

# Sex does not sell: the argument for using the terms “anamorph” and “teleomorph” for fungi

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## Abstract

Using the adequate morph terminology is an important tool for describing the different stages of fungi with their often hidden and flexible sexual processes. These processes play significant roles in the evolution and spread of pathogenic fungi as well as their antifungal resistance. Their knowledge is also the base for control of human and plant pathogenic fungi as well as strain improvement in biotechnology. Among all organisms, the heterokaryotic stage, i.e., the intermediate stage between plasmogamy and karyogamy is unique for Ascomycota and Basidiomycota. These fungi show a high flexibility of sexuality by the gradual reduction of sexual processes in the teleomorphs and the occurrence of genetic recombination processes in the anamorphs. Our lack of knowledge about such details of development in most species of fungi justifies maintaining the unique morph terms “anamorph” and “teleomorph” in mycology instead of an incorrectly simplified application of the ontogenetic terms “asexual” and “sexual.”

**Keywords** Apomixis · Autogamy · Dikarya · Horizontal chromosome transfer · Nomenclature · Parthenogamy · Pezizales · Phylogeography · Spermatization

## Introduction

Anamorphic fungi were named as early as in the eighteenth century without knowledge about their relationship to teleomorphic stages. This connection with teleomorphic stages was published for the first time in 1854 for *Aspergillus glaucus* (L.) Link by Anton de Bary (Seifert and Samuels 2000). This discovery gradually showed the need for globally accepted terms for distinguishing between both morphs, since different terms had been existing in different languages, such as “perfect stage” and “imperfect stage.” Because of the uprising discussion whether different stages of the same species could be named differently, M.A. Donk

(1960) adopted a morphological approach to naming. He proposed the term “anamorphosis” to refer to the conidial or presumed asexual morph, the Greek prefix “ana-” referring to the incomplete development. Although this term was already used in other contexts (e.g., geology, optics, religion), its introduction into mycology did not cause confusion. In contrary, Hennebert and Weresub (1977) proposed the analogous term “teleomorph” for the presumed sexual morph, the Greek “teleo-” referring to a complete process including sexual reproduction. In contrast to the preceding terms, “anamorph” and “teleomorph” focused on the element “morph,” whereas the prefix *ana-* (directed towards a goal) and *teleo-* were as biased by the anthropocentric perspective as the previous terms, such as “perfect/imperfect.” Although the new morph terms were defined as intuitively as the previous versions, they gained wide acceptance. Later, a terminology was proposed that distinguished conidial stages and sexually reproducing stages on the basis of the presumed nuclear divisions found in each: mitosis in anamorphs and meiosis in teleomorphs. Thus, “mitotic” replaced “asexual stage” or anamorph, and “meiotic” replaced “sexual stage,” but this new terminology was never widely adopted (Seifert and Samuels 2000). The common practice of naming the two stages of the same fungus separately as anamorphs and

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teleomorphs was legitimized for dikaryotic fungi (Dikarya = Ascomycota and Basidiomycota) as an exception in the International Code of Botanical Nomenclature until 2011 (since the end of 2011 called International Code of Nomenclature for algae, fungi, and plants; McNeill and Turland 2011).

Although the terms anamorph and teleomorph are used in the newest version of the Code (Shenzhen Code, Tom May, pers. comm.), we are now experiencing a tendency of editors and reviewers of mycological publications to suppress the terms anamorph and teleomorph in favor of “asexual stage/morph” and “sexual stage/morph,” a policy supported by Hawksworth (2013). In a published response, Seifert (2016) defended the usage of these terms against censorship. The attempts to suppress the morph terms come from a misguided belief that familiar terms will make mycology to more accessible to students and other disciplines. However, the existence of anamorphs and teleomorphs is unique to the Dikarya and the terms sexual stage or asexual stage oversimplify and can obscure a complex and highly interesting life cycle.

As it becomes clear from closer examination of Ascomycota and Basidiomycota (Dikarya), which comprise the vast majority of fungal species, the morph terms refer rather to morphology, and the terms “asexual” and “sexual” to ontogeny and are not simply each other’s synonyms. While the morphological stage of a fungus can be described comparatively easily, the sexual processes are complicated, differ even among species in the same genus, and in most species are only fragmentarily known. Therefore, we suggest defining the teleomorph as phenotype in which reproduction occurs by including meiosis or loss of meiosis and the anamorph as phenotype in which reproduction occurs without meiosis and without its loss. Below we present the reduction of sexuality in the teleomorph and the introduction of sexual processes in the anamorph in order to illustrate the “diffuse” sexuality in fungi.

Although we no longer provide separate names for the respective anamorphs and teleomorph in a single life cycle, these morphs still represent unique patterns of gene expression in the life cycles of dikaryotic fungi, and these patterns cannot be adequately expressed by terms that are used for other groups of organisms. Doing so will only obscure the unique features of the sexual processes in the life cycles of Dikarya in comparison to other organisms.

The sexual process in the Dikarya is not necessarily binary with “males” and “females” uniting and producing offspring, as is the case with most other sexually reproducing organisms. Attempts to define “sex” in a sense that would include fungi are comparatively rare (Gäumann 1964; Vreeburg et al. 2016). Only detailed knowledge about the sexuality of fungi, however, would justify speaking of asexual or sexual (Seifert and Samuels 2000). For most fungi, assigning sexual functions occurs by generalization from a few better known species

and not by scientific observation in the actually investigated species. By mycological progress (such as in the same name journal), we experience that mycological disciplines split into those focusing on the cell biology and development of one or few model species and those dealing with the ecology and diversity of many species. The deep insights of the former into the life of a single fungus tend to ignore that other groups of fungi may have completely different expressions. Focusing on the diversity of fungi, however, often leads to rather reductionistic cladistics or quite speculative or trivial ecological conclusions. Although the author is not familiar with experimental study of sexual processes in fungi, an overview of the different forms of sexuality in Dikarya presented mainly from the secondary literature (only the figures are original) is attempted below as an incentive to connect the diverging mycological disciplines.

## Sexuality in fungi

Sexual processes include a regular sequence of fusion of compatible cells (plasmogamy), fusion of haploid nuclei (karyogamy), and meiosis. In animals with a diplontic life cycle, karyogamy and meiosis are separated by the proliferation of diploid cells. Gametes are the product of meiosis and, therefore, considered to be formed sexually. Plasmogamy, however, is immediately followed by karyogamy. In the anthropocentric view, the closely consecutive sexual processes of meiotic gamete production, fusion of male and female gametes and fusion of their nuclei are considered sexuality par excellence, but in non-diplontic life cycles, this view reveals its limitations. In diplohaplontic organisms, gametes are formed by mitosis of haploid cells, and are thus formed asexually. With regard to plasmogamy, gametes undergo sexual fusion. Here meiosis is only indirectly included among sexual processes but gives rise to the haploid generation. Hence, plasmogamy and subsequent karyogamy can be considered more appropriate for applying the term sexual than meiosis. Some authors focus on karyogamy as *the* sexual event but implicitly also may include the steps following karyogamy as well as preceding karyogamy in the next generation (Vreeburg et al. 2016). Hitherto, it has not been possible to define a single event as sexual that would fit all life cycles in all kingdoms of organisms. In fungi as well as other organisms, sexuality should include meiosis, plasmogamy, and karyogamy (Miles 1993). In fungi, although we usually consider spores being meiotically derived from a zygote as sexual, this does not exclude the possibility that mitotically formed spores can function as gametes as well when their main function is plasmogamy, e.g., in “spermatia” of certain groups of Ascomycota and Basidiomycota. In most Dikarya, however, the mitotically formed cells of hyphae growing out from meiotically

produced spores serve as gametes when they fuse by plasmogamy (Vreeburg et al. 2016).

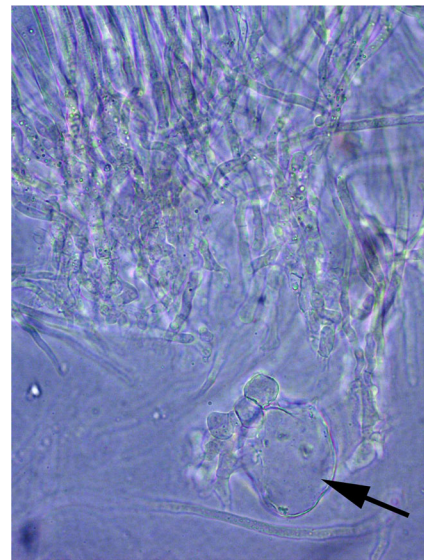
In contrast to all other organisms, the two sexual fusion processes plasmogamy and karyogamy do not follow each other immediately in Dikarya but are separated by a stage *sui generis*, hyphae (or yeast cells) with paired haploid nuclei (Gäumann 1964; Vreeburg et al. 2016). These nuclei do not fuse with each other but divide simultaneously mitotically and form new identical pairs which are distributed to the daughter cells. This stage with paired nuclei is often truly dikaryotic, i.e., characterized by two nuclei per cell, but multinucleate cells containing several pairs of nuclei also frequently occur in Dikarya, e.g., in *Morchella* species (Gäumann 1964). The number of nuclei per cell can be highly variable, from one to several, even within the same mycelium (not simply “mono”- or “di”karyotic) as well as in spores derived from the same conidiophore or sporoma (Kües et al. 2016). The observation of variable numbers of nuclei has, therefore, led to erroneous interpretations as karyogamy and meiosis in anamorphs (Evans et al. 2003; Kraepelin and Schulze 1982). The term “homokaryotic” might be more appropriate than “monokaryotic” and “heterokaryotic” than “dikaryotic” (Clemençon 2012), referring to the lack or presence of paired nuclei with each of both nuclei (“karyon”) being derived from a different (“hetero-”) cell by the preceding plasmogamy.

## Reduction of sexuality in the teleomorph

In Pezizales, particularly Pyronemataceae, sexuality and different examples of its reduction were discovered very early, because ascogonia can be detected comparatively easily with light microscopy (Gäumann 1964; Fig. 1). The “typical” (and in many textbooks often single) case of plasmogamy is that of gametangiogamy, which is initiated by dissolving contacting cell wall areas of an antheridium and an ascogonium, followed by transfer of the nuclei from the antheridium to the ascogonium (Fig. 2), where pairs of compatible nuclei are formed and shifted to outgrowing heterokaryotic hyphae.

Some deviations from the regular sexual processes can be found among species of the same genus (Fig. 3) and may be taxonomically significant. It is, therefore, impossible to make extrapolations from one species to even closely related species without detailed study. Reduction of sexuality is, of course, highly relevant for speciation, but understanding of such evolutionary processes is only exceptionally aimed at in rather mechanically conducted cladistics, although they are called “phylogenies.” The below terminology is adopted from Gäumann (Gäumann 1964) and may deviate from the usage by other authors.

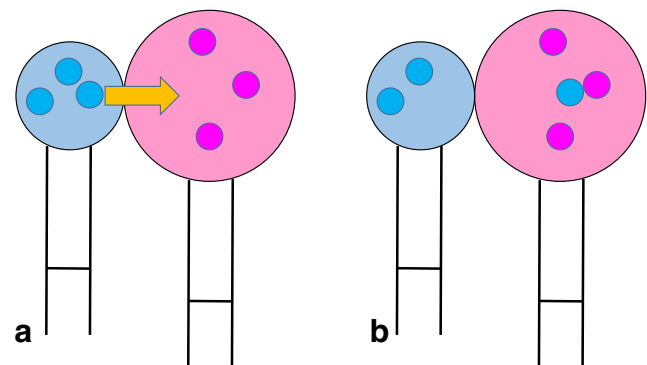
**Spermatization of the antheridium** The antheridium is reduced in size and may be dispersed like a spore, lacking the ability to germinate and produce hyphae; it is only capable of



**Fig. 1** Ascogonium of *Cheilymenia* sp. (arrow) from a squash mounting (Germany, Frankfurt am Main, on wall, Oct. 10, 2008 R. Kirschner 3248)

transferring, typically, a single haploid nucleus to a receptive cell (Fig. 4). The receptive cell can be an ascogonium or a hyphal cell (for simplification, the trichogyne—a filamentous outgrowth of the ascogonium which actively or passively gets into contact with the spermatium—is omitted here). In some groups, e.g., rust fungi (Pucciniales/Uredinales), complex spermogonia are developed (Fig. 5). In such cases, the reduction of the multinucleate antheridium to a uninucleate spermatium appears to be secondarily compensated for by the mass production of spermatia and their enhanced dispersal. Particularly, in such cases, the distinction between spermatium and conidium can be obscure (see below).

**Parthenogamy** The antheridium is lost (or it is present but does not provide nuclei). In order to achieve pairings of nuclei from two cells, fusion of the ascogonium and its “sister cell” takes place (Fig. 6). This does occur not only in Pezizales, but also other Ascomycota, e.g., Eurotiales



**Fig. 2** “Typical” plasmogamy in Pezizomycotina between an antheridium (blue) and an ascogonium (pink) by dissolving contacting cell wall areas (a) and transfer of nuclei from the antheridium to the ascogonium (b, indicated for one nucleus)



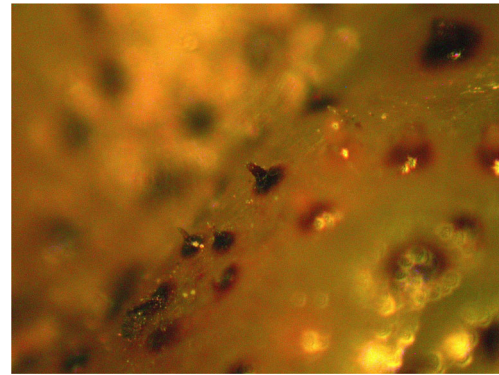
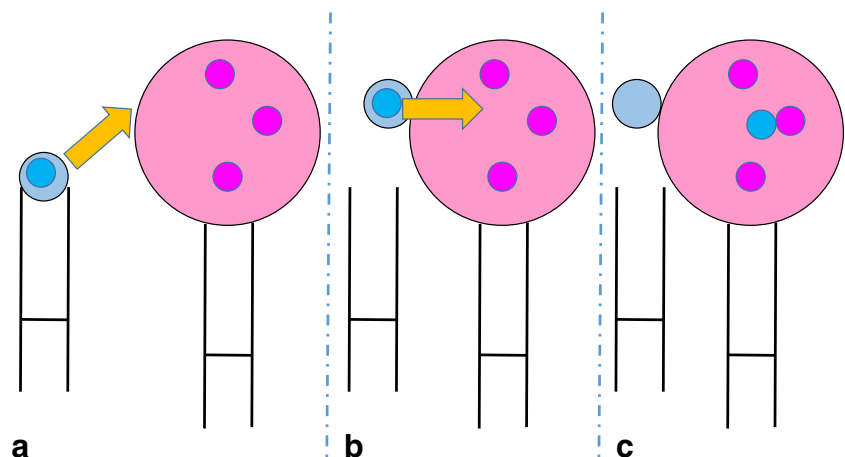
**Fig. 3** *Scutellinia* sp., a member of Pyronemataceae (Pezizales), where different modes of reduction of sexuality have been recorded (Taiwan, Hsinchu County, Qionglin Township, Apr. 18, 2014)

and Phyllachorales [*Polystigma rubrum* (Pers.) DC., *Rhytisma punctatum* (Pers.) Fr.] (Gäumann 1964).

**Autogamy** No fusion of compatible cells occurs, but pairing of nuclei within one and the same cell (Fig. 7).

**Somatogamy** Not only the antheridium has been lost, but also the ascogonium. Fusion takes place between cells of undifferentiated hyphae leading to the formation of heterokaryotic cells (Fig. 8). This mating behavior not only is common in Agaricomycetes but also occurs in Ascomycota, e.g., species of *Morchella* (Fig. 9) and *Neurospora tetraspora* Dania et al. (Gäumann 1964). The homokaryotic mating cells may be called gametes, but they differ from gametes in other organisms by being hermaphroditic, i.e., donating and receiving at the same time (Vreeburg et al. 2016). Gäumann (Gäumann 1964) considered the somatogamy as a sexual process, but the later development of basidiomata from the heterokaryotic mycelium as asexual. The sexual function of plasmogamy may have been transformed into parasitic exploitation of nutrients by the hyphae of some mycoparasitic fungi, such as species of *Tuberulina* (Basidiomycota) and *Parasitella* and other mycoparasitic

**Fig. 4** Spermatization is indicated by reduction of the antheridium which only contains a single nucleus (a) which after plasmogamy (b) is transferred to the ascogonium (c)

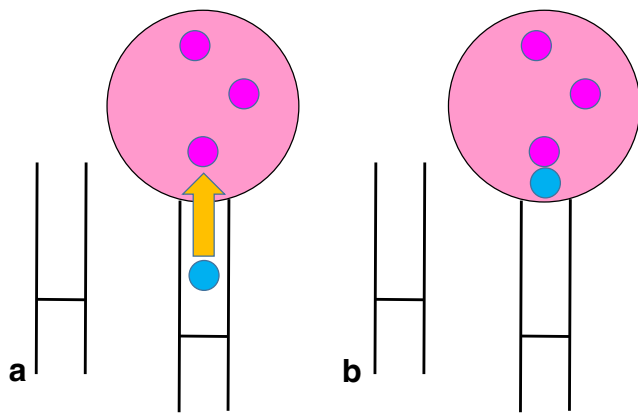


**Fig. 5** Spermogonia of the rust fungus *Puccinia caricis-araliae* Kakish. & Q. Wang (Taiwan, Mar. 17, 2011, R. Kirschner 3458)

zygomycetes (Bauer et al. 2004; Jeffries and Young 1994). This would be a special reduction of sexuality.

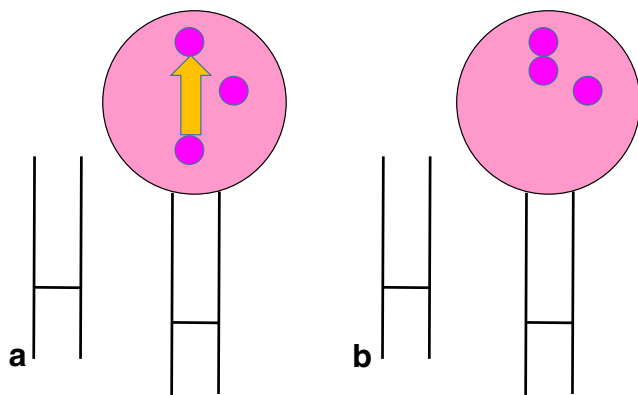
**Apomixis** No fusion of nuclei (karyogamy) and no meiosis occur. A diploid stage is not established. Apomixis occurs frequently in certain species of the Saccharomycetales (Gäumann 1964). In Agaricomycetes, particularly, Agaricales, examples are known where typical agaricoid basidiomata are formed, but without heterokaryotization (dikaryotization). Fusion of nuclei and meiosis has not been found in the basidia of this basidiomata (Petersen and Methven 1994). Sexual processes are lost, but the morphology of the sporoma is that of a teleomorph. Among Pucciniomycotina, cases of basidium development are known in the rust genus *Endophyllum*, where basidia and basidiospores are formed without karyogamy and meiosis (Gäumann 1964). Since it is more difficult to prove the absence of something than its presence, the cases of proposed haploid apomixis in fungi need careful further examination (Clemençon 2012; Prillinger 1982).

**Discordant distribution** The occurrence of the teleomorph may be spatially and temporarily limited compared to the widespread anamorph. In addition to the examples provided

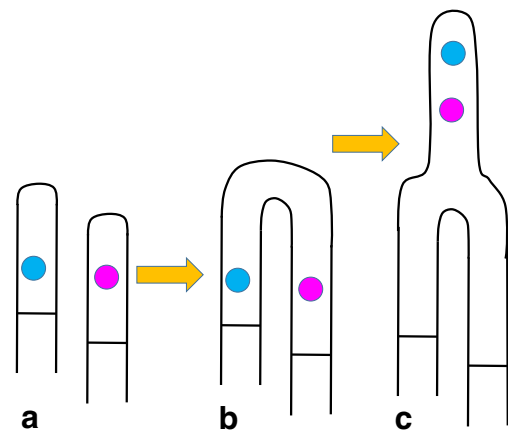


**Fig. 6** In parthenogamy, the antheridium or its function is lost; a haploid nucleus of a sister cell of the ascogonium is transferred to the ascogonium (a) and pairs with a nucleus in the ascogonium (b)

by Seifert and Samuels (2000), *Beauveria* is particularly interesting because its *Cordyceps* teleomorphs are thus far known only from East Asia, whereas their anamorphs can be found widespread and worldwide (Shrestha et al. 2014). The neotropical species *C. locustiphila* does not have a *Beauveria* anamorph and should not be combined into *Beauveria* (Pelizza et al. 2018). Restriction of the teleomorph to a limited geographic region and widespread distribution of the anamorph indicate the geographic evolutionary origin of these fungi in the area of teleomorph distribution and subsequent clonal spread to other regions. In other fungi, whose teleomorph appears rarely, reduction of sexual reproduction in favor of clonal dispersal might be prevalent when a stable environment is ensured. For example, the fungal symbionts of leaf cutter ants (Formicidae, Attini) are reared in the ants’ subterranean nests under optimal conditions for mycelial growth and are transferred to newly established nests by young queens (Piepenbring 2015). The basidiomata of the symbiotic Leucoprineae appear only during decline of the ant nest. In contrast, the termite symbiotic *Termitomyces* species are not transmitted by the new termite progeny that found new nests, but the symbiosis has to be newly established by



**Fig. 7** In autogamy, the antheridium or its function is lost; haploid nuclei of the ascogonium pair with each other (a, b)



**Fig. 8** Somatogamy is initiated by close proximity of two compatible homokaryotic hyphae (a) and proceeds with plasmogamy of the hyphal cells which thus function as gametes (b). A new heterokaryotic hypha with paired nuclei is formed (c)

new acquisition of the fungus. The lack of vertical transmission in termites is correlated with frequent and regular development of basidiomata. Many lichenized Ascomycota rarely form ascomata so that they are treated as “largely asexual” (Tripp 2016). Occurrences of ascomata in such lichens, however, may change over time and perhaps be triggered by changing environmental factors (Obermayer 2008). Actually, sexual processes of such asexual lichenized fungi are simply too poorly understood, as demonstrated by biologically absurd phrases such as “gain of sexuality from asexual ancestors” (Tripp 2016). Molecular genetic methods now allow the detection of sex-related genes in fungi without known teleomorph, which indicates that rare (“cryptic”) sexuality is widely present in fungi hitherto only known as asexual.



**Fig. 9** *Morchella conica* is an example of an ascomycete which lost the formation of antheridia and ascogonia and forms multinucleate cells with paired nuclei by somatogamy (Germany, Frankfurt am Main, Leipziger Strasse, Apr. 19, 2010)

Although actual sexual processes have not yet been confirmed and can be considered rare compared to the reproduction of the anamorph, they must be present and play an important role in the speciation of these fungi. Cryptic sexuality is still widely neglected in phylogeographic studies (Seifert and Samuels 2000; Tripp 2016), in spite of increasing evidence by molecular genetic study.

## Sexual processes in the anamorph

As mentioned above, the stage with paired nuclei can reproduce independently from the homokaryotic stage as well as the truly sexual meiotic stage. The reproduction itself can be asexual with respect to the absence of karyogamy and meiosis, but itself is based on mating of cells.

**Somatogamy** Homokaryotic cells reproduce asexually by forming conidia or yeast cells but at the same time can function as gametes and donate as well as receive nuclei from other homokaryotic cells. Heterokaryotic mycelia, though being a product of sexual fusion, may form heterokaryotic conidia. Since genetic recombination may have taken place prior to the production of conidia, these conidia compared to conidia produced from homokaryotic mycelia are not purely asexual. Furthermore, the heterokaryotic cell can act as a gamete by plasmogamy and by transferring a nucleus to an additional homokaryotic cell; this is known as the Buller phenomenon. Compared to homokaryotic hyphae, the sexual function of the heterokaryotic cell is limited by being able only to donate, not to receive nuclei. By this transfer of nuclei, genetic recombination is possible without karyogamy and meiosis (Peraza-Reyes and Malagnac 2016).

**Spermatization** Conidia of some fungi do not only disperse the species, but they can also transfer nuclei (i.e., gene flow) and thus play an important role in heterokaryotization. Watling (Watling 1979) and Clemençon (2012) presented the example of homokaryotic conidia of *Coprinopsis cinerea* (Schaeff.) Redhead et al. and did not favor the term asexual even for mitotic monokaryotic spores which serve as spermatia. Experimental evidence shows that the conidia of *C. cinerea* can have both functions. Conidia also of certain species of Ascomycota can alternatively act for dispersal and for donating their nuclei to a receptive hypha, e.g., in certain species *Fusarium* and *Neurospora* (Gäumann 1964; Seifert and Samuels 2000). Whether mitospores serve as “conidia” or “spermatia” cannot be concluded from morphology alone, but only by observation of their behavior. For example, in most species of Meliolales, Phyllachorales, and Rhytismatales due to lack of experimental evidence, we do not know whether the phialospores serve as true conidia, i.e., have the capability to germinate with hyphae and produce

new colonies, or only function as spermatia by transferring a haploid nucleus to a receptive cell for heterokaryotization (Piepenbring 2015). Further examples are given by Seifert and Samuels (2000). In these and many more fungi, when “asexual reproduction” and spermatization cannot morphologically be distinguished, anamorph terms such as “coelomycetes,” “pycnidia,” “phialides,” and “conidia” are applied. There is no mistake when these terms are used as descriptive morphological terms, whereas in this context, the term asexual as a functional term can only be used when heterokaryotization can demonstrably be excluded.

**Non-meiotic recombination** Besides these deviations from the regular sequence of fusion of cells (plasmogamy), fusion of nuclei (karyogamy), and meiosis, sexual processes occurring without meiosis in fungi do occur. Here, undifferentiated hyphal cells may fuse even without the involvement of mating types or sexual compatibility and may transfer nuclei, chromosomes, chromosome fragments, or genes. For a schematic figure, see Mehrabi et al. (Mehrabi et al. 2011: Fig. 2). When a temporary diploid nucleus is formed, this process is called parasexual (in fungi this definition differs from that applied in bacteriology), but it seems that it is practically more easily to prove asexual recombination than how this recombination takes place in detail, e.g., whether fusion of two nuclei is or is not involved (Mehrabi et al. 2011; Shahi et al. 2016a). Compared to the typical sequence of sexual processes, only meiosis is missing here. These processes are difficult to detect, because they occur among hyphae or conidia of the anamorph without the formation of ascomata or basidiomata (the teleomorph). It appears that asexual heterokaryon formation (leading to asexual recombination) by conidial anastomosis tubes occurs more easily than by hyphal anastomosis (Shahi et al. 2016b). Since genetic recombination occurs by fusion of cells and maybe even karyogamy, this behavior is not strictly asexual. The most exciting recent discovery in this field was that of the intraspecific transfer of chromosomes responsible for host specific pathogenicity between different strains of certain *Fusarium* species (Mehrabi et al. 2011). This finding inspires new hypotheses about host jumps and speciation in the evolution of plant pathogenic fungi. This genetic recombination may be unique among eukaryotes and further illustrates the high flexibility of fungi with respect to sexuality. It was perhaps a precondition even for inter-kingdom gene transfer from fungi to insects with strong ecological impact (Moran and Jarvik 2010).

## Conclusions

The unique heterokaryotic stage, i.e., the intermediate stage between plasmogamy and karyogamy, particularly of Basidiomycota, the reduction of sexual processes in the

teleomorphs of certain species of Dikarya, the occurrence of parasexuality and other sexual processes in anamorphic fungi, and our lack of knowledge about such details of development in most fungi justify maintaining the unique mycological terminology of anamorph and teleomorph instead of an incorrectly simplified application of the terms asexual and sexual. From the modes of reproduction, we can conclude that asexual and sexual behaviors are not strictly separated in fungi. As indicated above, somatogamy and spermatization can occur in both stages.

Knowledge of the high variation between completely sexual and asexual reproduction was presented in old textbooks, such as early as in Gwynne-Vaughan and Barnes (1927), and particularly in Gäumann (Gäumann 1964), who talked of “reduced” and “blurred” sexuality as well as “crisis of sexuality,” but this topic gradually disappeared from mycological syllabi. Understanding of sexual processes, however, is fundamental for getting insights in causal connections involved in the evolution of fungi (Prillinger 1982) besides merely defining statistically supported terminal clades. Replacing the morph terms with asexual and sexual in order to conform to non-mycological disciplines may be an adequate simplification for educational purposes as long as the teacher is aware about its limitations. Suppression of the morph terms in scientific mycological publications, however, rather indicates the decline of fundamental mycological and phylogenetic knowledge and education due to the prevailing molecular reductionism or due to attempts to harmonize mycological terminology with the terminology in other groups of organisms. The diversity of sexuality in fungi provides unique opportunities for approaching particular genetic and cell biological questions which cannot be solved by using animal (including human) and plant models. In zoology, evolutionary developmental biology (evo-devo) has boosted understanding of phylogeny. In fungi which in contrast to animals much more commonly have two independently reproducing morphs with separate evolutionary traits, evo-devo is still to be established. Using the adequate morph terminology is an important tool for describing the often hidden and flexible sexual processes in fungi, which play important roles in the evolution and spread of pathogenic fungi as well as their antifungal resistance. Their knowledge is the base for application in suppressing pathogenic fungi as well as in strain improvement in biotechnology. These chances for strengthening mycology as a unique discipline should not be obscured by imposing an imprecise usage of asexual and sexual in order to abandon the particular mycological terms anamorph and teleomorph.

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few months before his death, he confirmed to me his concern about the tendency to suppress these terms and expressed his preference for them. Tom May is thanked for the information about the actual stage of the Code. Insights into the horizontal chromosome transfer were possible by joining the FEMS congress in 2011 supported by the Ministry of Science and Technology, Taiwan (NSC 100-2621-B-008-001-MY3). The author is very grateful to the editors of the special issue for providing the space for this opinion dealing with a matter which is not much important in itself, but only by the need of defending a little piece of scientific freedom and thinking. Three anonymous reviewers are particularly thanked for their constructive and highly inspiring suggestions, which considerably improved the message of this text.

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