (1795–1815), Greville (1823–1828), Krombholz (1831–1846), and Corda (1837–1854). Many other regional overviews or monographic treatments with colour illustrations of various quality were published until recently, for instance in Central Europe by Bresadola (1929–1930), Schaeffer (*Russula* 1942–1943), Neuhoff (*Lactarius* 1956), Moser (*Phlegmacium* 1960), Poelt & Jahn (1963), Singer (Boletaceae 1965, 1967), Einhellinger (*Russula* 1985), Stangl (*Inocybe* 1989), and Marxmüller (*Russula* 2014). – Worldwide, numerous regional **field guide books** for mushrooms and other fungi, illustrated by colour photos, were produced and fill the market, especially since they became comparatively cheap through digital photography. Meanwhile, this modern trend covers nearly all organismic groups whose species can be distinguished, at least to some degree, macroscopically.

One of the most **influential mycologists of the macroscopic era of mushroom research** was Elias Magnus Fries (1794–1878) with his „Observationes mycologicae" (1815–1818), „Systema mycologicum" (1821–1832), „Epicrisis systematis mycologici" (1836–1838), and „Hymenomycetes Europaei" (1874). In addition, he also summarized the knowledge of lichens

of his time (1831). The founder of the French mycological society, Société mycologique de France, Lucien Quélet (1832–1899), studied mushrooms of his home country and described several new species. The protestant priest and teacher Paul Kummer (1834–1912) published books for the identification of mushrooms, mosses and ferns, and Petter Adolf Karsten (1834–1917) explored the mycoflora of Finland (Karsten 1871–1879). Lewis David von Schweinitz (1780–1834) first explored the fungi of the Oberlausitz together with Johann Baptista von Albertini (1769–1831) as first author (1805), then those of North Carolina (1822) and middle Northern America (1832). Mr. Mushroom, William Alphonso Murrill (1869–1957), collected more than 75.000 specimens of agarics, hydnums and polypores, preferably in North America, and described around 1.700 new species.

The **registration and documentation of biodiversity** is an everlasting and meritorious task with more than 300.000 listed publications (Web of Science, June 2015). Several articles in this volume are dealing with these topics: fungi of Bavaria by Andreas Bresinsky, and of the Tropics by Meike Piepenbring et al. 2016; lichens of Germany by Volkmar Wirth et al. (2016), lichens of the Alps by P eter O. Bilovitz & Helmut Mayrhofer, and lichens of Tibet and the Himalajas by Walter Obermayer.

First activities to recognize cryptogams:

- **Observation in the field of small plants and plant-like organisms: cryptogams.**
- **Classification in algae, mosses, ferns, and fungi.**
- **Documentation of species diversities in regional floras.**
- **Habit and macrostructure illustrations.**
- **Regional and general taxonomic treatments.**
- **Global biodiversity registration.**

3. A first research boom: light microscopy

A gradual turn **from macroscopic recognition to microscopic characters** for the distinction of cryptogams marks the general transition from the older collectors to the younger research generations. This chapter intends to articulate the new dimension for understanding organisms by revealing their cellular body plans. No other method than **light microscopy has the allround potential** for this purpose. Therefore, this method never lost its importance in structural studies of organisms. The examples mentioned here are intended to show this fact, however, they should not at all be considered as a comprehensive historical outline.

The Dutch spectacle-makers Hans Jansen and his son Zacharias (1585–pre1632) are said to have invented a compound microscope, and Marcello Malpighi (1620–1694), Robert Hooke (1635–1703), and Anton van Leeuwenhoek (1632–1723) were the first to use it for studying biological samples. Pier Antonio Micheli's (1679–1737) „Nova genera plantarum iuxta Tournefortii methodum disposita" (Micheli 1729) was a major step in the knowledge of cryptogams, including fungi with microscopic structures like spores. It was the merit of Johannes Hedwig (1730–1799) **to study cryptogams with the light microscope intensively** (1799–1803), and to succeed in identifying antheridia and archegonia as sexual organs of mosses (1798, 1801). To differentiate fungi from seed plants, Hedwig introduced the term „**spore**" for propagules of fungi which are produced in „**sporangia**" (Hedwig 1798). – There were eminent fieldworkers and fungal taxonomists at the end of the 18. and the 19. century in Central Europe who also used the light microscope for improving their investigations. The French physician and microscopist, Joseph Henri Léveillé (1796–1870), discovered **asci** with ascospores, and **basidia** producing basidiospores (Léveillé 1837), and Louis René Tulasne (1815–1885) studied the **developmental stages of the rusts** (Tulasne 1853, 1854a), improved their classification and underlined the differences to smuts (Tulasne 1853, 1854b). Many of his contributions (Tulasne & Tulasne 1847) were illustrated by excellent microscopic drawings of his brother Charles Tulasne (1816–1884). The golden period of Italian lichenology, 1830–1861, is treated in this volume by Pier Luigi Nimis.

The Swiss Karl Wilhelm Nägeli and Simon Schwendener were **prominent microscopists**, at first collaborating in Munich, and attracting various talented students continuing light microscopic investigations on cryptogams (Fig. 3). Nägeli discovered the **spermatozoids of ferns**, and Schwendener was heavily attacked when he published his light microscopic discovery of the **dual nature of lichens**. Paul Lorentz and Hubert Leitgeb studied the **anatomy and ontogeny of bryophytes**, while Karl Eduard Cramer focused on **algae**, and Carl Prantl on **ferns**. Cell division studies were the objectives of Maximilian Westermaier, and Carl Correns became a well-known geneticist and one of the rediscoverers of Mendel's laws. The different plant cell and tissue structures, elaborated by the eminent microscopists, Heinrich Schenck and Ernst Küster, were indicative for their functional specialisations. Thus, research in plant anatomy gradually switched into physiological and metabolic studies. Pioneers for applying new chemical and physico-chemical methods were Gottlieb Haberlandt, Georg Volkens, Wilhelm Ruhland, and Kurt Noack. Other fields were applied disciplines, like agronomic botany, in which Otto Warburg succeeded, and water ecology, including algae as bioindicators, an objective of Richard Kolkwitz.

The genealogies of prominent researchers firmly document their **broad academic education** that allowed them to cover several groups of organisms effectively and to be capable of developing new and progressive methods.

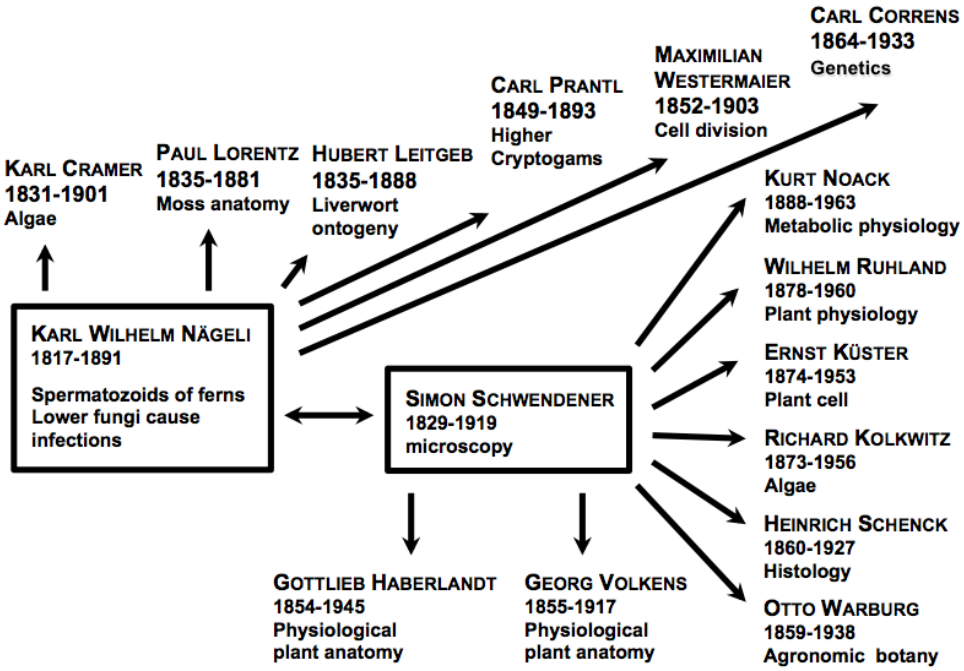


Fig. 3: The **academic schools of Karl Wilhelm Nägeli and Simon Schwendener**. This simplified overview illustrates the basic role of microscopic studies in diverse cryptogams. The knowledge of cellular ground plans is essential for all groups of organisms and for all kinds of research methods. It underlines the historical importance of structural biology for the development, the progress and further understanding of other disciplines, like anatomy, histology, developmental and metabolic studies, physiology, and genetics. – Another important context is documented in this scheme: two centres of leading researchers and their schools with far reaching influence. – Finally, the approximate timespan from 1850–1950 is covered here. It is intended to show the dependency of research progress from newly invented technical methods, and the rapid dominance of objectives dealing with functional aspects. (Graphic: F. Oberwinler)

Anton de Bary (1831–1888) was a successful academic teacher whose students and their pupils continued effectively in different fields of cryptogamic research (Fig. 4).

In all disciplines of cryptogamic research, the use of the light microscope expanded the understanding of these organisms on the level of their cellular constructions with major implications on functional aspects, including the cellular interaction with their substrates. Mycologically, this early period culminated in de Bary's „Morphologie und Physiologie der Pilze, Flechten und Myxomyceten" (1866), and „Vergleichende Morphologie und Biologie der Pilze, Mycetozoen und Bacterien" (1884), books widely distributed and estimated through the early English translation „**Comparative morphology and biology of the fungi, Mycetozoa, and bacteria**" (1887).

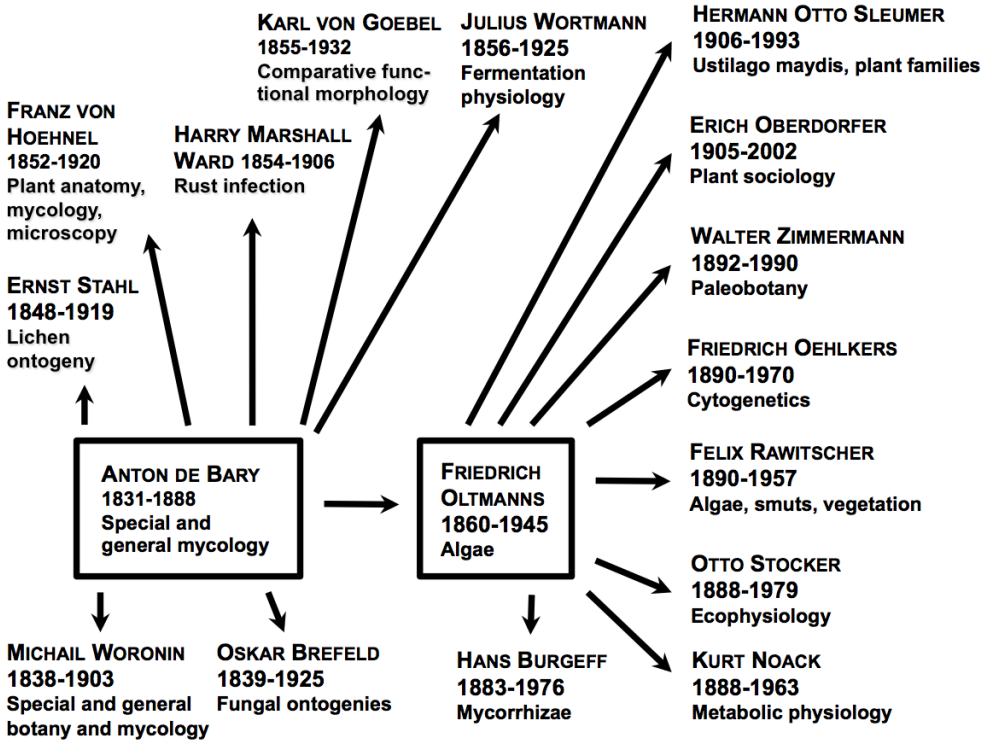


Fig. 4: The **academic schools of Anton De Bary and Friedrich Oltmanns**. A timespan of 150 years of botanical research is covered here, indicating the impact of strongly influential scientists. The keywords for the research fields of individual scientists have to be taken as cut-outs of their activities. However, they clearly indicate the broad spectrum of research with new techniques approached by them, including the transitions to higher plants. (Graphic: F. Oberwinkler)

A high standard of correct cellular illustrations of fungi was already reached in the times of de Bary (l.c.), Tulasne & Tulasne (1847), Brefeld (1881, 1883, 1888, 1895a, 1895b, 1912), Sappin-Trouffy (1896), Thaxter (1896–1931), and others. In „Les hyménomycètes d'Europe" (Patouillard 1887), Narcisse Théophile Patouillard (1854–1926) put particularly emphasis on **microscopic characters of higher** basidomycetes. John H. Corner (1906–1996) published monographs of difficult and species-rich plants (*Ficus*) and fungal genera (*Clavaria*, Corner 1950, and others). He was one of the first studying and illustrating the cellular morphology of higher basidiomycetes (e.g. Corner 1932, 1935). In addition, he was a pioneer of exploring and documenting Southeast Asian fungal flora over many years. In a multi-annual project John Eriksson (1921–1995) and coauthors, published the „The Corticiaceae of North Europe" (1973 following) with excellent line drawings by the senior author.

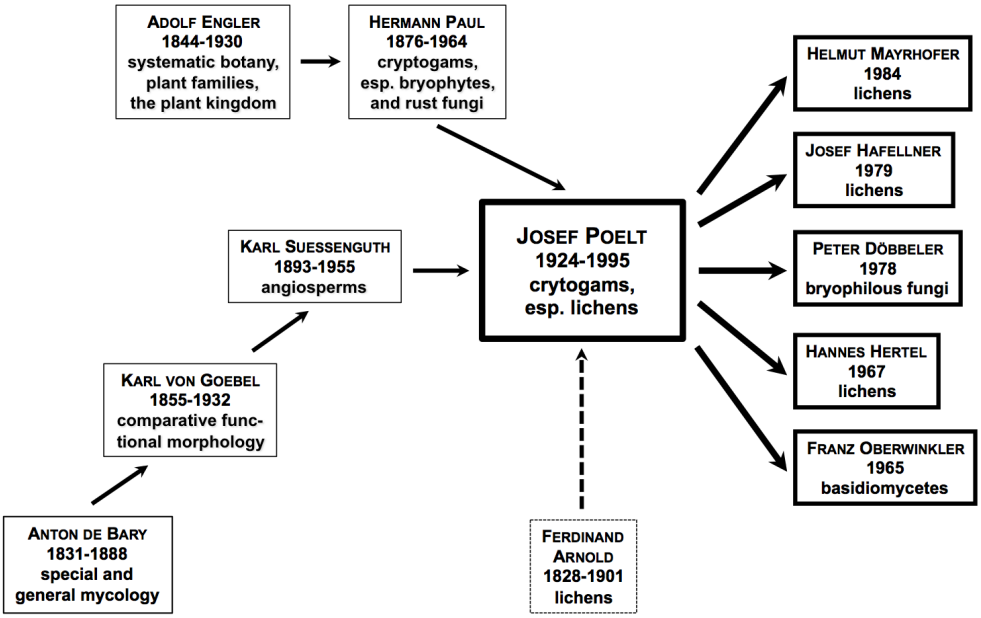


Fig. 5: The **academic school of Josef Poelt** and its ancestors, originating from Anton de Bary (compare Fig. 4), and leading through Karl von Goebel to Karl Suessenguth, Poelt's doctorate supervisor. Poelt himself considered Ferdinand Arnold as his most important scientific advisor through his collections and publications. Five of Poelt's students became university teachers. They are listed here chronologically by the year of their doctoral examination. (Graphic: F. Oberwinkler)

Josef Poelt founded his **world-wide studies of lichens** on macro- and microscopic characteristics. His impact on research in cryptogams and his academic school (Fig. 5) are separately dealt with in this volume by Hannes Hertel. Nevertheless, his three most influential publications on European lichens, „Bestimmungsschlüssel europäischer Flechten" (Poelt 1969, Poelt & Vězda 1977, 1981) shall be mentioned here, too. Some special monographic works are those on **foliicolous lichens** by Santesson (1952) and Lücking (2008). In addition, other selected **regional lichen floras** are listed chronologically: Clauzade & Roux flora (1985) of Western Europe, written in Esperanto, lichens of North America by Brodo et al. (2001), of the Greater Sonoran Desert region by Nash et al. vols. 1–3 (2002, 2004, 2007), flora of New Zealand lichens by Galloway (2007), and of Great Britain and Ireland by Smith et al. (2009).

Karl von Goebel's „**Organographie der Pflanzen**", his magnum opus of comparative morphology of plants, was published in three editions with three volumes (1928–1933), 2885 pages and 2608 illustrations, most of them origi-

nal drawings of von Goebel (see Fig. 4) from microscopic preparations. The second volume contains **bryophytes** and **pteridophytes** (von Goebel 1930).

Original illustrations are of essential value because they directly document the quality of the author's investigations. In addition, Gäumann (1959, p.11) quoted „that every illustration somehow reflects the personality of the author", a statement that should be kept in mind by textbook writers and students.

From „**Rabenhorst – Kryptogamenflora von Deutschland, Österreich und der Schweiz**", only „Die Lebermoose Europas", part I and II by Müller (1954, 1957), with excellent microscopic illustrations, are cited. Another long lasting great work is „**The Hepaticae and Anthocerotae of North America**" (Schuster 1966, 1969, 1980 and 1992, cited only with four volumes). The illustrated Moss Flora of Antarctica (Ochyra et al. 2008) is a recent and outstanding study.

For **algae**, the basic work of Oltmanns (Fig. 4) in three volumes (Oltmanns 1922, 1923) has to be mentioned. „Die Süsswasser-Flora Deutschlands, Österreichs und der Schweiz", a multi-author series, was founded by Pascher in 1914, and continued until volume 15 with pteridophytes and phanerogams by Glück (Pascher 1936).

Oscar Brefeld, Ernst Stahl, Franz von Höhnel, and Julius Wortmann, students of Anton de Bary (Fig. 4), continued **mycological research**, focussing on different topics, inclusive of physiological disciplines. Karl von Goebel covered a broad spectrum of botanical research, including **different cryptogamic fields**, and he was the founder of the botanical garden in München-Nymphenburg. Friedrich Oltmanns became a famous **phycologist** and another successful academic teacher. His student Hans Burgeff was a **pioneer in mycorrhiza** research, especially of orchids on a world wide scope. Kurt Noack was student of Oltmanns and Schwendener and became a plant physiologist. Ecophysiology was developed to the main research field of Otto Stocker. **Algae, smuts, and vegetation types** were the main objectives of Felix Rawitscher. Friedrich Oehlkers focused on cytogenetics, and Walter Zimmermann on paleobotany. Plant sociology was the main research field of Erich Oberdorfer, while Hermann Otto Sleumer primarily studied the **sexuality of *Ustilago maydis***, and then became a well known plant taxonomist, revising especially tropical families.

The availability of the **new techniques had an high impact on the progress of cryptogamic research** for which some examples are given (Figs. 6, 27, 28; Tab. 2). – Before the period of 1590, when Jansen and his son constructed the first light microscope, handlenses were used. The first to observe biological objects with self-made, **compound microscopes** were Galilei, Hooke and Leuwenhoek. Nearly 100 years later, 1768, a newly designed mi-

croscope by d'Albert d'Ailly (1714–1769) had no impact on further development of light microscopy. Genius inventions were **immersion objectives**, first with water by the American Robert Tolles, 1858, then with glycerin and canada balsam. The German Ernst Abbe (1840–1905) introduced the oil immersion objectives (Abbe 1873) that were produced commercially by Carl Zeiss (1816–1888) already 1877. When studying tuberculosis, Robert Koch (1843–1910) used these oil objectives and Abbe's condenser and detected the tubercle bacillus. – Since high-quality Zeiss light microscopes were on the market and were successfully used for basic and applied studies, they also became integral instruments in biological investigations, including research in cryptogams. Indispensable for technically perfect light microscopy is the optimization of resolution by evenly illuminating the field of view, known as **Köhler illumination** (Köhler 1893). August Köhler (1866–1948) pioneered also light microscopy with ultraviolet light, thus initiating fluorescence microscopy in 1904.

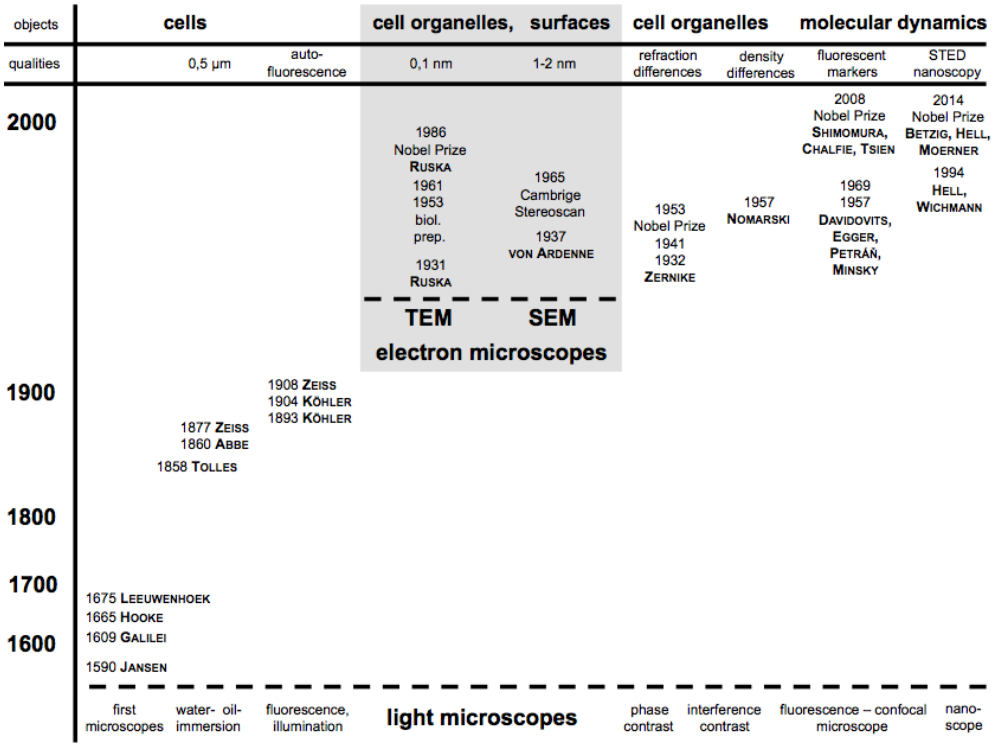


Fig. 6: Time table for the invention of microscopes and their constructors. Some of the instrument's qualities and main study objects are listed. Further details in the text. (Graphic: F. Oberwinkler)

Already from 1930–1960 light microscopic tools had been expanded by **phase- and differential interference contrast** techniques, both often suc-

cessfully applied in thin preparations, preferably one cell layer thick. For his invention of phase contrast microscopy, Frits Zernike (1888–1966) was awarded the Nobel Prize for Physics in 1953. Living, unstained biological preparations are often studied with Nomarski interference contrast microscopy, introduced 1957 by the Polish-French physicist Georges Nomarski (1919–1997), providing pictures of three dimensional appearance. Finally, **confocal microscopy** uses point illumination and a pinhole in front of the detector to eliminate out-of-focus light, a principle for the development of a scanning microscope in 1955, patented by Marvin Minsky 1957. The American researchers Paul Davidovits & David Egger (1969, 1971) collaborated with the Czechoslovak Mojmír Petráň in constructing the confocal laser scanning microscope. By developing the stimulated emission depletion, STED, Hell & Wichmann (1994) succeeded to break the diffraction barrier, thus reaching a **super-resolving fluorescence microscopy** with nano dimension resolutions.

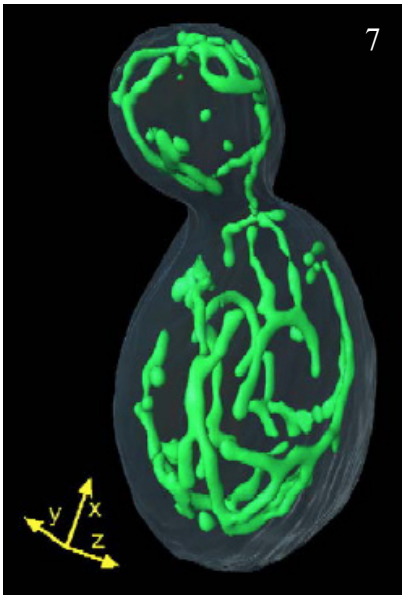
A renaissance of light microscopy by new techniques and their impact on cryptogam research

The compilation of data in figure 6 intends to show the influence of newly developed microscopic techniques on biological research. In the first part of chapter 3, the immense impact of light microscopic studies in cryptogams until the 1950s was discussed. Then, in addition, electron microcopic investigations were tardily carried out in various lower plants, later on more intensively. This will be briefly dealt with in chapter 5.

Within a certain period of „modern research“, light microscopy was often considered as out of date. However, this was shortsighted regarding the basic implications of structural biology on the cellular level, especially when living organisms have to be examined. Therefore, experts put emphasis on overcoming the physical constraints of classical light microscopy. These attempts were very successful in **fluorescence microscopy**, a method that allows non-invasive imaging of organelles in living cells, specifically labeled by biological markers. When it was established for daily research, **confocal scanning microscopy** became widely used, and its successful application is documented by nearly 287.600 publications, listed in Web of Science, end of June 2015. The resolutions of earlier confocal laser-scanning microscopes are strongly overcome by **4Pi-confocal microscopy**, invented by Hell (1990).

The 4Pi laser scanning fluorescence microscope has an improved resolution up to 100–150 nm. – *Saccharomyces cerevisiae*, „**the yeast**“, and „**the model organism of eukaryotes**“ has served for all kinds of basic research, and, as well known, for applied ones especially (see chapter 6). The yeast was used for live cell confocal microscopic studies (Egner et al. 2002, Jacobs 2006, Fig. 7). It was found „that mitochondria are highly dynamic organelles that are frequently dividing and fusing, changing size and shape and travelling

long distances throughout the life of a cell". – The analysis of protein distributions in cell organelles reached new qualities by super-resolution microscopy, **nanoscopy**, which ultimately led to diffraction-unlimited optical resolution. In October 8, 2014, the Royal Swedish Academy of Sciences has decided to award the Nobel Prize in Chemistry for 2014 to Eric Betzig, Stefan W. Hell, and William E. Moerner for their ground-breaking work that optical microscopy has brought into the nanodimension. – Now, **correlative microscopy** appears to be of actual interest (Bianchini et al. 2015), because it combines the observation of the cells and their organelles under life conditions with fixed material for electron microscopy.



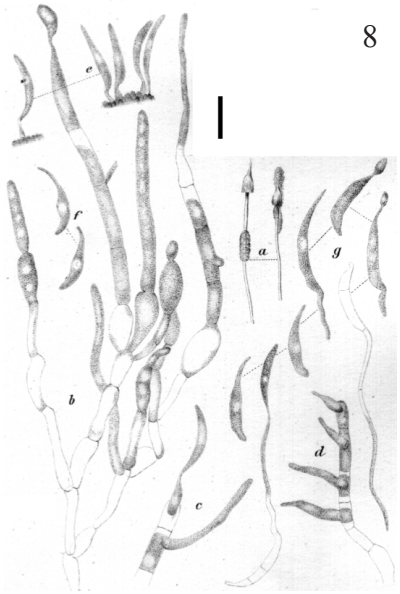


Fig. 7 to the left: Mitochondrial network of a live budding *Saccharomyces cerevisiae* cell recorded with a beam-scanning multifocal multiphoton 4Pi-confocal microscope, MMM-4Pi, at an equilateral resolution of ~100 nm. The mitochondrial matrix was labeled with the green fluorescent protein, GFP, and is displayed as a surface-rendered 3D-data stack. The cell wall has been stained with calcofluor white and displayed after interactive contour tracing. Each arrow length = 1 µm. From Egner et al. (2002), modified in Jacobs (2006).

Fig. 8 to the right: *Jola hookeriarum* Möller nov. gen. et nov. sp., original illustration of Möller (1895b), drawings from living fungus. **a** habitus of *Jola h.* growing on moss seta (to the left), and seta and spore capsule (to the right), natural size; **b-g** light microscopy, bar = 10 µm. **b-d** different stages of basidial development. Note details in cytoplasm distribution: nearly empty generative hyphae after probasidial development; nearly empty probasidia after metabasidial development; during basidiospore development the cytoplasma moves through the sterigmata (d) into the basidiospores (c). **e** tips of sterigmata, emerging from the slimy basidiocarp and carrying asymmetrically inserted, nearly mature basidiospores. Note that each basidiospore is monokaryotic. **f** ejected basidiospores with initial stages of germination. **g** formation of secondary spores. Note transport of cytoplasm into secondary spores.

Observation of living cells is a traditional and frequently practised method in light microscopy. Without any stain, developing stages of cells or cell compartments can be seen, e.g. swimming flagellates, moving cytoplasma, enlarging vacuoles, or occasionally stages of dividing nuclei. Such studies can also be applied to cryptogams (Figs. 8, 16). However, mobile particles smaller than 0.5 µm cannot be resolved with normal light microscopy. To observe subcellular structures and their migration, fluorescent microscopy is particularly suitable. In super-resolution light microscopy **the green fluorescent protein, GFP**, is frequently used as a report of expression. The GFP gene can be introduced in bacterial and eukaryotic host cells, including fungi (Fig. 7) through various procedures. For the discovery and development of GFP, Osamu Shimomura, Martin Chalfie, and Roger Y. Tsien were honoured by the Nobel Prize in Chemistry 2008.

Substantial progress in knowledge of cryptogams through light microscopy:

- **Observation of living cells, cell complexes and organs.**
- **Different cellular construction of algae, bryophytes, ferns, and fungi: single cell → filament, single cell → tissue → organ differentiation.**
- **Detection of taxon-specific microscopic features.**
- **Life cycle elucidation including mitotic and meiotic nuclear division, propagation and sexual reproduction.**
- **Organismic interactions, especially in parasitic and symbiotic systems.**
- **Live observation of subcellular organelles.**
- **Detection of proteins.**

Further potential applications:

- **Observation of organismic interactions through living cells and cell complexes.**

4. The model group rust fungi

After a period of 70 years, recognizing rust fungi as plant parasites in the field, **the combination of microscopic studies and infection experiments were path-breaking to understand host alternation in the black rust's ontogeny**. Basic and applied research were developing quickly and led to regional floras on the one hand and to infection and physiological experiments on the other. The latter were coupled with ultrastructural investigations for elucidating cellular interacting processes in the subcellular and the physio-

logical context. Experimental results clearly showed that rusts had a strong potential in mutations, thus quickly infecting genetically changed hosts again. When *Puccinia graminis* f. sp. *tritici* Ug99 was detected, a global initiative was established to explore the microevolution of this strain and others with molecular methods.

The rusts, **Pucciniales**, are taken here as a **model group** to document developing research methods and their consequent application over **200 years** in a strongly condensed timeline overview (Fig. 9). Three additional papers in this volume are dealing with rust fungi: Peter Zwetko & Paul Blanz interprete the morphology of aeciospores, Reinhard Berndt discusses the Pucciniosiraceae, and Blanz & Zwetko present remarks on species concepts in European florae of rust fungi.

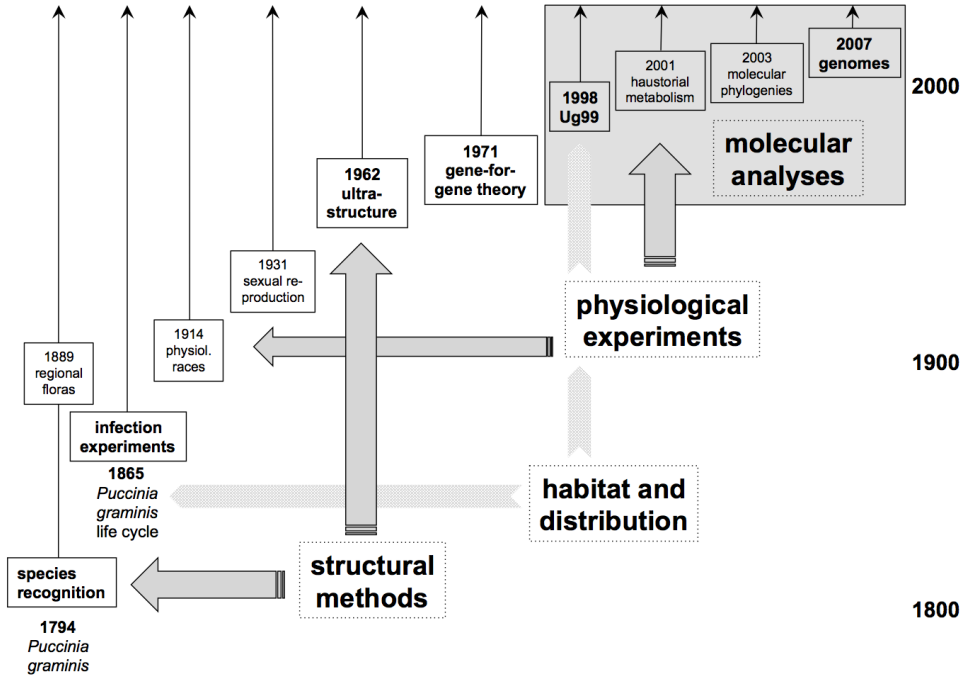


Fig. 9: Overview of **major steps in research on rust fungi**, showing the development and application of new methods. Arrow-headed lines indicate continuous application of older methods throughout subsequent generations. (Graphic: F. Oberwinkler)

1) Taxonomic **recognition** of the black rust, *Puccinia graminis* by Persoon (**1794**); germ pores in urediniospores and teliospores and germination of the latter ones (Tulasne & Tulasne 1847); rusts are basidiomycetes (Tulasne 1853); major classification of rust fungi (Tulasne 1854b).
2) Clarification of the black rust **life cycle** (Fig. 10) in combining infection experiments with light microscopic examinations (de Bary **1865**, 1867, Petersen 1974).

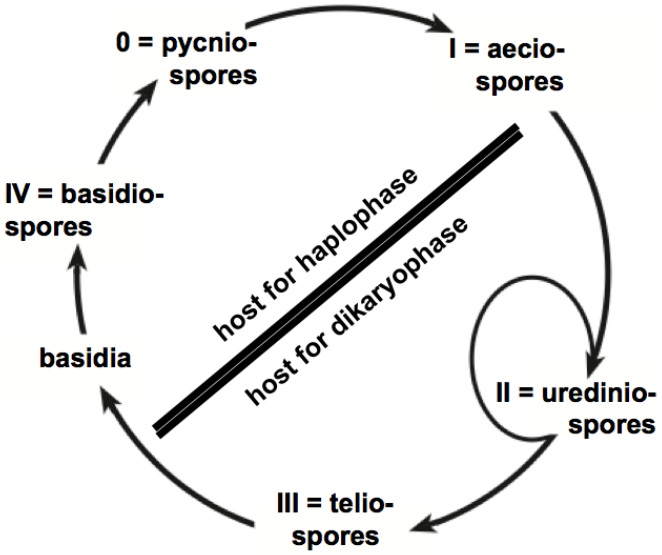


Fig. 10: Life cycle of the black rust, *Puccinia graminis*, based on the original discoveries of Anton de Bary: The hosts for the dikaryophase are grasses, including cereals, while the haplophase can infect and grow only on *Berberis-Mahonia* species. The developmental sequence of spores is fixed, however, urediniospores (II) are capable for repetition, resulting in a vegetative propagation of the dikaryophase with potentials for epidemic spread outs on cultivated, useful grasses. Teliospores (III) function as resting spores and finally as diploid probasidia, producing meiosporangia with meiospores, i.e. basidia with basidiospores (IV). In sexual reproduction, pycniospores (0) are involved as providers of compatible haploid nuclei. Dikaryotization occurs in primordial hyphae of aecia which finally produce dikaryotic aeciospores (I). These are unable to infect the haplophase host, and they rely exclusively on species of the Poaceae. (Graphic: F. Oberwinkler)

3) The compilation of data to get information about the **geographical distribution** of rusts started with Plowright and his monograph of the British Uredineae and Ustilagineae (Plowright **1889**), followed by McAlpine with rusts of Australia (1906), and the British rust fungi of Grove (1913). Compare subparagraph 13.
4) Rust host ranges and taxon separation were based on **host specificity** by proposing „formae speciales“ (Eriksson **1894**).
5) **Cereal rusts** play the most important role as parasites in agricultural ecosystems and their management. Because of their economical importance they were already comprehensively treated by Eriksson & Henning (**1896**). The exploration of these rusts is one of the most fascinating chapters in microscopy, functional and experimental mycology and biology in general. It also reflects precisely the availability and consequent progress of elucidating the origin of interacting partners, infection processes, resistance mechanisms, geographical distribution, continuous microevolution of hosts and parasites, and global scientific and commercial initiatives to conquer the spread out of new cereal rust epidemics.

6) **Nuclear behaviour** of rusts with karyogamy in teliospores and meiosis in basidia were studied by Sappin-Trouffy (**1896**).

7) The abbreviation of macrocyclic heteroecious rust cycles to microcyclic autoecious ones by infection of basidiospores only of the previous aecial host led to propose **Tranzschel's law** (Tranzschel **1904**, Shattock & Preece 2000).

8) **Cytological studies of infection** by urediniospores were carried out by the former de Bary student Harry Marshall Ward (1904).

9) Rust fungi with **alternating hosts** and their biological relations were summarized by Klebahn (**1904**).

10) The complexity of rust **life cycles** required a specific **terminology**: pycnium (spermogonium), aecium, uredinium, telium with corresponding spore forms (Arthur **1905**; Cunningham 1930, Hughes 1970, Hiratsuka 1973). Spermogonia were classified and used for taxonomy by Hiratsuka & Hiratsuka 1980, and Hiratuska & Sato 1982).

11) **Physiological races** within „formae speciales" of *Puccinia graminis*, based on infection types (Stakman **1914**) led to differential host sets for the wheat black rust (Stakman & Levine 1922, Stakman et al. 1962).

12) Basidio- and aecio-**spore discharge** in *Puccinia graminis,* described by Buller (**1924**), recognizing a droplet at the base of the basidiospore prior to its discharge. Meiosporangial „germination" is strongly influenced by external conditions, like air, water, or solid support and varies accordingly with ballistospores, hyphae, and hyphae with appressoria (Bauer & Oberwinkler 1986a, b).

13) An extensive **taxonomic paper of the Uredinales** was first published by Dietel (**1928**), followed by the manual of the rusts in United States and Canada by Arthur (1934), and the conspectus of the rust fungi of the USSR by Tranzschel (1939). The most comprehensive regional treatment of rust fungi was Gäumann's „**Die Rostpilze Mitteleuropas** mit besonderer Berücksichtigung der Schweiz" (**1959**). The Rust Fungi of cereals, grasses and bamboos were dealt with by Cummins (1971), and Majewski (1977) compiled the rusts of Poland and neighbouring countries. In the second edition of „Die Rostpilze Österreichs" (Poelt & Zwetko 1997) 496 species were treated. McKenzie (1998) listed 234 rust species for the flora of New Zealand, and Berndt (2013) 68 species with 57 new reports for French Guiana. Compare subparagraph 3.

14) Craigie (**1931**) found that rust fungi are heterothallic with **sexual reproduction**.

15) The **genetics of pathogenicity** in *Melampsora lini* was studied by Flor (**1946**), who introduced the **gene-for-gene theory** (**1971**).

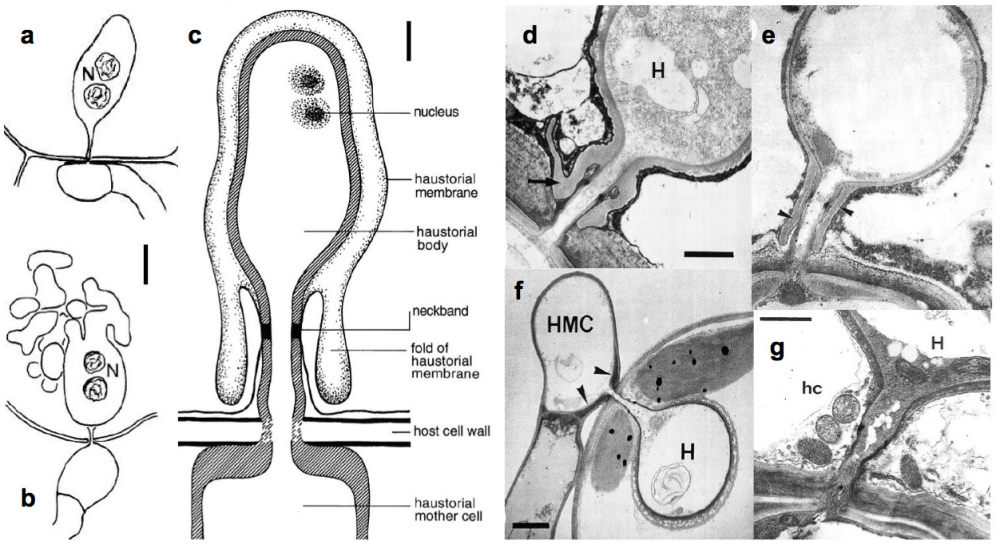


Fig. 11: Haustoria from melampsoraceous rusts (Berndt & Oberwinkler 1995, 1997). **a** and **b** light microscopic illustrations of *Melampsorella* spp., N nuclei of the haustorium, bar = 5 µm. **a** *Melampsorella symphyti* with unlobed haustorium, **b** *Melampsorella caryophyllacearum* with lobed haustorium. **c** Schematic illustration of the velopedunculat haustorial type, bar 1 = µm. **d-g** transmission electron micrographs, d-f bar = 1 µm. **d** *Calyptospora goeppertiana*, penetration peg, haustorial neckband body; the neck is sheathed by a fold of the extra-haustorial matrix which reveals a characteristically bent rim (arrow), H haustorial body. **e** *Thecopsora areolata*, overview of D-haustorium and penetration site. Haustorial neck covered by a thin fold of the extrahaustorial matrix (arrowheads). **f** *Thecopsora galii*, overview of haustorial mother cell (HMC) and haustorium (H); the wall of the mother cell is thickened around the penetration site; the thickening of the HMC wall (arrowheads) is located near the mother cell septum. **g** *Melampsorella symphyti*, haustorial neck, penetration site, and proximal part of haustorial body (H); neck naked, not wrapped into a fold of the haustorial membrane; bar 1 = µm.

16) In a first edition, the **genera of rust fungi** were treated by Cummins (**1959**), a second edition was published in 1983 by Cummins & Hiratsuka, and a third one by the same authors in 2003.

17) **Ultrastructural studies** in rust fungi were undertaken when the technical prerequisites were sufficiently developed. Surprisingly, **simple septal pores** were found in rusts (Jones 1973, Hardwick et al. 1975, Markham 1994, compare Oberwinkler & Bauer in this volume). **Haustoria** (Fig. 11) of rust fungi were already observed light microscopically by de Bary (1884) and illustrated by Sappin-Trouffy (1896), with remarkable structural details, especially when preparations from living hosts and parasites were studied. Detailed developmental cytological studies, combined light microscopy with SEM (Quilliam & Shattock 2003), and finally with confocal microscopy, were used for 3-D imaging (Sørensen et al. 2012). – Electron microscopically, the cellular interaction of rust haustoria with host cells was studied intensively. Besides general structural features, as

penetration channel, neckband, extrahaustorial matrix (Ehrlich & Ehrlich 1962, Ehrlich et al. 1966, Hardwick et al. 1971, Ehrlich & Ehrlich 1971, Heath 1971, Heath & Heath 1971, also special, taxonomically relevant structures, as gymnopedunculate and velopedunculate haustoria were detected (Berndt et al. 1994; Berndt & Oberwinkler 1995, 1997). The structural aspects of the dikaryotic haustorium together with metabolic functions were treated by Mendgen & Deising (1993), Voegele et al. (2009), and Voegele & Mendgen (2011). – Also ultrastructural details of nuclear divisions in **mitosis** (Harder 1976a, b) and **meiosis** could only be studied adequately by transmission electron microscopy (O'Donnell & McLaughlin 1981a, b, c).

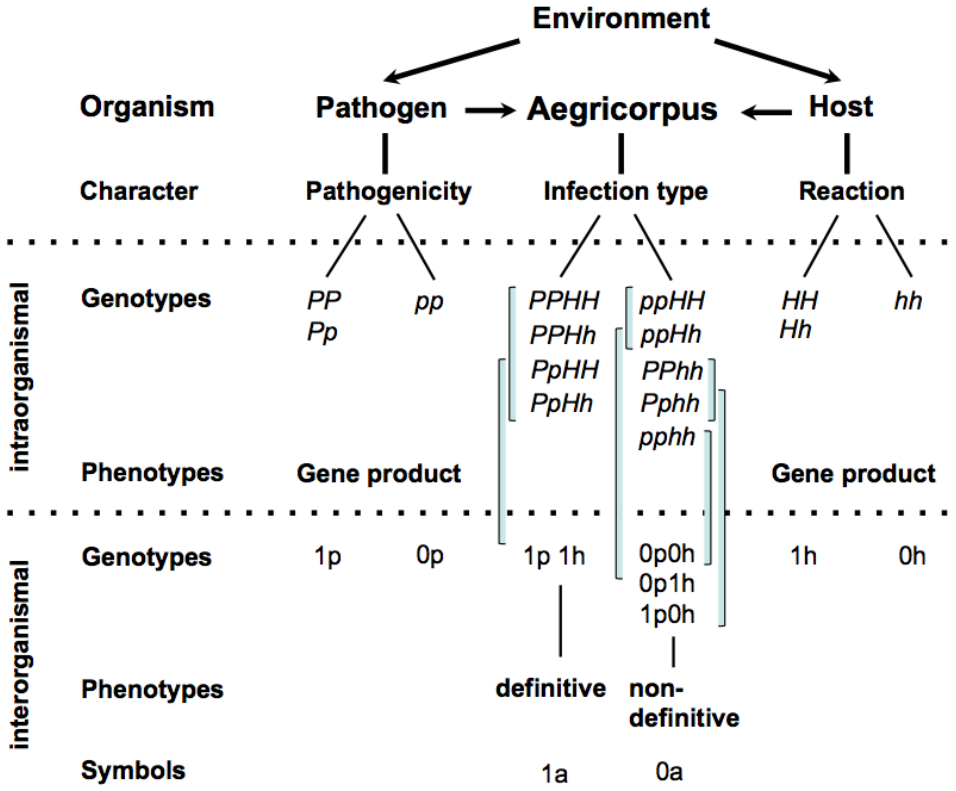


Fig. 12: An **expanded version of the gene-for-gene model** showing interaction of interorganismal genetics representing corresponding gene pairs typical of cereal rusts. *H, h, P, p* = alleles for reaction of the host and pathogenicity of the pathogen, numbers indicate loci (after Loegering 1969, 1984).

18) The result of coevolution is a functional structure of host and pathogen together, named **aegricorpus** by Loegering (**1969**, **1984**, Fig. 12). However, the genotypes are of the symbionts. This implies that a cultivar/culture may carry genes for resistance and avirulence, and likewise may be

susceptible or virulent. Pathogen and host are organisms, and both together, as a functional unit, are considered as a third organismal entity, the aegricorpus. Characters are defined as variations in phenotypes, genetically characterized by more than one allele at a locus. Nine possible combinations constitute the aegricorpus with homo- and heterozygous genotypes of the pathogen and host. The infection type is aequivalent to the intraorganismal phenotype of the aegricorpus and neither of the host nor the pathogen. Neither reactions of the pathogen in axenic culture nor those of the host itself can therefore be representative for the interaction physiology. Browder (1985) summarized this theoretical concept that „a definitive parasite genotype interacting with a definitive host genotype in a definitive environment results in a definitive phenotype."

19) The **worldwide distribution of *Puccinia graminis*** is a result of agricultural attempts to grow wheat in all regions with favourable abiotic conditions. In many of these areas the parasite has become **independent of the primary host** *Berberis* (Anikster & Wahl **1979**).

20) **Lytic enzymes** in early dikaryotic infections include primarily chitin deacetylase, proteases and acidic cellulases, then pectin methylesterases, neutral cellulases, and polygalacturonate lyases (Mendgen & Deising **1993**).

21) During the ontogeny of the infection process, signals of the plant direct the fungal growth outside and inside the host, and the parasite was assumed to interfere with the **signalling** systeme of the host (Heath **1997**).

22) Fluorescence microscopy was applied for studying **endocytosis** of germ tubes of *Uromyces fabae* urediniospores (Hoffmann & Mendgen **1998**), using the dye FM4-64. The pathway of FM4-64 internalisation by endocytosis was also demonstrated in *Aspergillus nidulans, Botrytis cinerea, Magnaporthe grisea, Neurospora crassa, Phycomyces blakesleanus, Puccinia graminis, Rhizoctonia solani, Sclerotinia sclerotiorum*, and *Trichoderma viride* by Fischer-Parton et al. (2000). These results indicated a generally distributed mechanism in fungal hyphae.

23) A **first representative molecular phylogeny** (Fig. 13) of rust fungi was mainly based on north temperate species (Maier et al. **2003**). Nevertheless, this study confirmed several taxonomic groupings, used in traditional classifications, e.g. Melampsoraceae, Cronartiaceae, Coleosporiaceae, Phragmidiaceae, and the genus *Gymnosporangium*. On the other hand, Pucciniastraceae were split in two groups, fern inhabiting rusts were not monophyletic, and the genera *Puccinia* and *Uromyces* were mixed in one cluster. In addition, **coevolutionary trends** could be deduced from the phylogenetic tree: (a) A general line passes from coniferes to angiosperms. (b) Rust fungi with Pinaceae-alternation have a basal position. (c) Rosaceae are hosts for two groups of rusts, heteroecious and autoecious ones.

(d) Dicot-Monocot host alternations are frequent in advanced groups, as well as autoecious species. (e) In addition, host jumps may have obscured the coevolution with higher taxonomic host groups (VAN DER MERWE et al. 2008). (f) Apparently, fern rusts are not placed in a basal position. – This phylogenetic hypothesis sheds also light on **habitat conditions**: (a) Coniferous forests, including fern vegetations represent geologically old biomes. (b) Deciduous forests constitute younger habitats, and (c) vegetations with dominating herbaceous plants are ecologically marginal or secondary under natural situations. Often, the latter ones have short vegetation periods with a quick growth of plants until seed production. Also the percentage of annuals is mostly high. Such host conditions certainly had a selective pressure on rust pathogens, favoring those with autoecious life cycles.

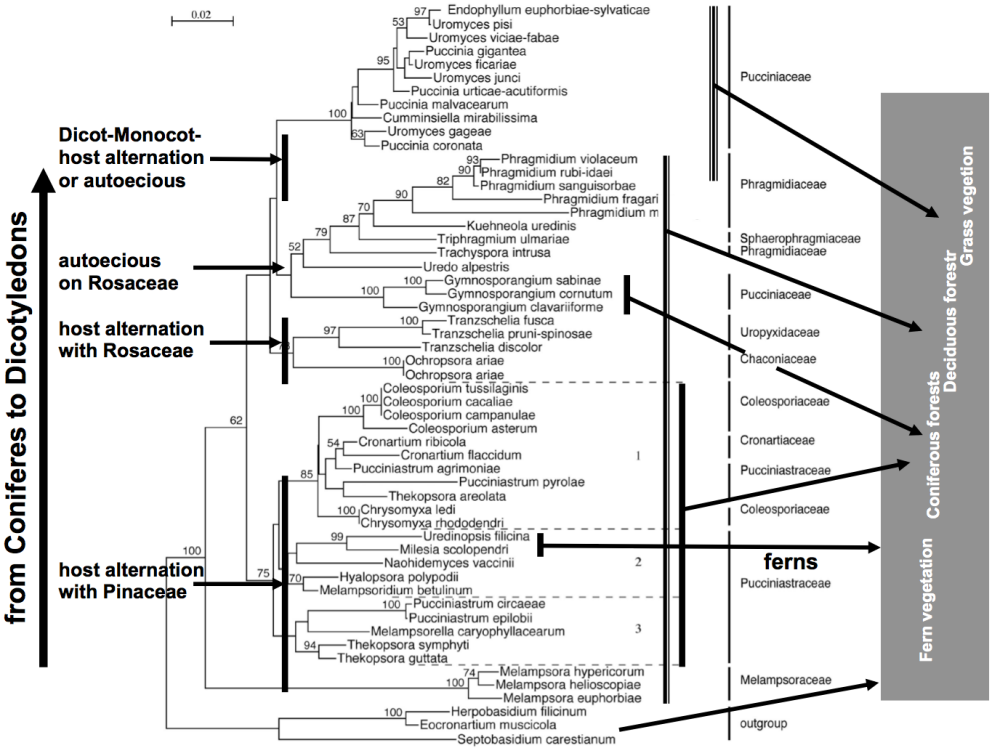


Fig. 13: Phylogenetic hypothesis for the rust fungi, Pucciniales, with main host dependencies and major vegetation units (tree after MAIER et al. 2003). (Graphic: F. OBERWINKLER)

24) In **1998** a new race of *Puccinia graminis* f. sp. *tritici* (*Pgt*), **Ug99** (American nomenclature: TTKSK), was detected in Uganda (PRETORIUS et al. 2000). This race was virulent for most of the commercial wheat cultivars grown in Eastern Africa, South Africa, Yemen, and Iran. Consequently,

the fungus spread out in the following years over this geographical region (Fig. 14). It is the first race of the black rust that had virulence to resistance genes Sr31 together with other virulence genes of *Triticum aestivum* origin, and Sr38, originating from *T. ventricosum* (Jin et al. 2008, Tab. 1).

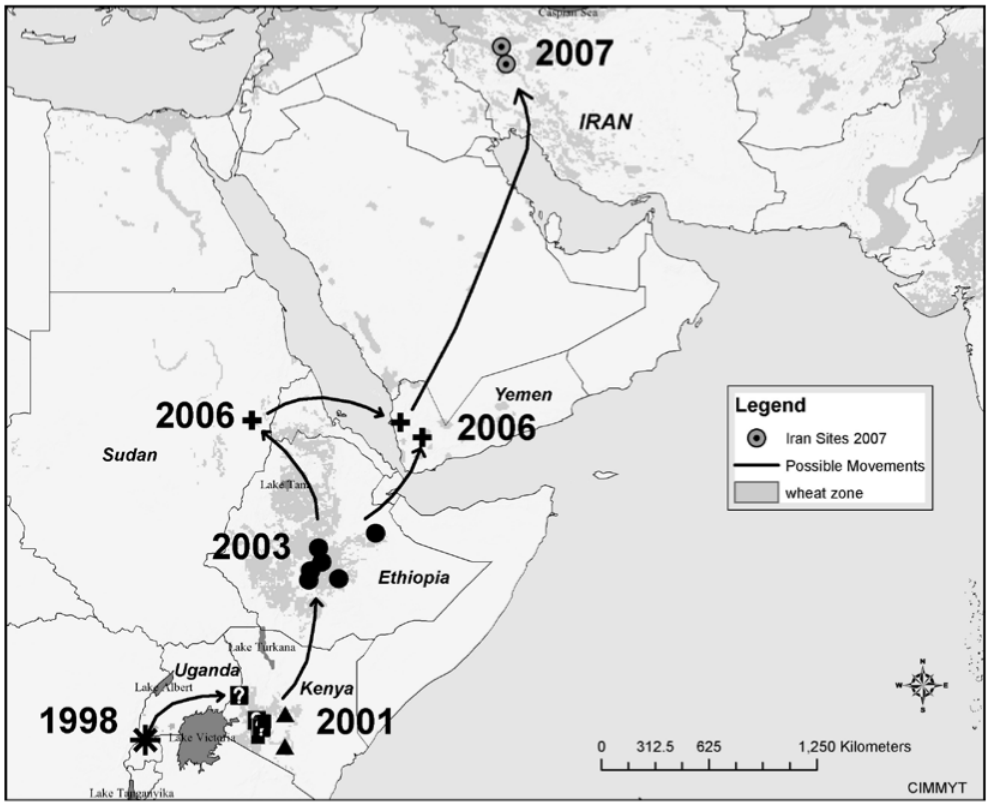


Fig. 14: *Puccinia graminis* f. sp. *tritici* Ug99 locations in 2009; from Hodson et al. (2009). Ug99 originated in Uganda and was characterized in 1999. It was detected in Kenya 2001, in Ethiopia 2003, in Sudan and Yemen 2006, and already 2007 in Iran.

25) The threat of Ug99 for world wheat production led to the establishement of a global rust initiative in 2005, later named **Borlaug Global Rust Initiative** (BGRI). A broad range of research activities is involved, comprising not only resistance breeding, but also pathogen virulence studies, host-pathogen genetics, breeding, and finally agronomic and economic parameters play a most important practical role (McIntosh 2009, McIntosh & Pretorius 2011). Within the BGRI, the global cereal rust monitoring system, GCRMS, focused on Ug99, in two countries in 2007, 15 in 2009, and over 20 in 2011 (Singh et al. 2011). – Population diversity of *Puccinia graminis* is assumed to be sustained through sexual cycle on alternate hosts. A *Pgt* population decline east of the Rocky Mountains of

North America, resulted in a single race remaining in the last decade (Jin et al. 2014). Babiker et al. (2015) detected a new gene on the long arm of chromosome 7A in the spring wheat landrace PI 374670 with resistance for Ug99.

Tab. 1: Summary of the known status of the Ug99 race group in 2010, twelve years after its appearance in Uganda. The North American nomenclature system is used for race acronyms. Often Ug99 races named by the addition of their key virulence (+) or avirulence (-) characters. In addition, the first detection of the strains in the countries in question is listed (after Hodson et al. 2012).

Race[1]	Common alias	Key virulence (+) or avirulence (-)	Country (year of 1st detection)
TTKSK	Ug99	*+Sr31*	Uganda (1998), Kenya (2001), Ethiopia (2003), Sudan (2006), Yemen (2006), Iran (2007), Tanzania (2009)
TTKSF		*-Sr31*	South Africa (2000), Zimbabwe (2009)
TTKST	Ug99 + Sr24	*+Sr31, +Sr24*	Kenya (2006), Tanzania (2009), Eritrea (2010)
TTTSK	Ug99 + Sr36	*+Sr31, +Sr36*	Kenya (2007), Tanzania (2009)
TTKSP		*-Sr31, +Sr24*	South Africa (2007)
PTKSK		*+Sr31, -Sr21*	Ethiopia (2007), Kenya (2009)
PTKST	Ug99 + Sr24	*+Sr31, +Sr24, -Sr21*	Ethiopia (2007), Kenya (2008), South Africa (2009), Eritrea (2010), Mozambique (2010), Zimbabwe (2010)
TTKSF+		*-Sr31*	South Africa (2010), Zimbabwe (2010)

26) The **floral scent** production in the pseudoflowers of Brassiceae species, induced through infections **of *Puccinia monoica*** is considered as a combination of attractives for pollinators that effect sexual outcross of the parasite (Raguso & Roy **1998**). A gene expression profiling, undertaken by Cano et al. (2013) revealed down-regulated genes in the plant for transcription, reproduction, floral organ development, anthocyanin and terpenoid biosyntheses, and up-regulated ones for vegetative organ development, carbohydrate transport, wax biosynthesis, and L-phenylalanine metabolisme. In this floral mimicry 31 differentially regulated plant genes were detected that obviously were induced by the rust pathogen. – An **insect-mediated reproduction** of *Puccinia arrhenatheri* was already reported in **2002** by Naef et al., and insect-transmitted *Puccinia punctiformis* urediniospores were studied by Wandeler & Bacher (2006). The latter fungus has an intensive scent in its pycnidial stage, hence its former name *P. suaveolens*. Surprisingly, this developmental stage has not been considered in potential transmitter activities though there is often a considerable overlap in the appearance of pycniospores and urediniospores in close by host communities.

27) It was logical to assume that **nutrient flow** from the autotrophic host to the heterotrophic parasite is mediated by **haustoria**, but Voegele et al. (**2001**) were the first to demonstrate experimentally that hexose uptake

occurs in these interactive compartments in *Uromyces fabae*. Plant sucrose is cleaved by fungal invertase and the monosaccharides are taken up by the hexose transporter, hexose is metabolised in gycolysis and the pentose phosphate pathway, while D-fructose is converted into mannitol (Voegele & Mendgen 2011). Also amino acid uptake takes place through haustoria (Struck 2015).

28) First results in the **genomic era of rust fungi** were derived from *Puccinia striiformis* f. sp. *tritici* (Cantu et al. **2011**, Zeng et al. 2013), *Puccinia graminis* f. sp. *tritici* and *Melampsora larici-populina* (Duplessis et al. 2011), *Melampsora lini* (Nemri et al. 2014), and *Hemileia vastatrix* (Talhinhas et al. 2014). These rusts lack genes encoding essential assimilatory enzymes, suggesting that they obtain the reduced versions of these nutrients from the host (Garnica et al. 2014).

29) The limitations of culturing rust fungi led to a **reappraisal of fieldwork** in *Puccinia striiformis* f. sp. *tritici* (PST) with a „field pathogenomics approach by transcriptome sequencing infected wheat leaves collected from the field“ in the United Kingdom (Hubbard et al. **2015**). A dramatic shift in the PST population of the country has been detected, suggesting that exotic pathogen lineages were introduced recently.

30) For economical calculations about the **costs of black rust research**, Pardey et al. (**2013**) developed an ecological-niche model with a probabilistic risk assessment. They estimated „that a sustained investment of $51.1 million per year (2010 prices) in stem-rust research could be justified economically“. This annual research and development „expenditure is equivalent to investing $0.23 per hectare of wheat in 2009; by comparison, U.S. wheat farmers spent $34.56 per hectare on seed in 2009.“

31) **A future scenario to answer key questions in plant pathology**, including research on rust fungi, is considered as a multi-dimensional approach (Saunders **2015**). These theoretically promising considerations are, fortunately, and at least partly, realised already.

Tab. 2: An overview of **research methods, applied to cryptogams incl. of cyanobacteria, and a selection of results**, suited for a discrimination of the organismic groups. No attempt was made to compile a comprehensive list. (Orig.)

	light microscopy	**electron microscopy**	**chemical methods**	**molecular methods**
ferns	oogamy, spermatozoids, cellular interactions	chloroplasts, gametes, fertilization, sporogenesis	chlorophyll a, b, starch, cell wall polysaccharides, secondary metabolites	phylogenies, class I KNOX and class III HD-Zip genes
hornworts	cellular morphology, chloroplasts with pyrenoids	isokont, chloroplasts, pyrenoid and spore ultrastructure	chlorophyll a, b, starch, cell wall polysaccharides	plastid genome, phylogeny
mosses	cellular morphologies, interactions	isokont, chloroplast ultrastructure	chlorophyll a, b, starch, cell wall polysaccharides	phylogenies, targeted mutageneses
liverworts	cellular morphology interactions	isokont, chloroplast ultrastructure	chlorophyll a, b, starch, cell wall polysaccharides	phylogenies
green algae	uni-, multicellular morphology, isoogamy, fungal symbioses	isokont, 2membranous plastids, mitochondira, various thylakoid arrangement	chlorophyll a, b, starch, carotene, xanthophylls, cell wall with sulfated polysaccharides, sex pheromones	phylogenies, xantophyll-dependent photoprotection, lipid metabolism, carotenoid biosyn.
heterokonts	uni-, multicellular morphology	heterokont, mitochondrial cristae, chromoplast	chlorophyll a, c, sterol synthesis, mannitol metabolism	phylogenies, functional gene annotations
false mildews	mostly unicellular, filamentous, branching, gametes, sporangiophores, haustoria	heterokont, gametogenesis, haustoria	cellulose, glucans, hydroxyprolin	kinesin motor proteins, metabolic pathways and compounds, phylogenies
red algae	uni-, multicellular morphology, akont	thylakoids unstacked, phycobilisomes	chlorophyll a, d, phycobiliproteins, floridean polysaccharides	toxins, genome projects, phylogenies
cyanobacteria	single cells, trichomes, colonies, hormogonia, heterocysts, prokaryotic, centro- and chromoplasm, plant and fungal symbioses	plastids with 2 membranes, thylakoids, polyhedral bodies, phycobilisomes	chlorophyll a, b, phycobilins, cyanophycin, peptidoglucans, polyphosphate, nitrogen fixing, cyanotoxins, bioactive compounds	biogenesis of cell organelles, nitrogen assimilation, carbon acquisition, genomics, circadian clock
lichens	dual nature, cyanobacteria, algae, mycosymbionts	asco-, basidiomycetous mycobionts, cellular interactions	chlorophyll a, b, phycocyanin, specific secondary metabolites	algae, cyanobacteria, fungi paraphyletic
fungi	opisthokont, akont, yeasts, filaments with apical growth, fruitbody constructions, ontogenies	Spitzenkörper, septal types, nuclear divisions, cell organelles, interactive structures	heterotrophy, chitin, exoenzymes, diverse secondary metabolites, antibiotics	endocytosis, HEX self-assembly, phylogenies
slime molds	plasmodial, acellular fructifications	phagocytosis	diverse secondary metabolites	phylogenies, population genetics
cell walls	present or not, ornamentation	present or not, ornamentation	cellulose, xylan, lignin, chitin, proteins	interconnections of polysaccharides
nuclei	nuclear divisions	mitosis, meiosis, SPBs, microtubules	nucleic acids, chromatin regulation	genes, genomes
cytoplasm	movement	ER, membranes	metabolic activities	actin, microtubule, cytoskeleton
vacuoles, vesicles	changing size and position	membranes, contents	metabolic reactions	genomic regulations
plastids	structure and position	membrane and thylakoid constructions	photosynthesis	plastid genomes
eukaryotic flagellae	structure, position and orientation	axonemes of 9 pairs + 2 central single microtubules, basal body	actin, α- and β-tubulin, dynein arms	multiheaded motor proteins, dynein regulatory complex
additional cell organelles		membranes, mitochondria, ribosomes	lipid layers, diverse protein granules, etc.	mitochondrial energetics, etc.

Model group rust fungi:

- **Obligate parasites of higher plants.**
- **Host alternation with complex life cycles → microcylic abbreviations.**
- **Coevolution with hosts and host jumps.**
- **Dependencies on geological vegetation changes.**
- **Particularly suitable for tracking the historical sequence of research methods.**
- **Successful interdisciplinary research efforts.**
- **Ug99 and its global agricultural and economic impacts.**

Further challenges:

- **Elucidation of rust's evolutionary origin.**
- **Studies in macro- and micro-coevolutionary systems.**
- **Multi-dimensional plant pathology.**

5. Electron microscopy for cell interior structures

Two technical developments revolutionized approaches in structural biology in the middle of the 20th century, **electron microscopy** and the unexpected developments in light microscopy to overcome the physical limitations of light resolution. After the construction of the first **transmission electron microscope**, TEM, 1931 (Knoll & Ruska 1932, Ruska 1934) by Ernst Ruska (1906–1988), it was not until 1945 that it was applied in cell biology. This required additional technical innovations, i.e. appropriate chemical fixation, at first with potassium permanganate, then osmium tetroxide, and embedding protocols for biological samples, and the development of ultramicrotomes, 1948–1953 and later on, for cutting the material. Primarily, studies in animal and human samples were carried out, but plants and fungi followed quickly. More than 50 years after his pioneer works in transmission electron microscopy, Ruska was awarded the Nobel Prize in Physics in 1986.

After first applications of TEM in bacteriological research (Marton 1941), crucial technical problems in studying eukaryotes were the **fixation of living samples, embedding and ultrathin sectioning** with microtomes (Porter et al. 1945, Palade 1952). By mastering these techniques and their successful application, Albert Claude (1899–1983), George Palade (1912–2008), and Christian de Duve (1917–2013) were honoured by the Nobel Prize in Physiology and Medicine 1974 for their discoveries concerning „the structural and functional organization of the cell".

The **scanning electron microscope**, SEM, was invented by Manfred von Ardenne (1907–1997) already 1937 (Ardenne 1940), but its general application in biology had to wait until the Cambridge Scientific Instrument Company produced the Stereoscan 1965. Since then, surface structures of biological samples are preferably studied by SEM, a high percentage being recruited from spores of crytogams, mostly decorated by specific spore wall ornamentations.

Because there was no other research technique available for reaching magnifications and resolutions of this dimension, a plethora of electron microscopic studies were carried out since the 1950s. Most cell organelles of many organismic groups were investigated electron microscopically, thus leading to a unique **boom in structural biology** (Fig. 27) with a countless number of detailed information. For the purpose to compare methods' impacts on research applications and results in cryptogams see table 2.

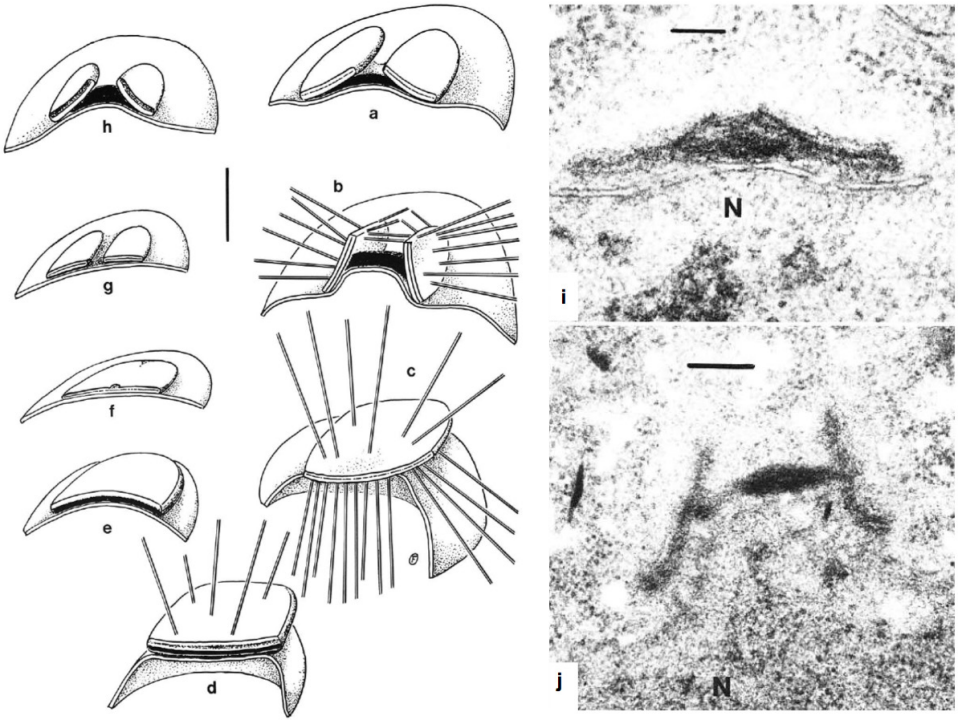


Fig. 15: *Cryptomycocolax abnormis*: **a-h** diagram of spindle pole body, SPB, development during meiosis. **a** middle prophase I, **b** late prophase I, **c** metaphase I, **d** late telophase I, **e-g** successive stages at interphase I, **h** interphase II or mitotic interphase. Bar = 1 µm. **i** longitudinal section of prophase I SPB, the discs multilayered and connected by a middle piece. Discs appear separated from the nuclear envelope by an electron-transparent zone. A ribosome free zone surrounds the cytoplasmic side of the SPB (N = nucleus). Bar = 0.1 µm. **j** late prophase I SPB. The discoidal elements are in an upright position with respect to the nucleus (N). Bar = 0.2 µm. From Oberwinkler & Bauer (1990).

Only few examples for transmission electron microscopy in fungi are mentioned here, haustoria of rusts (Fig. 11), and spindle pole bodies (SPBs, Fig. 15) in the basidiomycetous mycoparasite *Cryptomycocolax abnormis*. SPBs are nuclear associated organelles, involved in spindle organization (Fig. 15b–d), and therefore essential for nuclear division. The SPB cycle includes its splitting as a precondition in nuclear division. For further information about the ultrastructure in Basidiomycota, I refer to Oberwinkler & Bauer in this volume.

Micro-computed tomography, micro-CT, has the potential of 3-D non-destructive imaging and is widely applied in medical disciplines. In a **combined approach with SEM and light microscopic studies**, Pallua et al. (2015) tried to elucidate hyphal textures in *Hericium coralloides*. The authors believe that they provided „an approximation of the evolutionary effictiveness of this bizarrely formed basidioma type in terms of the investment of tissue biomass and its reproductive output (production of basidiospores)".

Substantial progress in knowledge of cryptogams through electron microscopy:

- **Observation of cells and cell organelles.**
- **Different subcellular construction of plants and fungi.**
- **Detection of taxon-specific submicroscopic features in cell organelles.**
- **Elucidation of cell organelle cycles, including mitotic and meiotic nuclear division.**
- **Ultrastructural features of organismic interactions, especially in parasitic and symbiotic systems.**
- **Three dimensional photographing of cell surfaces and cell complexes.**

Further potential applications:

- **Combined application with fluorescent microscopy.**

6. Experimental approaches: from cultures to biotechnology

Sexuality and genetics

Though Joseph Gottlieb Kölreuter's (1733–1806) experimental studies focused on pollination of flowering plants, he also studied fungi and suggested to have clarified the **secret of cryptogamy** (Kölreuter 1777). Together with Karl Friedrich Gärtner (1772–1850) he definitely confirmed the sexuality of plants as detected first by Rudolf Jacob Camerarius (1665–1721). – When

studying Zygomycetes, Christian Gottfried Ehrenberg (1795–1876) recognized fusion of terminal cells, zygogamy, as **sexual reproduction** (Ehrenberg 1819).

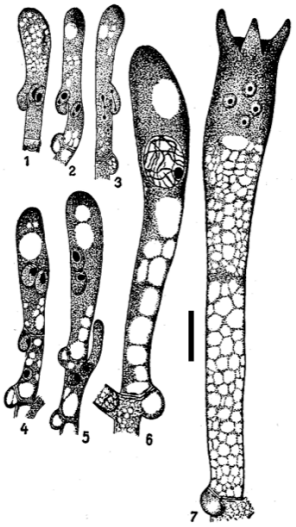


Fig. 16: **Basidial development** in *Armillaria* illustrates the sexual reproduction from the dikaryotic (1-5) to the diploid stage (6) with immediately following meiosis (7) in one cell, the meiosporangium basidium, typical for holobasidiomycetes. The microscopic details clearly prove the nuclear behaviour during karyogamy and meiosis, and cytoplasmic changes with an accumulation of vacuoles in the basal part. This is a prerequisite for having cytoplasm available during basidiospore production on top of the meiosporangium. The example demonstrates the power of light microscopy when living cells are observed with high magnification. Bar = 5 µm. From Kniep (1928).

Tab. 3, 4: Results of mating experiments of basidiomycetes. The letters are used for genetic factors, in the case of Aa etc. localized on homologous chromosomes. **3**: In the case of several *Coprinus* species and other agarics, two individuals of the same species and from different localities were used for mating experiments of haploid mycelia. Four haploid mycelia, 1, 2, 3, 4, resulted from hybrid basidiocarps which were crossed with four parental haplotypes. **4**: In the mating experiment with haploid mycelia from one single *Schizophyllum commune* basidiocarp, only mycelium 10 reacts with all mycelia AB and all aB, indicating that it carries factor b, but neither A nor a. An explanation is that A or a mutated what is expressed by A_1b. From Kniep (1928).

3

	AB	AD	CB	CD
	1	2	3	4
AB	–	–	–	+
ab	+	+	+	+
Ab	–	–	+	+
aB	–	+	–	+
CD	+	–	–	–
cd	+	+	+	+
Cd	+	+	–	–
cD	+	–	+	–

4

		AB	AB	Ab	aB	AB	Ab	aB	ab	Ab	A_1b
	S	1	2	3	4	5	6	7	8	9	10
AB	1	–	–	–	–	–	–	–	+	–	+
AB	2	–	–	–	–	–	–	–	+	–	+
Ab	3	–	–	–	+	–	–	+	–	–	–
aB	4	–	–	+	–	–	+	–	–	+	+
AB	5	–	–	–	–	–	–	–	+	–	+
Ab	6	–	–	–	+	–	–	+	–	–	–
aB	7	–	–	+	–	–	+	–	–	+	+
ab	8	+	+	–	–	+	–	–	–	–	–
Ab	9	–	–	–	+	–	–	+	–	–	–
A_1b	10	+	+	–	+	+	–	+	–	–	–

One of the most impressive results of DE BARY's investigations was the elucidation of the life cycle of the black rust, *Puccinia graminis* (Fig. 10). This milestone marks the begin of experimental mycology through artificial infections of plants, necessary for deciphering the host spectrum of each rust species (compare chapter 4). – Experiments with **culturable fungi** were intensivley conducted by BREFELD (1881–1912) to elucidate life cycles. His advice encouraged Alfred MÖLLER (1860–1922) to collect, to study intensively by microscopy and to cultivate South Brazilian fungi. His richly illustrated books (MÖLLER 1893, 1895a, b) are pioneer works in mycology. – Karyological studies to elucidate sexuality were carried out by several microscopists (Fig. 16), and fungal cultures were heavily used for **mating experiments** by KNIEP (1881–1930) to study sexual reproduction of diverse groups (Tabs. 3, 4).

Despite KNIEP's outstanding merits as experimental pioneer in sexuality of lower plants, with an enormous amount of published data, there are only few or even no citations of his publications in later times. However, a laudable comment can be found in MÄGDEFRAU's „Geschichte der Botanik" (1992), p. 215: „Die allmähliche Enthüllung der Basidiomyceten-Entwicklung ist ein treffendes Beispiel dafür, wie ein schwieriges Problem mit Sorgfalt, wohlüberlegter Methodik und zähem Fleiß allen Irrwegen zum Trotz schließlich doch zur Lösung geführt werden kann." – The American mycologist John ‚Red' RAPER (1911–1974) first studied the mating behaviour in the aquatic „fungus" *Achlya*, a genus of the fungal imitating **Oophyta**, then continued with KNIEP's model organism ***Schizophyllum commune*** for further elucidating the genetic control of sexual reproduction in mushrooms. Reproductive isolation was considered the final step in speciation by TAYLOR et al. (2006), and that genetic isolation may precede morphological changes. The genome sequence of *S. commune* revealed that one-third of the 471 genes predicted to encode transcription factors are differentially expressed during sexual development. In reviewing contributions about the evolution of fungal sexal reproduction, HEITMAN et al. (2013) stressed general principles of the origins of mating-type loci, sex chromosomes, and sexual reproduction involving tetrapolar, bipolar and unipolar cycles. The study of MAIA et al. (2015) reinforced tetrapolarity as the ancestral state of all basidiomycetes. – For **volvocine algae**, GENG et al. (2014) demonstrated genetic continuity between mating-type specification and sex determination pathways, and predicted that „these findings will enable a deeper understanding of how a master regulator of mating-type determination in an ancestral unicellular species was reprogrammed to control sexually dimorphic gamete development in a multicellular descendant."

Biochemistry and physiology

A brief selection of **chemical methods applied in cryptogam research is listed in table 2**. These comprise only the cell wall macromolecules cellulose, lignin and chitin, different pigments in photosynthesis and its products, few

chemical components of cell organelles and major secondary metabolisms and metabolites. As an example for the latter, **lichens** shall serve here because of their **abundant secondary metabolites** (Fig. 17), for which more than 700 have been recorded so far. One of the first were vulpinic acid, detected by the French chemist and pharmacolgist Antoine Bébert in the 1830s, and usnic acid by the German W. Knop (1844). A first milestone in lichen chemistry was the book of Wilhelm Zopf (1846–1909) „Die Flechtenstoffe in chemischer, botanischer, pharmakologischer und technischer Beziehung“ (Zopf 1907), followed by comprehensive treatments of Hesse (1911), Asahina (1934), Asahina & Shibata (1954), Culberson (1969, 1970), Culberson et al. (1977), Huneck & Yoshimura (1996), Huneck (2001), and many others. An overview on the methods applied for the identification of lichen substances was given by Leuckert (1984). – Surprisingly, the metabolism of an early Devonian terrestrial macrofossil, *Spongiophyton minutissimum*, could be identified as belonging to a lichen, and not to another organism (Jahren et al. 2003). This finding may indicate the importance of **lichens in Paleozoic terrestrial ecosystems**.

The diversity of natural **metabolites in fungi** is treated by Dirk Hoffmeister in this volume.

Industrial *Tremella fuciformis* development in Taiwan is presented by Jee-Chen Chen also in this volume.

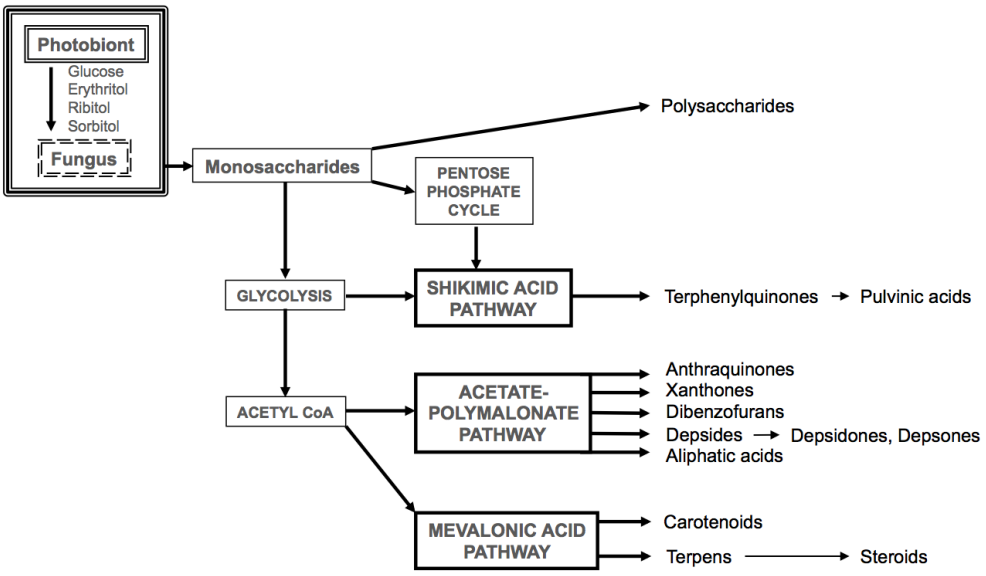


Fig. 17: Simplified scheme of metabolisms and groups of **secondary metabolites in lichens**. Compiled from literature cited in the text. (Graphic: F. Oberwinkler)

Most **secondary metabolites in lichens** are the derivatives of **three main biosynthetic pathways** (Fig. 17). The following is a **selection of compounds which were also studied under pharmaceutical aspects** (Gómez-Seranillos et al. 2014):

Shikimic acid pathway: **Pulvinic acids**: Norstictic acid from *Sticta*; Vulpinic acid from *Letharia* (Burlando et al. 2009).

Acetate polymalonate pathway (polyketide pathway): **Xanthones**: Lichexanthone from *Parmotrema* (Brandão et al. 2013); **Dibenzofurans**: Usnic acid from *Alectoria* (Gollapudi et al.1994), *Parmelia* (Kumar & Müller 1999), *Usnea* (Sultana & Afolayan 2011), *Xanthoparmelia*, and other species (Ingólfsdóttir 2002). **Depsides**: Alectoronic acid from *Parmotrema*; Atranorin from various *Parmelia* (Kumar & Müller 1999) and *Parmotrema* (Honda et al. 2010) species, and *Pseudevernia furfuracea*; Evernic acid from *Evernia prunastri* (Burlando et al. 2009); Lecanoric acid from *Parmelia* and *Parmotrema* (Lopes et al. 2008) species; **Depsidones**: Hypostictic acid from *Pseudoparmelia*; Menegazzic acid from *Usnea*; Norstictic acid from *Usnea* (Sultana & Afolayan 2011); **Aliphatic acids**: Protolichesterinic acid from *Cetraria* (Türk et al. 2003) and *Parmelia* (Goel et al. 2011) species.

Mevalonic acid pathway: **Terpenes**: Glutinol from *Usnea* (Choudhary et al. 2005).

Single-cell cryptogams and their biotechnological potential

Yeasts were characterized light microscopically as single-cell fungi, and Theodor Schwann (1810–1882) found that fermentation of „the yeast“, *Saccharomyces cerevisiae*, is its anaerobic metabolism (Schwann 1837), producing ethanol and carbondioxide. Sugar was identified as the substrate for this process (1838) by Charles Cagniard-Latour (1777–1859), a revolutionary result, 1860 verified by Louis Pasteur (1822–1895) (Pasteur 1860) and further investigated by Julius Wortmann (Fig. 4) who founded the first yeast pure culture laboratory in Geisenheim (1895).

The search term „yeast research“ delivered 57.600 articles in Web of Science in June 2015, and clearly underlines that it is an important discipline in basic and applied research. There is a big yeast community of researchers worldwide realising multi-author compendia, like „The Yeasts“ in three volumes, comprising 2080 pages (Kurtzman et al. 2011).

Various research disciplines are involved in yeast biotechnology, as biochemical and molecular methods, biotransformations and pathway engineering including fermentation approaches (Walker 1998). A simplified overview is given in figure 18.

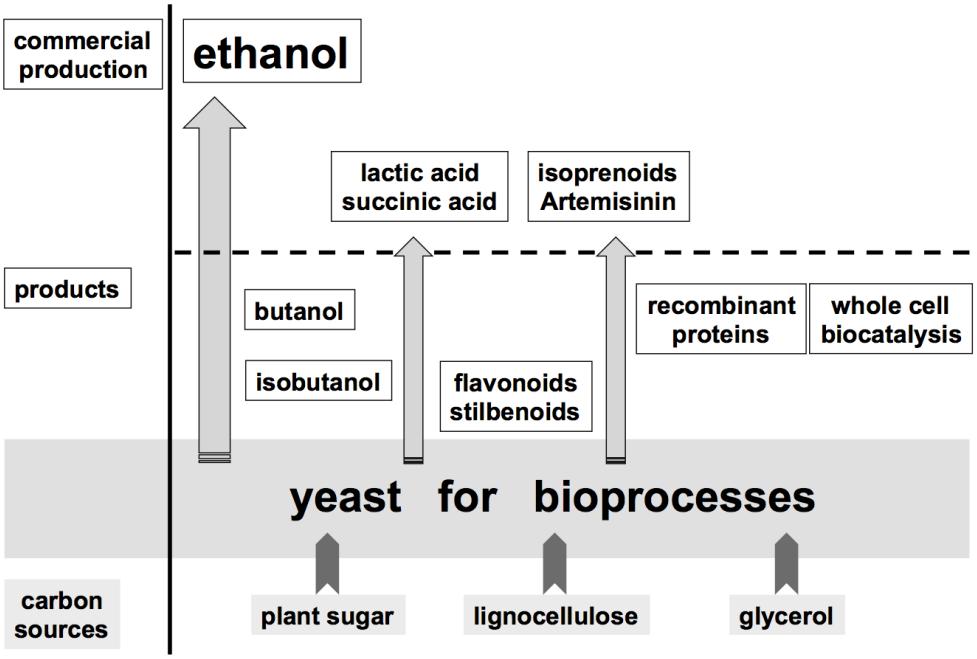


Fig. 18: Diagrammatic overview of **bioprocesses in yeast biotechnology**. Explanation in the text. (Graphic: F. Oberwinkler)

To grow yeast in quantities required for technological production, mostly plant sugar, lignocellulose and glycerol are used. **Ethanol** production has a long history and still dominates yeast biotechnology. Also the production of lactic and succinic acids reached industrial standards (Mattanovich et al. 2014). Similar attempts are going on in bioprocessing for butanol, isobutanol, flavonoids, and stilbenoids. A commercially profitable production of **Artemisinin** was reported by Paddon et al. (2013). This was a first success in synthetic biology for a pharmaceutical agent, demonstrating the incredible potential of available technologies (Paddon & Keasling 2014). The future yeast cell factories will be assembled into genetic modules for fast transfer between strains which will benefit from progress in bio-computational methods (Kavšček et al. 2015).

Characters of yeasts and substantial progress in yeast research:

- **Yeasts are easily culturable single-celled fungi.**
- **The capability of *Saccharomyces cerevisiae* to switch from aerobic metabolism to anaerobic fermentation led to the oldest and most efficient biotechnological application.**
- **Bioprocessing of various commercially important products is already practised.**

Further potential developments:

- **Synthetising an optimal yeast for a given production process.**

The use of **microalgae as production systems** are considered helpful to solve the problems of feed, food, and fuel supply (Fig. 19). For that purpose strain selection and genetic engineering, process, and reactor design and integration into environmental mass and energy fluxes is required (Fresewinkel et al. 2014).

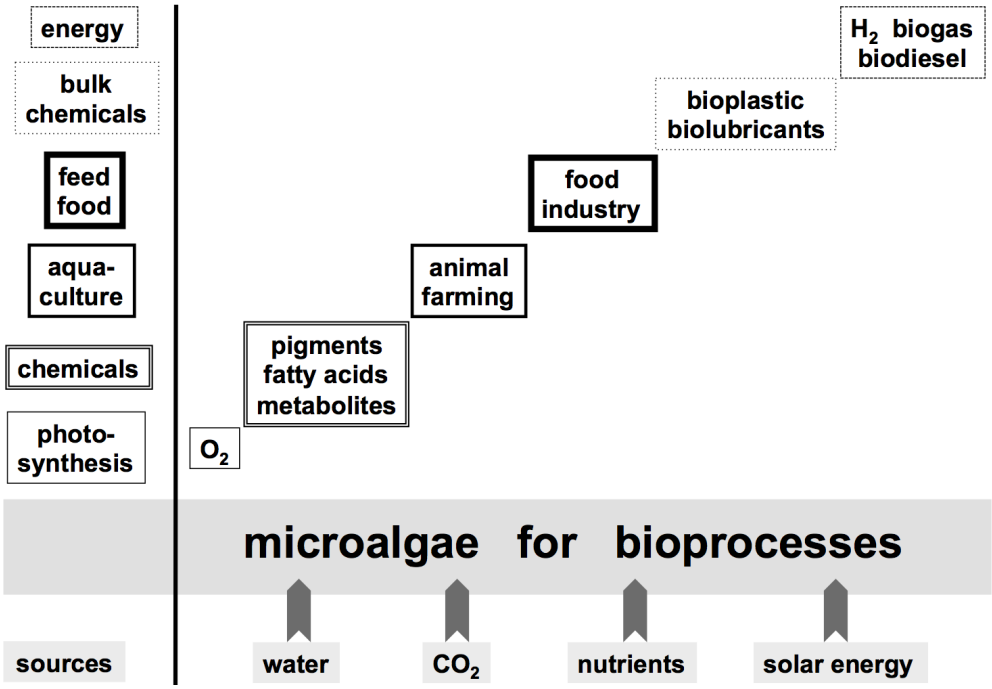


Fig. 19: Diagrammatic overview of **bioprocesses in microalgae biotechnology**. Explanation in the text. (Graphic: F. Oberwinkler)

Sources for the **cultivation of microalgae** are water, CO_2, nutrients, and solar energy. As photoautotrophic organisms they produce O_2. Future food **production** is estimated of highest social and economic priority. Concurrently, also animal farming, especially fish dietetics (Roy & Pal 2015), appears to be similarly important. Metabolic capacities of microalgae shall be used to produce pigments, fatty acids, edible oils (Klok et al. 2014), and other metabolites as well as bioplastics and biolubricants. Finally, microalgae may play a considerable role to provide energy as H_2, biogas and biodiesel.

Well known **phytohormones** in higher plants, as abscisic acid, auxin, cytokinin, ethylene, and gibberellins, have been found also in microalgae. Assuming from genome-based metabolic reconstruction, Lu & Xu (2015) suggest

that phytohormone biosynthesis pathways originate from those in ancient microalgae.

Macroalgae play an important role as food, especially in East Asian countries. Culture techniques for them have long, historically based tradition.

Physcomitrella patens, described already by Hedwig (1801) as *Phascum patens*, is the only moss species with a prospective use for biotechnology. The species is molecularly excellently characterized and considered as a genetics' milestone (Strotbek et al. 2013). It has been employed for glyco-engineering in bioreactors and already targeted for therapeutic proteins, like monoclonal antibodies (Decker et al. 2014).

Green micro-cryptogams and their biotechnological importance:

- **Providers for additional feed and food.**
- **Producers of useful metabolites in bioreactors.**
- **Renewable energy supplier.**

Further potential developments:

- **Synthetising targeted products.**

7. The molecular revolution in biology

Gene based phylogenies

After traditional methods of comparative character analyses and cladistics, phylogenetics were revolutionized when molecular techniques were well established and applied for all organismic groups. In July 2015, Web of Science listed for algae 7.800, for bryophytes 600, for ferns 500, for lichens 500, and for fungi 15.200 articles upon the query „molecular phylogeny", published within the timespan of 25 years. **Major steps in molecularly based phylogenies** of plants and fungi were comparative analyses, primarily of 5S rRNA, then of 18S rRNA and 26S rRNA, followed by multi-gene analyses, and finally by genome comparisons.

Fox & Woese elucidated the **architecture of 5S rRNA** and its relation to function (1975), Hori et al. sequenced it from the cellular slime mold *Dictyostelium discoideum* (1980), and Olsen et al. (1983) clarified its secondary structure. The phylogenetic position of the dinoflagellate *Crypthecodinium cohnii* was based on 5S rRNA characterization by Hinnebusch et al. (1981), containing a computer simulation of its evolution. On the basis of 5S rRNA sequences, Walker & Doolittle (1982) „redivided" basidiomycetes, and sequenced eight basidiomycetes and fungi imperfecti (Walker & Doolittle 1983). Gottschalk & Blanz (1984) found highly conserved 5S ribosomal

RNA sequences in four rust fungi and an atypical secondary structure in *Microstroma juglandis*, a specialised parasite on *Juglans* that later was found to belong to the smut fungi. Their continuing studies were contributions for better understanding systematics and phylogeny in basidiomycetes (Gottschalk & Blanz 1985). By then, the **unique power of molecularly based phylogenies** became evident, however the technical difficulties to shorten sequencing times were still not overcome. – In 1986, Hori & Osawa discussed the evolutionary changes in 5S rRNA secondary structure and a phylogenetic tree of 352 species (Hori & Osawa 1986). The evolution of eukaryotes and their relation to archaebacteria was analysed by Wolters & Erdmann (1986) through cladistic analyses of 5S rRNA and 16S rRNA secondary and primary structures, and further enlarged by comparative computer and biochemical analyses (Erdmann et al. 1987). Comparing ribosomal RNA sequences, Vossbrinck et al. (1987) suggested that microsporidia are extremely ancient eukaryotes.

After the first period of sequencing 5S rRNAs, an explosive development followed with expanded protocols as mentioned above. This era will not be further traced here for fungi, but few examples are given for Viridiplantae below. Meanwhile, **phylogenetic hypotheses are derived from comparisons of genomes**. The sampling in figure 20 is representative in parts for Basidiomycota (Sharma et al. 2015). Actually, this tree widely confirms earlier basidiomycetous phylogenies based on multi-gene, and even most of single gene analyses. – More details can be found in **phylogenetic treatments of basidiomycetes** of Dominik Begerow for smut fungi, of Jee-Chen Chen for *Tremella*, and of Zhu-Liang Yang for Boletaceae and Amanitaceae in this volume.

The diversity and evolutionary lines in green plants, **Viridiplantae**, are manifold, including aquatic alga, terrestrial cryptogams and higher plants. The algal phylogeny with the example of ***Chlamydomonas***, and based on nuclear ribosomal RNA genes, was studied by Jupe et al. (1988). Molecular studies in colonial green flagellates (Buchheim & Chapman 1991), and the Chlamydomonadales (Buchheim et al. 1996), followed, the latter based on comparison of ribosomal RNA sequences from the nucleus and the chloroplast.

Pröschold et al. (2001) used nuclear-encoded SSU rRNA sequences of 32 strains of *Chlamydomonas*, *Chloromonas* and *Chlorogonium* for a taxonomic revision, together with 132 strains of **Chlorophyceae**, a well-supported molecular phylogeny of the group. Exhaustive 18S rRNA phylogenetic analyses revealed 21 strongly supported clades within phylogenetically redefined **Volvocales** (Nakada et al. 2008). An integrative approach with multigene analyses and comparative light and electron microscopy was applied by Matsuzaki et al. (2012) to elucidate the phylogeny of *Chloromonas*, Volvocales. – The phylogeny and **molecular evolution of the green algae** was critically reviewed by Leliaert et al. (2012). The Streptophytes were characterised by the synapomorphic lateral flagella, the glycolate oxidase, flagellar peroxidase and a

GaA/B gene duplication. **Green land plants and their algal relatives** Charophyceae, Zygnematophyceae, and Colechaete share phragmoplasts, plasmodesmata, branching, apical cell growth, sexual reproduction, dessication resistant zygospores, cellulose synthesising rosettes, and the absence of functional plastid tufA.

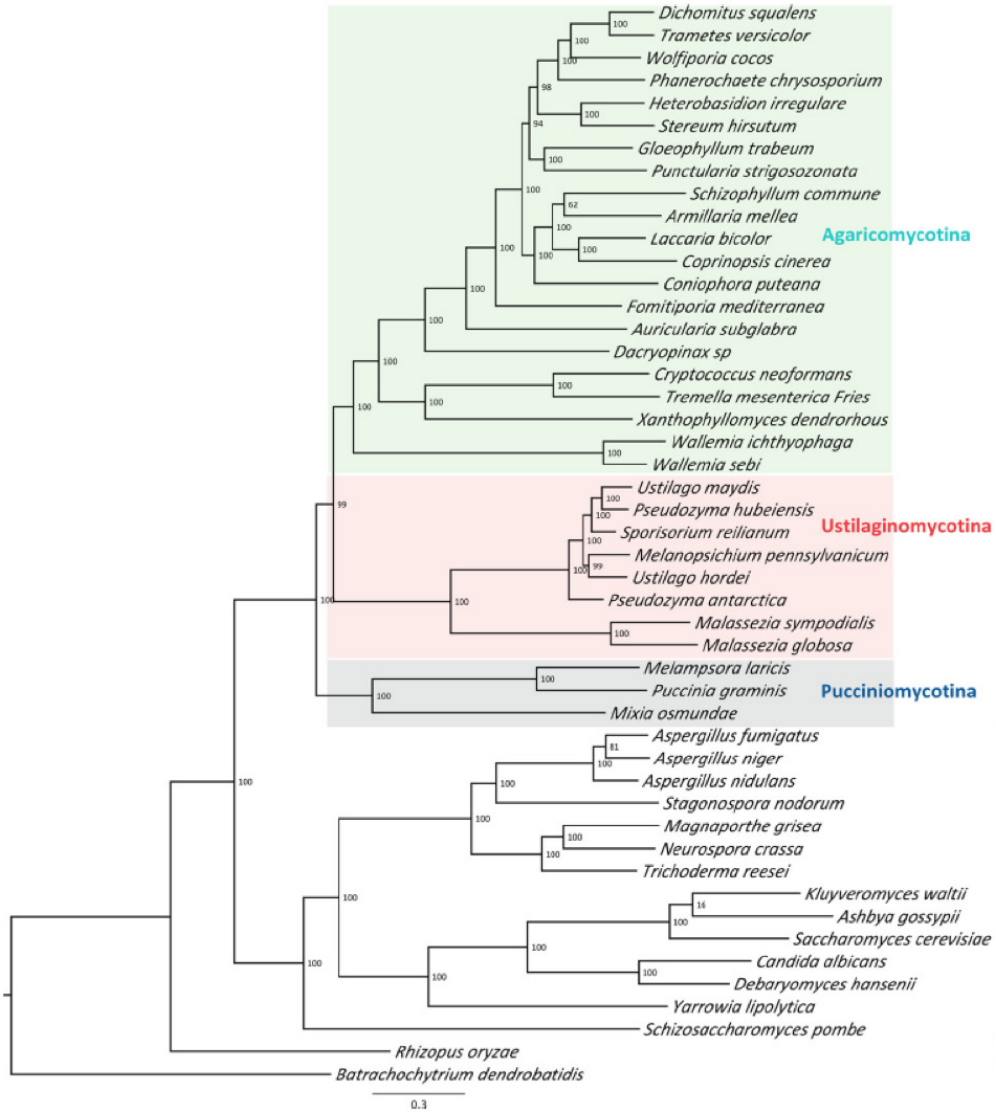


Fig 20: Fungal phylogeny based on 48 genomes. Numbers on branches indicate support from 1000 bootstrap replicates. From Sharma et al. (2015).

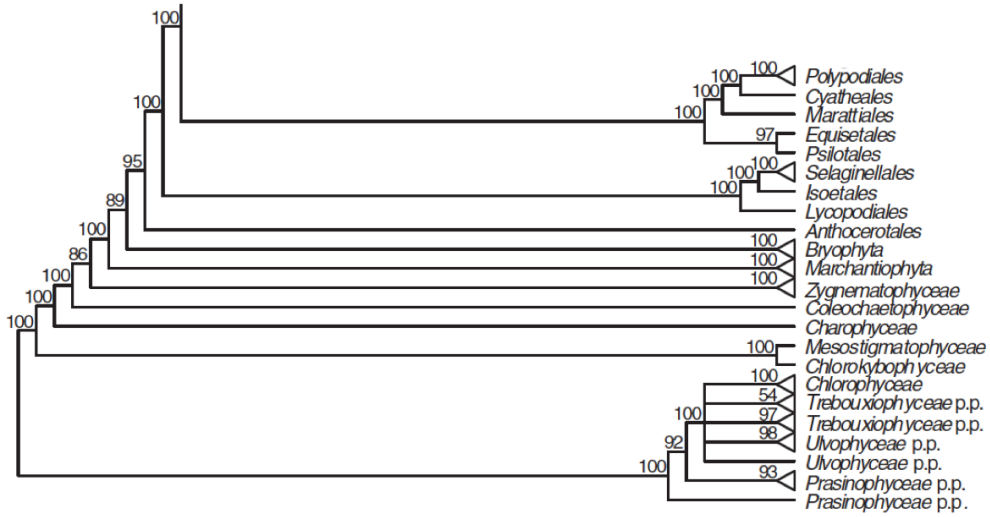


Fig. 21: Section for cryptogams of a tree of Viridiplantae inferred from the RY-coded (RY) analysis. Data set derived from 78 protein-coding genes of the plastid genome. Terminals with a triangle represent collapsed clades with > 2 taxa. From RUHFEL et al. (2014).

Protein-coding sequence data for 78 genes from 360 diverse green plant taxa with complete or nearly complete plastid genome sequences were assembled by RUHFEL et al. (2014). They found i.a. that **Zygnematophyceae are sister to Embryophyta**, and that Equisetales and Psilotales are sister of Marattiales and the leptosporangiate ferns (Fig. 21).

Tab. 5: Genomes of cryptogam species (selection). The arrangement is in a time sequence from below upwards. Note that corresponding contributions over more than 10 years were exclusively published in Science and Nature. Compare text. Orig.

year	species	higher taxon	authors	journal
2015	*Xanthophyllomyces dendrorhous*	Basidiomycota	SHARMA et al.	BMC Genomics
2013	*Chondrus crispus*	Rhodophyta	COLLÉN et al.	Proc Natl Acad Sci USA
2012	*Wallemia sebi*	Basidiomycota	PADAMSE et al.	Fungal Genetics and Biology
2011	*Puccinia graminis* f.sp. *tritici*	Basidiomycota	DUPLESSIS et al.	Proc Natl Acad Sci USA
	Selaginella moellendorffi	Pteridophyta	BANKS et al.	Science
2010	*Schizophyllum commune*	Basidiomycota	OHM et al.	Nature Biotechnology
2008	*Laccaria bicolor*	Basidiomycota	MARTIN et al.	Nature
	Physcomitrella patens	Bryophyta	RENSING et al.	Science
2007	*Chlamydomonas reinhardtii*	Chlorophyta	MERCHANT et al.	Science
2006	*Ustilago maydis*	Basidiomycota	KÄMPER et al.	Science
2005	*Cryptococcus neoformans*	Basidiomycota	LOFTUS et al.	Science
2004	*Yarrowia lipolytica*	Ascomycota	DUJON et al.	Nature
2003	*Neurospora crassa*	Ascomycota	GALAGAN et al.	Nature
2001	*Encephalitozoon cuniculi*	Microsporidia	KATINKA et al.	Nature
1996	*Sacharomyces cerevisiae*	Ascomycota	GOFFEAU et al.	Science

The **genome sequence of *Saccharomyces cerevisiae***, „**The Yeast**“, **was released 1996 as the first of eukaryotes, the largest completely sequenced at that time** (Goffeau et al. 1996), a revolutionary breakthrough in which more than 600 scientists from over 100 laboratories were collaborating (Tab. 5). „The complete, ordered and non-redundant sequence provides an invaluable resource for the detailed analysis of cellular gene function and genome architecture“ (Mewes et al. 1997). – The genome of the eukaryotic, microsporidian parasite of uncertain phylogenetic position, ***Encephalitozoon cuniculi***, was sequenced by Katinka et al. (2001). – Galagan et al. (2003) sequenced the genome of the filamentous ascomycete, the genetic model fungus ***Neurospora crassa***. – „Genome evolution in yeasts“ was announced when ***Yarrowia lipolytica*** was fully sequenced (Dujon et al. 2004). – The genome of the human pathogen ***Cryptococcus neoformans***, an unusual basidiomycetous yeast, was released in 2005 (Loftus et al.). – One of the best studied fungal plant parasites, ***Ustilago maydis***, was completely sequenced by Kämper et al. (2006). – Key functions in animal and plant evolution were elucidated through the genome of ***Chlamydomonas reinhardtii***, (Merchant et al. 2007). – Insights into the conquest of land by plants were made possible through the genome of the moss ***Physcomitrella patens*** (Rensing et al. 2008). – Symbiosis characteristics were gained from the genome of the mycorrhizal basidiomycete ***Laccaria bicolor*** (Martin et al. 2008). – The world-wide distributed wood decomposer and model mushroom ***Schizophyllum commune*** was sequenced by Ohm et al. (2010). – The ***Selaginella moellendorffi*** genome identified genetic changes associated with the evolution of vascular plants (Banks et al. 2011). – Obligate biotrophy features were unraveled by the genomic analysis of the most serious cereal parasite, ***Puccinia graminis* f. sp. *tritici*** (see chapter 4), by Duplessis et al. (2011). – ***Wallemia sebi*** is adapted to osmotic stress, and sexual reproduction is not known, but may be cryptic, characteristics waiting for elucidation through genomic features (Padamse et al. 2012). – Genome structure and metabolic features in the red seaweed ***Chondrus crispus*** shed light on evolution of the Archaeplastida (Collén et al. 2013). – The genome of ***Xanthophyllomyces dendrorhous*** gave insights in acetyl-CoA pathways, and the evolution in Agaricomycotina (Sharma et al. 2015).

Biodiversity, barcoding and cryptotaxa

Exploring a regional flora and/or fauna is a long runner, now true not only for local aspects, but also for global ones. Floras and monographs with different scopes are convincing proofs. The latest approach to **explore biodiversity is barcoding**. The universal applicability of biodiversity detection with ITS sequencing is spectacular, just making clear that in many cases even not the tip of the iceberg is explored. There are some 20.000 articles published already, dealing with fungi and their diversities.

The question is, what is the detected organism? Or, even more provocative, **what is a species**? Biologists, seriously interested in this topic, know about the dilemma involved. This dilemma was nicely unrolled by John Taylor (2014) in his plenary talk at IMC X in Bangkok about *Neurospora*. Here is an extract: „What's a species? It depends: 2 phenotypic species, 5 biological species, 35 phylogenetic species. – Species breadth is limited by reproductive isolation; the narrowest species is an interbreeding population; and a SNP fixation index might measure divergence. – Genome wide association? You need the narrowest species. – Ecology? You must live with a broad species that may include fungi with different ecological functions."

In the case, „what is a species", I am quoting our own research in **Sebacinales**: a hitherto overlooked cosm of heterobasidiomycetes with a broad mycorrhizal potential (Weiss et al. 2004). More than ten years ago, the discovery of a surprisingly high number of new environmetal sequences/species of this relationship appeared to be unique, however, the eyecatcher titel „Sebacinales everywhere" (Weiss et al. 2011) could have been applied at that time already to many other genera/species, studied in a broader geographical and/or population range. For environmental sequences, their detection is the end of the story, in other words, new organisms have not been made available (Oberwinkler et al. 2013). – In addition, three laborious studies were carried out to elucidate the phylogenetic diversity and structure of these fungi associated with plant communities along an altitudinal gradient (Garnica et al. 2013), to understand the high genetic diversity at the regional scale and possible speciation in *Sebacina epigaea* and *S. incrustans* (Riess et al. 2013), and to detect unknown morphospecies that correspond phyloclades (Oberwinkler et al. 2014).

Khaund & Joshi (2014) intended to identify wild **edible mushrooms** of India by barcoding. In a study by Põldmaa et al. (2014), DNA barcoding aided the identification of fungus gnat species, allowing the conclusion that host diversity and trophic status determined gnat community composition. Finally, with improved techniques, older herbarium species can be barcoded, as was proven by molecular annotations of Murrill's *Russula* species (Looney 2015).

These examples may shed light on the **concepts for applying barcoding for biodiversity estimations** in plants and fungi (Chase & Fay 2009, Begerow et al. 2010, Schoch et al. 2012).

In **ferns**, Masuyama et al. (2002), and Liao et al. (2011) detected cryptic species in *Ceratopteris thalictroides*, Yatabe et al. (2009) in *Asplenium nidus*, Fayle et al. (2011) in epiphytes, Metzgar et al. (2013) in circumboreal reticulated *Cryptogramma*, and Dauphin et al. (2014) in *Botrychium*.

Similar findings were reported for **bryophytes** in *Rhynchostegium riparioides* by Hutsemékers et al. (2011), by Carter (2012) in *Scleropodium* cryptic diversity, by Yu et al. (2013) in *Cololejeunea lanciloba*, by Renner et al.

(2013) in *Lejeunea*, by Beike et al. (2014) in the *Physcomitrium-Physcomitriella* species complex, and by LI et al. (2015) in cryptic species of Plagiotheciaceae. Lang et al. (2014) concluded that DNA barcoding improves species identification of arctic *Dicranum*, but the combination of several markers, ITS1, trnL -F and rps4 –trnT, appeared necessary for reliable identifications.

In the **algae**, Chong et al. (2014) reported for glaucophytes a previously unrecognized cryptic diversity within *Cyanophora* and *Glaucocystis*. Metabarcoding was carried out by Nanjappa et al. (2014) in diatoms, Sissini et al. (2014) studied the diversity of the rhodophyte *Mesophyllum erubescens*, and Robuchon et al. (2015) the brown algal genus *Laminaria*. – In contrast, Schneider et al. (2015) found fewer taxa in *Chara* by barcoding ITS2 and matK than by morphological studies. – Also in **trentepohlian lichen photobionts** (Hametner et al. 2014), and in *Trebouxia* (Sadowska-Dés et al. 2014), species delimitations were investigated.

Finally, the successful application of barcoding for taxonomic and biodiversity applications implicitly made clear its forthcoming high potential for biosystems approaches. A high-throughput **DNA barcoding for ecological network studies** was shown by Toju (2015).

Which ITS is „better"? Blaalid et al. (2013) resumed that their results indicate that ITS1 and ITS2 to a large extent yield similar results when used as DNA metabarcodes for fungi. However, Wang et al. (2015) found that ITS1 is better than ITS2 in eukaryotes. Additionally, „shorter length of amplification product and lower GC content was discovered to be two other advantages of ITS1 for sequencing. In summary, ITS1 represents a better DNA barcode than ITS2 for eukaryotic species".

The impact of the molecular revolution in understanding cryptogams:

- **Gene and genome based phylogenies have reached a high degree of conformity.**
- **Fossil dating helps to calibrate molecularly based phylogenies.**
- **Genome sequences allow insights in metabolic functions and ecological adaptations.**
- **Barcoding touches biodiversity.**
- **Molecular approaches relativise species concepts.**

Further potential developments:

- **Genomically based backgrounds for organismic interactions.**
- **Population genomics for understanding microevolution.**
- **Biome genomics as a future challenge.**

8. Cryptogamic fossils, ecological changes and challenges

Cryptogams over 500 million years

Few remarks on fossil records of cryptogams are mentioned here because of their importance in understanding the historical context and global changes over very long geological times.

In a **stratigraphic arrangement of major plant fossils** (Fig. 22), MÄGDEFRAU (1968) positioned representative taxa: Algae known from the Cambrian. Earlier records refer to **stromatolites of cyanobacteria**, the „bluegreen al-

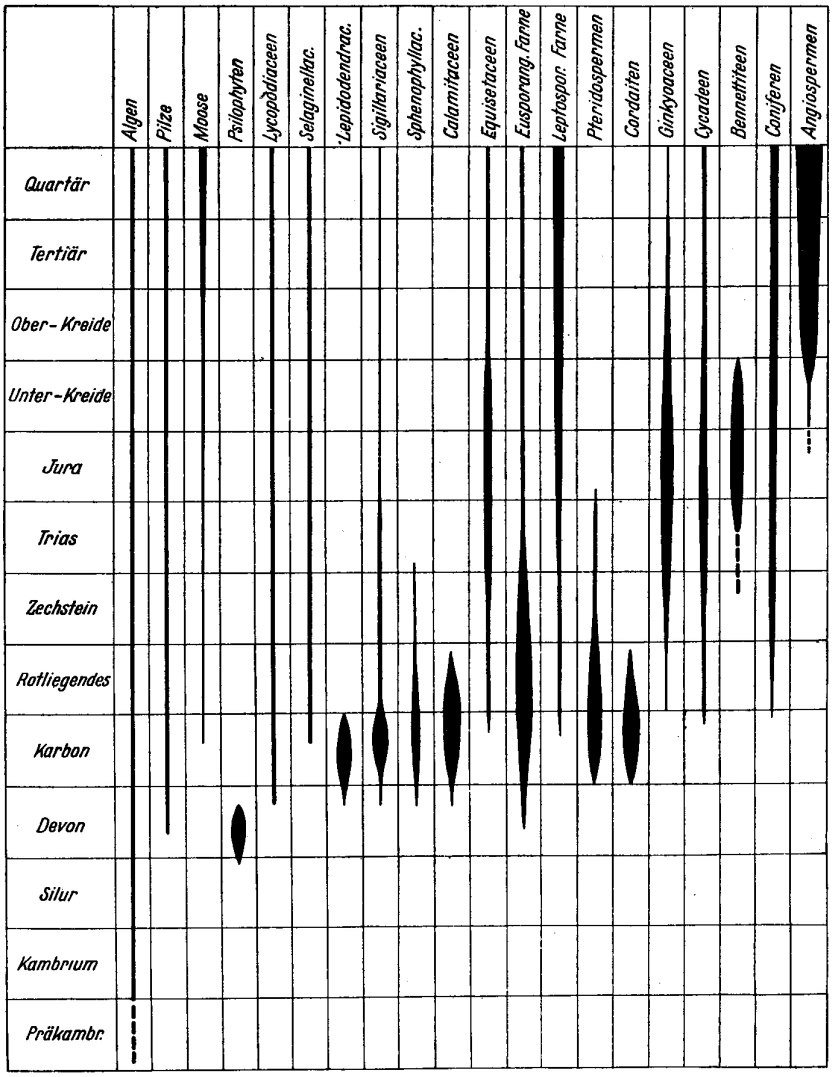


Fig. 22: Fossil records of most important plant groups, known until 1967. From MÄGDEFRAU (1968). For details compare text.

gae“, in former times included in cryptogams. Many fossils of **pteridophytes** are well preserved and suitable at best for phylogenetic reconstructions. **Psilophytes** are known from the Late Silurian but are extinguished already in the Upper Devonian when the bulk of other plant groups tardily began to develop. Several of them radiated strongly in the following Carbonian, as *Lepidodendron*, Sigillariaceae, Sphenophyllaceae, Calamitaceae, seed ferns Pteridospermophyta, and *Cordaites*. *Lepidodendron* became extinct at the end of the Devonian.

Calamitaceae, Sphenophyllaceae, and *Cordaites* disappeared in Middle Permian as parts of the **Permian-Triassic extinction event**. Few fungal fossils and the **oldest surviving vascular plants**, the lycopods, Lycopodiophyta, were known from the Devonian. Selaginellaceae, Equisetaceae, Leptosporangiates, and the non-cryptogamic Cycads, Ginkgoaceae, and Conifers were first recognized from the Middle to the Upper Carboniferous, and persisted over the times. Another non-cryptogamic group, the Bennettitales appeared in the Triassic and became extinct in the middle of the Cretaceous.

Ernst Friedrich Freiherr von Schlotheim (1765–1832) was the founder of scientific Palaeontology. He also introduced Linnéan binary nomenclature for fossils, thus making them „comparable“ to extant species. The major results of palaeobotanical research, including cryptogams, until the middle of the 20th century, were compiled in textbooks in German by Walter Zimmermann (1892–1980) in two editions, last one in 1959 (Zimmermann 1959), and Karl Mägdefrau (1907–1999) in four editions, last one in 1968.

For comparison with the state of fossil knowledge in 1967 (Fig. 22), newest data are compiled in figure 23. In the Ordovician of Wisconsin, Redecker et al. (2000) found fossilized hyphae and spores, strongly resembling extant **glomeralean arbuscular mycorrhizae**. – Globally widespread cryptogamic covers from mid-Ordovician times are assigned to ***Nematothallus*** (Nematophytes), suggesting affinities with lichenized fungi (Edwards et al. 2013). – Well-preserved **dasycladalean algal fossils** from the Silurian Kalana Lagerstätte in Estonia, described as *Palaeocymopolia silurica* by Mastik & Tinn (2015), show similarity to the extant species *Cymopolia barbata*, however, with lack of a calcium carbonate skeleton. – The early evolution of land plants from fossils from the **Downtonian** of England and Wales, first explored already by Lang (1937), was reconsidered by Elbert et al. (2012) and Edwards & Kenrick (2015), who understand the cryptogamic covers as small bryophyte-like organisms and lichens. – **Lower Devonian lichens**, *Cyanolichenomycites devonicus* with cyanobacterial photobionts, and *Chlorolichenomycites salopensis* with unicellular, presumably green algal symbionts, were described by Honegger et al. (2013). Fungal fruiting bodies could not be detected, however spores in a pycnidium were found in *C. devonicus*. For further reading, see Rosemarie Honegger in this volume, dealing with fossil lichens and their bac-

terial epi- and endobionts. – Since the early Devonian sedimentary deposit of **Rhynie chert** was discovered in 1910 west of Aberdeen, a bulk of important fossils of diverse organismic groups was detected, i.a. the early land plant genera *Aglaophyton, Asteroxylon, Horneophyton*, and *Rhynia*. Detailed microscopic studies of the last years unraveled *Zwergimyces vestitus* (Krings & Taylor 2012), and the fungal sporocarp *Mycocarpon* from the Rhynie chert (Krings et al. 2014). Already in 1993, Simon et al. used SSU sequences for a molecular clock to infer dates of divergences in the phylogenetic tree of **arbuscular mycorrhizal fungi**, and an estimated origin of AMF 353-462 Ma ago.

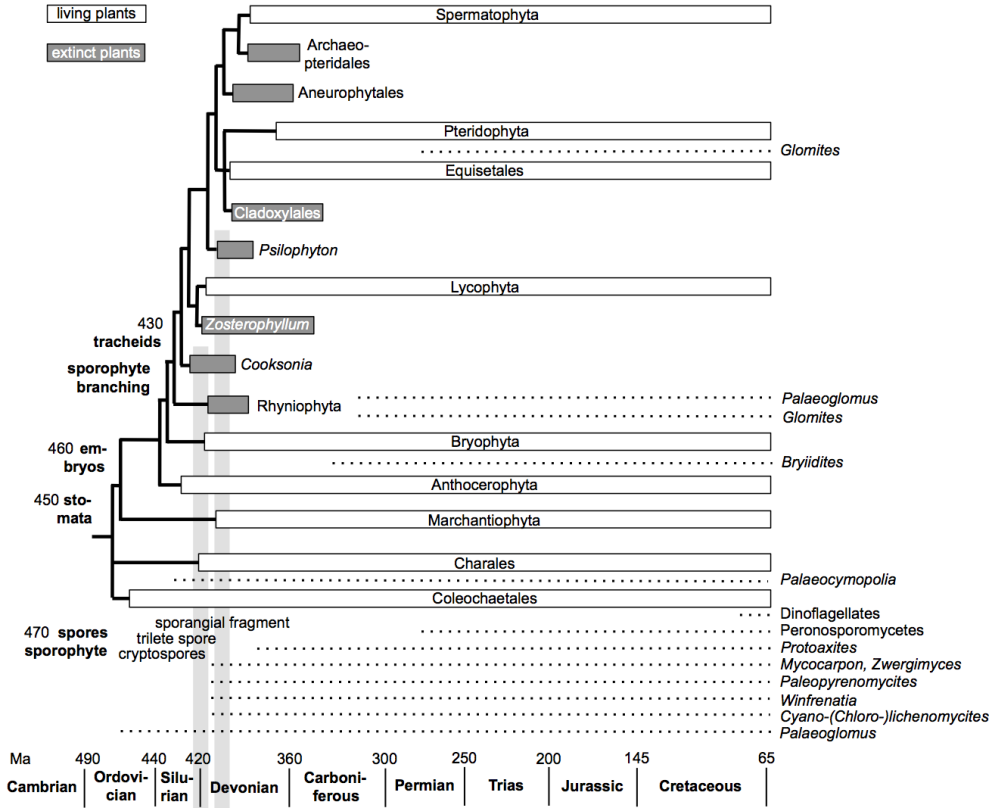


Fig. 23: Fossils of cryptogams. Geological periods at bottom, Downtonian and Rhynie chert included as vertical columns. Fossils indicated by dashed lines, extinct taxa by dark boxes, and still extant groups by unfilled frames. *Palaeoglomus, Winfrenatia, Palaeopyrenomycites, Mycocarpon, Zwergimyces*, and Peronosporomycetes cannot be associated with plants. The phylogenetic tree is adopted from Kenrick and Strullu-Derrien (2014), and strongly modified by compilations from various authors, cited in the text. Orig.

There is no agreement about the Devonian fossil logs of *Prototaxites*. Retallack & Landning (2014) suggest that the genus and its extinct order Nematophytales may belong to the Mucoromycotina or Glomeromycota, and reject interpretations of giant aquatic algae, carpets of liverworts, unpropor-

tionally huge fungal fruiting bodies or inflated lichens. – Apparently **saprobic Peronosporomycetes** from Middle Permian in Antarctica were reported from Slater et al. (2013). – **Dinoflagellate** cysts from the Upper Cretaceous in the Norwegian Sea were reported by Radmacher et al. (2015). – The oldest known **epiphyllous moss, *Bryiidites***, from the North American middle Cretaceous provides fossil evidence for a tropical maritime climate in central North America during the middle Cretaceous (Barclay et al. 2013). – The mycorrhizal fungus, *Glomites vertebrariae*, in the Permian seedfern *Glossopteris* of Antarctica was considered as of AMF by Harper et al. (2013) because of its strikingly similar vesicles and arbuscules. However, the authors reported also sparsely septate hyphae in the host roots, a feature unlike Glomeromycota. Therefore, dark septate endophytes were also discussed, and interpreted as additional fungi in *Glossopteris*. – Using high-throughput metabarcoding of **ancient DNA from arctic permafrost** sediment samples in Siberia, dated 16.000–32.000 radiocarbon years, Bellemain et al. (2013) detected 75 fungal OTUs from 21 orders, representing three phyla, most likely part of a fungal community as in similar, present-day soils.

Interactive systems I: symbiotic cryptogams conquering terrestrial biomes and influential abiotic factors

Beerling & Berner (2005) carried out a system's analysis of the physiological and geochemical processes involved in the coupled evolution of land plants and CO_2. During the evolution and diversification of terrestrial ecosystems in the Paleozoic, CO_2 concentrations were falling, implying that **first plants cooled the Ordovician** (Lenton et al. 2012). The approximate 90 % CO_2 fall, 480–360 Ma ago, coincides with glomeromycotan mycorrhization (AMF) of thallophytes, primarily conquering terrestrial habitats. Using standardized dual isotopic tracers (^{14}C and ^{33}P), Field et al. (2012) could demonstrate „that AM symbiosis efficiency (defined as plant P gain per unit of C invested into fungi) of liverwort gametophytes declines, but increases in the sporophytes of vascular plants (ferns and angiosperms), at 440 p.p.m. compared with 1,500 p.p.m. $[CO_2]_a$".The interference of early cryptogams with geochemical carbon cycle development is a future research challenge.

Interactive systems II: extant cryptogams and their organismic partners

Extrapolated from **extant symbiotic associations**, Mucoromycotina can be assumed as primary symbionts of terrestrial thallophytes (Bidartondo et al. 2011), replaced by allround successive Glomeromycota (Fig. 24). Later, losses of symbioses occurred several times, but also secondary gains by species of basidiomycetous Tulasnellales and Sebacinales and Ascomycota took place in liverworts (Kottke & Nebel 2005, Preussing et al. 2010a, b).

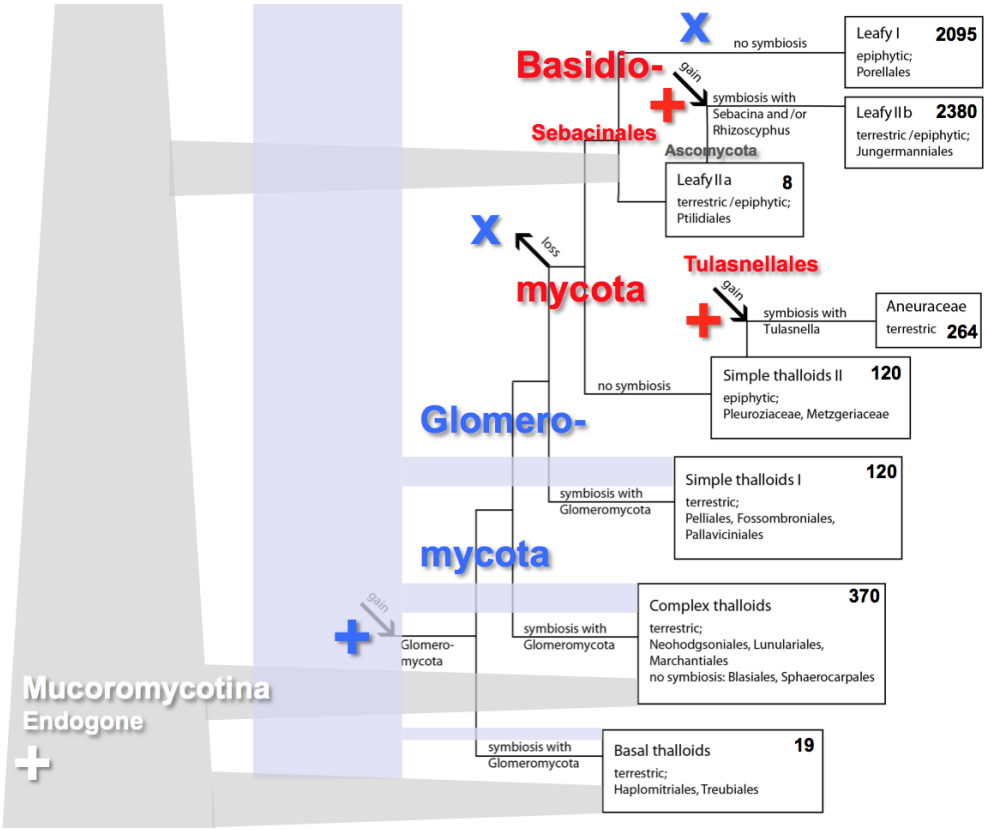


Fig. 24: Basal extant liverworts and their fungal associations may reflect historical mycothallus events. + gain, x = loss of fungal symbionts. Numbers in boxes refer to known species in 2011 (pers. comm. Martin Nebel 2012). Compare following text. (Based on Kottke & Nebel (2005), strongly modified and complemented)

Earliest terrestrial mycothalli had to cope with limited water and minerals, and had to be protected against extreme temperature fluctuations and heavy insolation. Crucial genes for the establishment of arbuscular mycothalli were studied by Genre et al. (2005) and Delaux et al. (2012). Strigolactone genes are involved in the pre-symbiotic stages and arbuscule formation, the latter together with subtilase and vapyrin, and a phosphate transporter delivers phosphorous into the host plant. – Recently, there are several reviews available dealing with the fascinating topic of the ascending life, marked with key events, and, surprisingly neglecting the adventures of interacting organisms. – By applying model selection theory to molecular phylogenies, Theobald (2010) tested **universal common ancestry** and found a strong support for the monophyly of all known life.

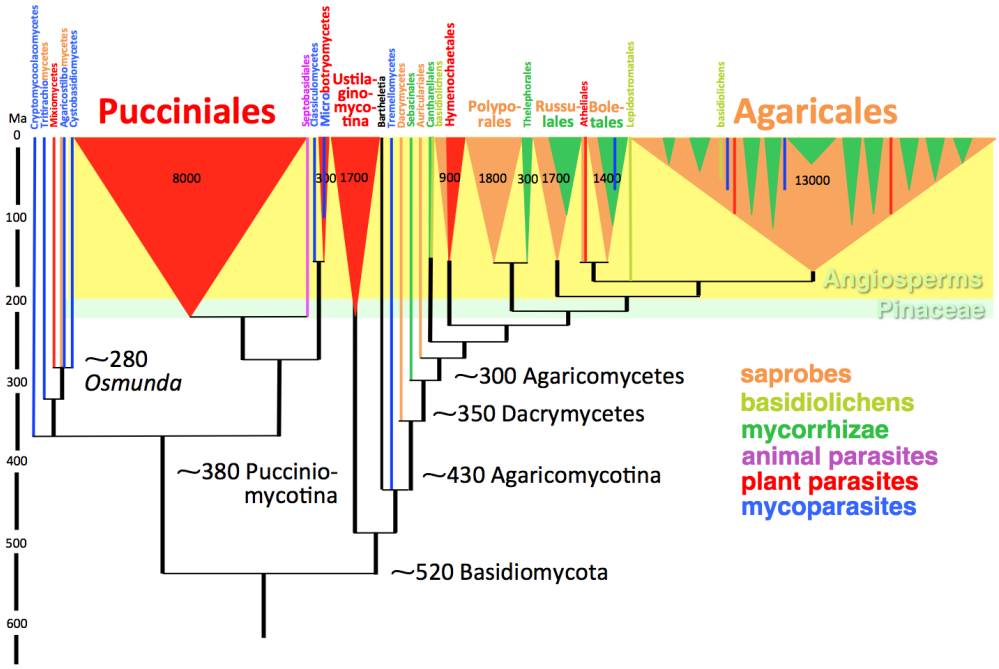


Fig. 25: Basidiomycota and their interactive systems representing principal nutritional modes. The geological appearance of Pinaceae and Angiosperms as most recent substrate suppliers is indicated by background colours. Numbers in the time scale and for approximate origins of taxa are in million years. Numbers in corresponding triangles are species estimations. The phylogenetic tree incorporates principal clades of Fig. 20, and includes additional taxa. Divergence dates are adopted from Taylor & Berbee's (2006) second scenario, applying fungal, animal and plant calibrations. (Graphic: F. Oberwinkler)

The **diversity of nutritional modes in extant basidiomycetes** can be projected in molecularly based phylogenies to their plausible origins (Fig. 25). There is strong evidence that **mycoparasitism** is a primary interactive strategy in basidiomycetes. However, various **plant parasites and mycorrhizal partners** quickly dominated in evolution, and continued to play most important ecological roles in plant communities. In addition, basidiomycetes are essential components in **saprobic decay of various substrates**, especially of wood. Even when common in certain vegetation types, **basidiolichens** are quantitatively limited in comparsion with ascomycetous lichens. They will be treated in the contribution on ultrastructure in basidiomycetes by Oberwinkler & Bauer in this volume. Livestyles, representative for basidiomycetes, have evolved indepently in various other fungal relationships and partly in Oomycetes. Coevolutionary trends of obligate parasites were already discussed in rust fungi (chapter 4). For them and others, organismal diversification needs to be accompanied by understanding host and biome interaction parameters, especially effector functions and targets (Kemen et al. 2015).

Interactive systems III: cryptogams and habitats

Historically, organismic studies started with fieldwork (chapter 2). As discussed for the black rust (chapter 4), understanding of host associations were mandatory to clarify the life history. Then, when agricultural needs changed the habitats drastically, fieldwork became another challenge to keep up with newly evolving, virulent strains.

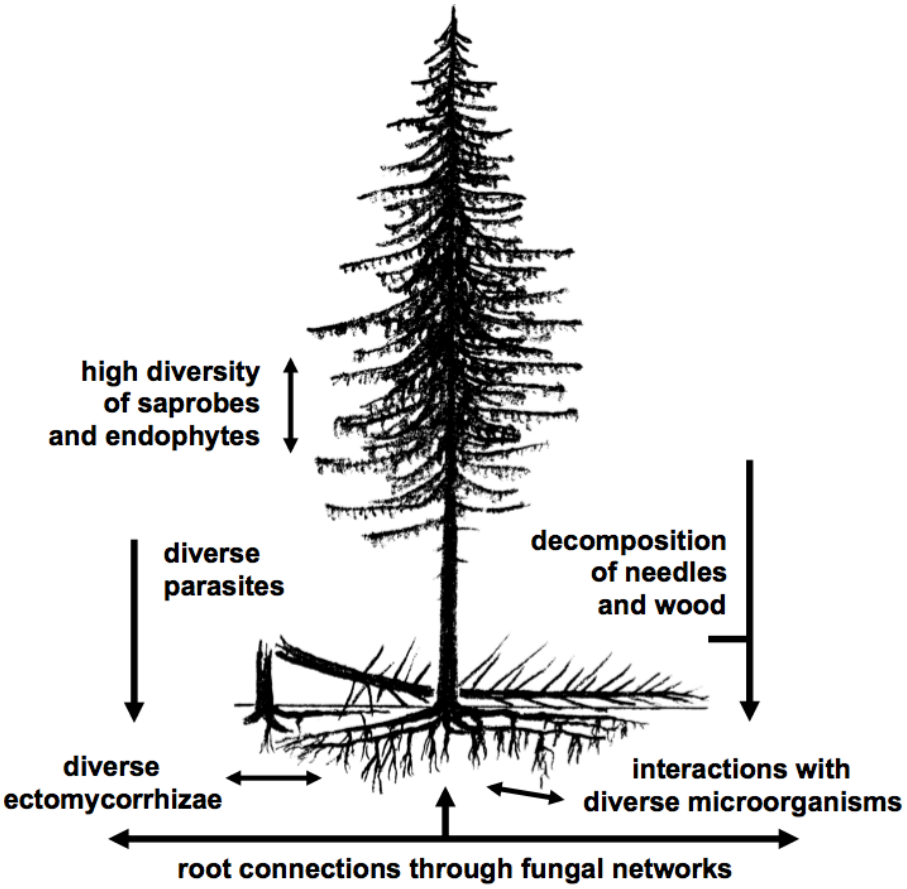


Fig. 26: Simple scheme of fungal plant interactions in spruce, *Picea abies*. Decidedly, this is a model of organismic interactions reduced to one plant species and an unknown number fungal participants. All other partners, like additional plants, including cryptogams, animals, and prokaryotes, are excluded. (Graphic: F. Oberwinkler)

Since the early 1970th, „**novel forest decline**“ was first recognized in Germany, successively affecting conifers and deciduous trees. Intensive basic research was initiated to elucidate causes for the symptoms. The interdisciplinary research approaches very much contributed to a better understanding of the organismic complexity of forest ecosystems. **Spruce** is taken here to refer to fungal partners (Fig. 26) for the purpose to discriminate between abiotic

and biotic, as well as parasitic, saprobic, and symbiotic interactions. **Ectomycorrhizal diversity** plays a crucial role for development and proper functions of spruce, including connections between tree individuals through hyphal networks. For further details compare the contribution of Ingeborg Haug on mycorrhizal diversification in South Ecuador in this volume. – The quality of soil and humus is markedly influenced by **wood and litter decay**, realised by a plethora of different species, including a high number of fungi. From habit appearance in late stages, brown and white rot have been distinguished for a long time. Comparative analyses of 31 fungal genomes led to the result that the white rot decomposer Auriculariales, ancestor of the Agaricomycetes, suggest the origin of lignin degradation, coinciding with the end of the Carboniferous period (Floudas et al. 2012). However, the distinction of the two decay modes, **white and brown rot**, based on the presence or absence of lignolytic class II peroxidases, was strongly relativised by Riley et al. (2014), with most of the authors of the Floudas et al. paper, comparing a broad range of gene families encoding plant biomass degrading enzymes of 33 basidiomycetes. In conclusion, these authors suggested now a **continuum of rot types** rather than a dichotomy between the two decay modes which are traditionally accepted. Comparison of genome sequences of the white-rot fungus *Cylindrobasidium torrendii* and the brown-rot fungus *Fistulina hepatica* reinforced the idea that wood decay mechanisms are phylogenetically intergrading (Floudas et al. 2015). – A detailed molecular study on fungal communities decomposing *Picea abies* logs was carried out in Sweden by Ottosson et al. (2015). 1910 fungal operational taxonomic units (OTUs) were detected from which 35 % were assigned to ecological roles, for the remaining bulk information is lacking.

Unfortunately, many other ecological and community networks must be skipped here. But there are several **additional and relevant contributions** in this volume on forest pathology by Gitta Langer, aphyllophoralean fungi as habitat builder by Ewald Langer, dependencies of fungi from plants by Roland Kirschner, hyperepiphyllic ascomycetes by Peter Döbbeler, lichen thallus as a microbial habitat by Martin Grube, lichenicolous fungi by Josef Hafellner, and bryophytes by Martin Nebel.

After half a millennium, global ecological challenges are culminating in integrative approaches of various disciplines to ensure viability and efficiency of natural, partly natural and secondary biospheres. Apparently, the progression from studies of relatively simple model systems to complex field conditions is the most important task in biology nowadays and in future because the processes involved „represent the combined effects of interactions among multiple species, environmental variation, and complex feedback mechanisms“ (Whitham et al. 2008). It requires network approaches to obtain data about interactions and responses of organismic assemblages (Bascompte 2009) in which cryptogams play essential roles. According to Prosser (2012) the relevance of modern techniques, as high-throughput sequencing, to im-

portant ecological questions is often unclear. Therefore, it is claimed for a „greater focus on ecological questions, more critical analysis of accepted concepts and consideration of the fundamental mechanisms controlling microbial processes and interactions in situ“. Convincing demands, similar to those by Saleem & Moe (2014) for multitrophic microbial interactions for eco- and agro-biotechnological processes. A forthcoming conference, „Functional genomics and systems biology: from model organisms to human health“, in October 2015, announces its goals anthropocentrically: „to improve our understanding of complex biological systems relevant to health and disease, these data, generated from disparate sources, need to be integrated in a biologically meaningful way“.

Cryptogamic fossils and the impact of cryptogams on ecosystems:

- **Cryptogams as fossil records.**
- **Fossil dating helps to calibrate molecularly based phylogenies.**
- **Mycothalli as first land plants.**
- **Mycorrhiza dominated vegetation types.**
- **Fungal parasites on land plants.**
- **Decomposition of organic substrates.**

Future urgent research:

- **Integrative analyses of global ecosystems.**

9. Data-driven research and bioinformatics

Exceptionally, but deliberately, I briefly mention **some personal experiences** over the last 40 years that quite emphatically had a direct and an ongoing impact on my own research in cryptogams.

I saw the first computer, actually an electronic typewriter with a screen, in Robert Bandoni's lab at UBC, Vancouver, in 1978. Three years later, we had, as one of the first ones, an external terminal in our institute, connected to the data processing centre of Tübingen University, down town in the city, where the printer was installed. – These days, internet did not exist. The quickest oversea's manuscript exchange by airmail, there and return, took at least three weeks. – Sequencing of 120 base pairs of 5S rRNA of *Puccinia poarum* in Paul Blanz's lab in my former institute required one week intensive work in 1982. Meanwhile, sequencers are nearly automated machines, so that the researcher's working place is no more in the wet lab, but alongside the computer. – Since internet is available reliably for global data search, researchers became evaluated without their own permissions. Huge data banks, as those

of Web of Science, allow each scientist, affiliated to a paying institution, to screen not only him- or herself about scientific output, implicitly identified with qualification, but anybody in the scientific community around the globe, unknowingly captured from that system.

Computers were the prerequisite for **data management** that quickly developed into an own discipline (for example Triebel 2009). Three primary nucleotide sequence databases, DNA Data Bank of Japan, European Informatics Institute, and GenBank, are interconnected and exchange new and updated data on a daily basis. The new webbased sequence management system UNITE (Kõljalg et al. 2013) is a database for molecular identification of fungi through ITS, generally applied in barcoding. That these technical achievements were revolutionary for scientific research is evident, and actually they need not to be reflected anymore.

Since genomes are being sequenced, data exploded exponentially (chapter 11, Fig. 28). In most cases, traditional biologists are unable to cope with this newly generated mass of sequences. The winged word appeared, „**Life out of sequence**“ (Stevens 2013), meaning in other words, bioinformatics had become the dominating discipline. There are top papers in which not only the first author but also the senior one is taken by a bioinformatician. This new development is usually meekly commented that biological questions were still set up by the biologists, resulting in an efficient interdisciplinary cooperation. Now, finally and definitely, **biological research is data-driven**, and its generally expected and mostly realised results are superbly designed graphs of various kinds, nearly always including phylogenetic trees with 100 % bootstrap values. Actually, these are the summaries of the papers. It is perhaps a philosophical question whether such kind of work is theoretical or not, even when it is clear that it is derived from experimental data. However, such data can also be predicted, as in the case of the basidiolichen *Dictyonema glabratum* (= *Cora pavonia*) for which 126 species have been reported recently (Lücking et al. 2014) and for which more than 400 species are suggested in a predictive model, nicely filled in a grid map of Central and South America. Maybe that this is an example for „data will be rich and reliable enough that doing a digital experiment by manipulating data will be considered the same thing as doing an experiment with cells and molecules“ (Stevens 2013). This example brings us to „**Big Data and its epistemology**“ (Frické 2015). Here, the question arises „whether Big Data, in the form of data-driven science, will enable the discovery, or appraisal, of universal scientific theories, instrumentalist tools, or inductive inferences“. Apparently, „data-driven science is a chimera“. Belcaid & Toonen (2015) consider it necessary to demystify computer science and „to help biologists understand some of the most important mainstream computational concepts to better appreciate bioinformatics methods and trade-offs that are not obvious to the uninitiated“. Finally, **Big Data biology is seen between eliminative inferences and exploratory experiments** by Ratti (2015).

Cryptogams and the data morass:

- **Data management.**
- **Data-driven research.**

Futuristic dreams:

- **Synthesis of ideas, experiments and selective data use.**

10. Publication strategies and problems

Increasing complexity of research processes and financing modalities were highly influential on publication strategies on a global scale during the last three decades. The shift from single-author to **multi-author papers** simply shows the facts. This is also true for research on cryptogams. As a rule, the first author has carried out most of the work, and the senior author provided the facilities, sometimes also the ideas and the money. Qualifying authorship credit is still mostly quantifying by dividing one credit equally among all co-autors, not counting their actual contribution. Already Katz & Martin (1997) noticed that collaboration is very difficult to define, partly because it is largely a matter of social convention among scientists. Coauthorship is also no more than a partial indicator of collaboration. According to Hagen (2013) a harmonic formula provides a straightforward quantification and a parsimonious solution of the byline hierarchy. Independent of these implications appears the simple statement of Servia-Rodríguez et al. (2015) that success lies at the centre of your co-authorship network. However, success in terms of **citation and h-index** depends very much on the research topics, and it heavily disadvantages younger researchers. To avoid blaming anybody, I have chosen two examples where I am involved as coauthor: „A higher-level phylogenetic classification of fungi“ (Hibbett et al. 2007) with 67 authors, was cited 815 times in June 2015 according to Web of Science. A publication on „Phylogeny of *Hyaloperonospora* based on nuclear ribosomal internal transcribed spacer sequences“ (Göker et al. 2004) with four coauthors has not been cited at that time in a refereed journal.

In the 1960s Thomson Reuters invented the **journal impact factor**, JIF, that influenced publication strategies heavily. In fact, young researchers are forced to publish in journals with an impact factor as high as possible and accessible in their specific discipline. However, it is no more a secret, that nonscientific criteria and even calculated manipulations effect the impact factor considerably. Consequently, „senior staff at societies and leading journals want to end inappropriate use of the measure“ (Callaway 2016).

More than others, high impact journals favour **eyecatcher titles** for their articles. As an arbitrary example, News from Science, weekly headlines, 08 May 2015, are cited: „Ebola persisted in doctor's eye for months", „Traffic noise blocks fish sex", „Podcast: A plant that finds diamonds, the evolution of pop music, and why Americans smile more than Russians and Chinese", „Graphene spray makes spider spin stronger silk....or die". Is this reflecting what is considered as essential today for mass consumers in the scientific community? – In April 2015, The Royal Society held the conference on „**The future of scholarly scientific communication**" (The Royal Society 2015). The Chair of the first session, Geoffrey Boulton, emphasized „that it was important to be radical in our thinking", and several contributors followed his advice, e.g. the **JIF** is „responsible for distorting journal editorial policies and author behaviour", and „**peer review** is faith-based (not evidence-based) slow, wasteful, ineffective, largely a lottery, easily abused, prone to bias, doesn't detect fraud and irrelevant. In the age of the internet, we no longer need it. We should publish everything and let the world decide. Peer review in journals only persists because of huge vested interests", and „**open access** is only really tinkering with the existing model". In fact, a free-thinking scientific community is active and successful, as is visible by ScienceOpen that was launched in May 2014 (Grossmann 2015a), and which actually (August 2015) offers already 1.5 million open access articles (Grossman 2015b).

Publish or perish:

- **Join multi-author papers.**
- **Follow scientific advertisement from paper title to journal.**

Hopeful future regulations:

- **Harmonic research and open access publication networks.**

11. Conclusions and outlook

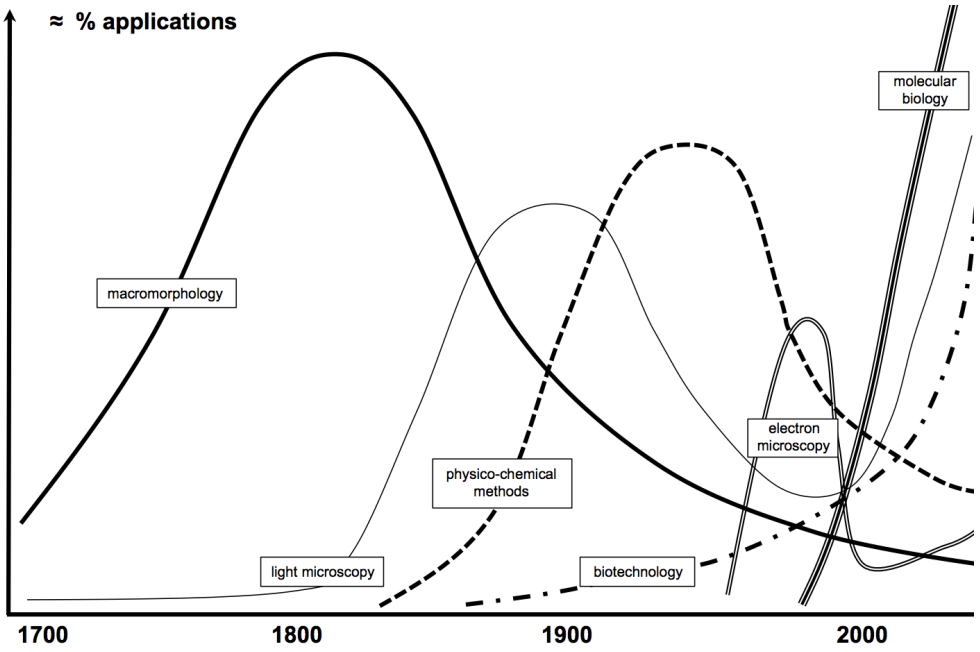


Fig. 27: Approximate application percentages of **successive main research methods** in biology over the last 300 years, with special reference to cryptogams, except lichens. (Graphic: F. Oberwinkler)

The brief outline and comments on changing research in cryptogams tries to analyse conditions and prerequisites for this development. Few collectors of „new organisms“ were followed by taxonomists of various kinds, and finally by specialized systematists. Regional and global monographs of selected taxa accumulated over the time, mostly usable only for the taxonomic experts. – Quickly, so-called general research methods were applied also for cryptogams. In a **historical sequence of techniques** available (Figs. 2, 6, 9, 27), these were light microscopic studies of cellular constructions, thus providing the grounds for forthcoming developments, than followed by physiological and ecological approaches, finally by molecular and partial to full genome analyses. However, none of the previous methods were completed. In contrast, they were used simultaneously, and quite often excessively, and facilitated by digitalizing equipments. – The result of this development is an exponentially increasing amount of data (Fig. 28). None of the experts themselves is able to overlook the data mass and the corresponding literature in his own field anymore. The selective interpretations of bioinformatics are consequently required, being the integral part of biological research in future. How the balance between biological questions and the essential data management will be handled now and after exploding in future, will be the most urgent challenge.

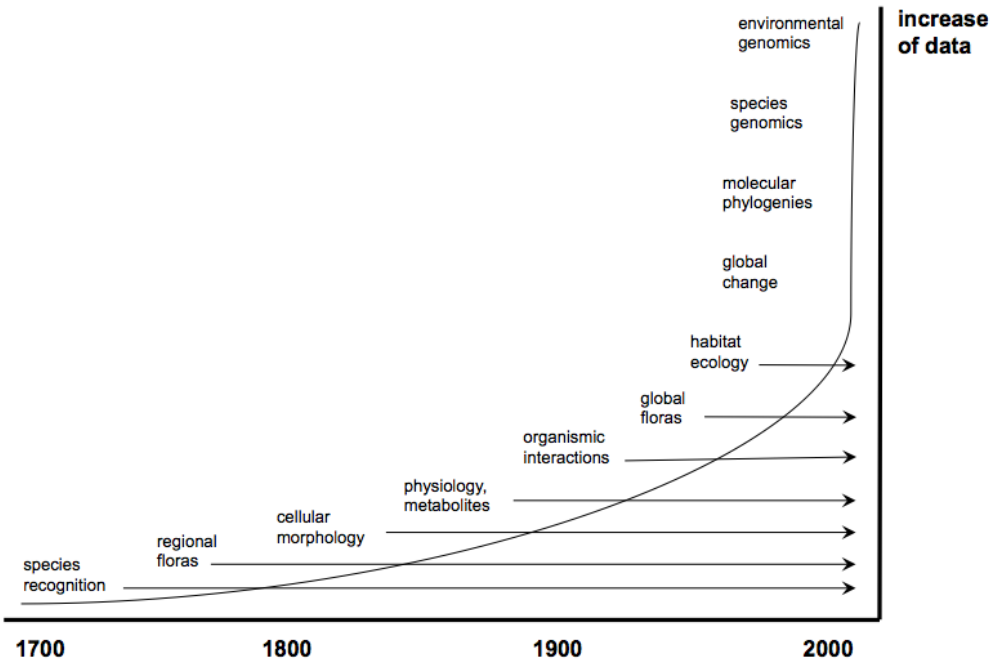


Fig. 28: Methods and fields in biological research over an approximate time of 300 years. This diagram is fully applicable to cryptogam research over that period, too. The diagram integrates and simplifies the data of Figs. 26 and 29. **The data curve illustrates the asymptotic increase of research output.** Arrow-headed lines shall indicate that former research methods were applied over the whole timespan of cryptogamic research. – In June 2015, nearly 416.000 publications for „biodiversity", 240.000 for „Molecular phylogeny", and more than 14.000 for the search term „environmental genomics" were listed in Web of Science. (Graphic: F. Oberwinkler)

Recognition of organisms by their habit appearance is as old as mankind. However, scientifically motivated distinctions of species is not much older than 500 years, except of folk medicinal purposes. When „macro-organisms" became interesting for former biologists, comparative macromorphology developed rapidly and culminated quickly (Fig. 27). It was the time of the great collectors and the beginning of intensive classifications. – Light microscopy required a long technical development and a pioneer attitude for researchers to apply it. Nevertheless, when well-equipped microscopes were available, light microscopy passed a track record. Its renaissance is similarily remarkable, and well understandable. The unique capabilities came through fluorescence and confocal techniques, and reached the possibilities to observe living cell organelles and even protein molecules. – Chemico-physical methods were then the winners in plant physiology, and biotechnology developed step by step. Both appeard to be unsurpassable. – Around the 1950s electron microscopes were technically adequately developed for practical work in biology. Electron microscopy's breakthrough was surprising, but also its decrease when mole-

cular techniques became available. These are nearly universally applicable and claim for first priorities in most fields, including research grants. – The coexistence and de facto **co-applicability of all methods** and their specific variants is an attribute of present times, and a challenge for coming joint applications.

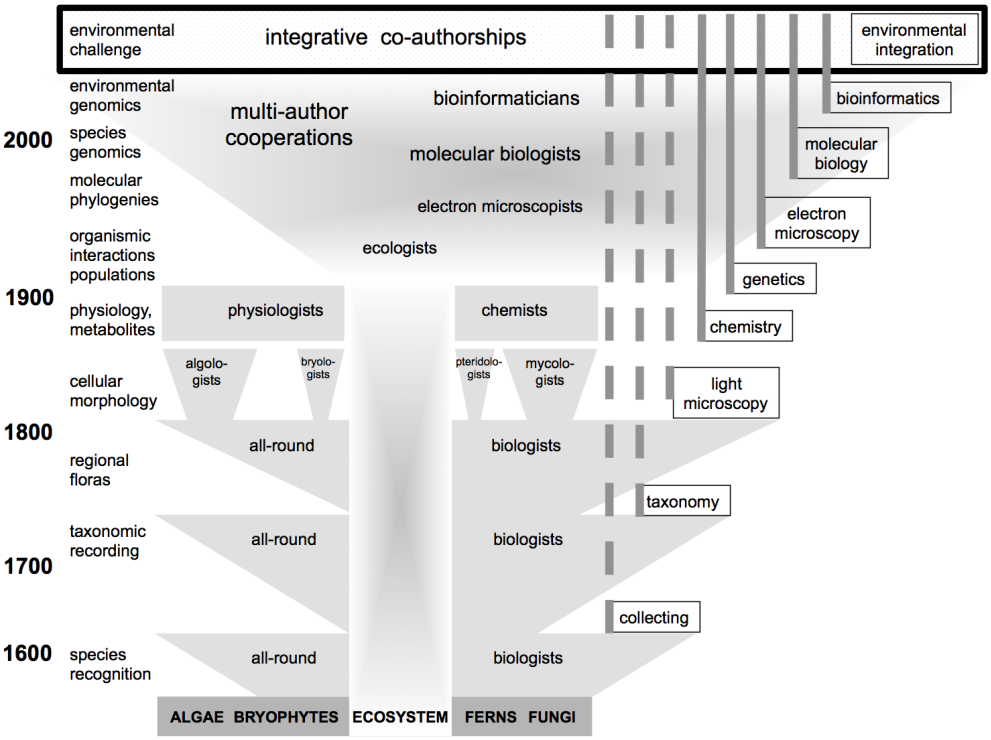


Fig. 29: Holistic view of individual and combined research capacities, the emerging, actual and prospective environmental challenge in biology in general, and with a special focus on cryptogams. Explanation in the text. (Graphic: F. Oberwinkler)

At times of the great herbalists, plants were recognized by habit as distinctive species. **One experienced physician** or pharmacist was covering all plants, including few cryptogams for medicinal applications. When scientific research developed (Fig. 29), also individual experts were capable to deal with the whole extent of known species. To master the quickly growing number of species, regional floras and taxonomic treatments were following, again, mostly the works of individual researchers. This „habitus-species“ approach was inherently accompanied by ecosystem characteristics of each species' habitat. So, even unconsciously, ecosystem parameters were in the mind of each field worker, and had some impact on species descriptions. – Increasing light microscopic work was accompanied by a first and significant reorientation in research fields. Careful microscopic studies were time consuming and con-

fronted with huge amounts of new data. Researchers with a restricted field of expertise, mostly in organismic groups, like algae or bryophytes, were the consequence. However, there were exceptions of still broadly expertised biologists.

When chemical methods became part of biological studies, the **splits in research competence** were much more drastic. At least as a rule, physiological and biochemical experiments in various fields required consequent laboratory presence. In addition, the generally important results in these fields appeared to justify the recommendation of more qualified research. A remarkable divergence resulted in progressively important and conventional disciplines. However, the limits of organismic groups appeared unimportant in general studies, but meaningful again, for example in chemosystematics. Exceptionally, there were and are biochemists with great expertise in field work and in systematics. – Similar attributes are also true for some electron microscopists, genetists, and molecular biologists. All of them, however, depend on the availability of the correct organisms for their special purposes. What the **correct organism** is, was traditionally defined by the expertised taxonomist, then by a voucher or culture name that correctly should include who has identified the sample. Genetics, physiology and molecular disciplines are overfilled with technical terminologies, certainly simplifying communication between specialists, but very much impeding the understanding of non-experts. – All together, **molecular techniques dominated** biological disciplines in the very short time of a few decades. Their integrative power lies in the affiliation of nearly all other biological disciplines.

12. Acknowledgement

The effort of Paul Blanz, Graz, to organize the Kerner von Maurilaun-Symposium in memory of Josef Poelt on the occasion of the 20th anniversary of his death, is very much appreciated. I am also grateful for Paul's suggestion to contribute an historical outline on research in cryptogams that were the main field of Josef's investigations. Hannes Hertel was so kind to comment critically on a first version of the manuscript. Careful proof-reading of my wife Barbara Oberwinkler is highly acknowledged. I thank editors and authors who kindly permitted copyrights of their illustrations reproduced in this article.

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