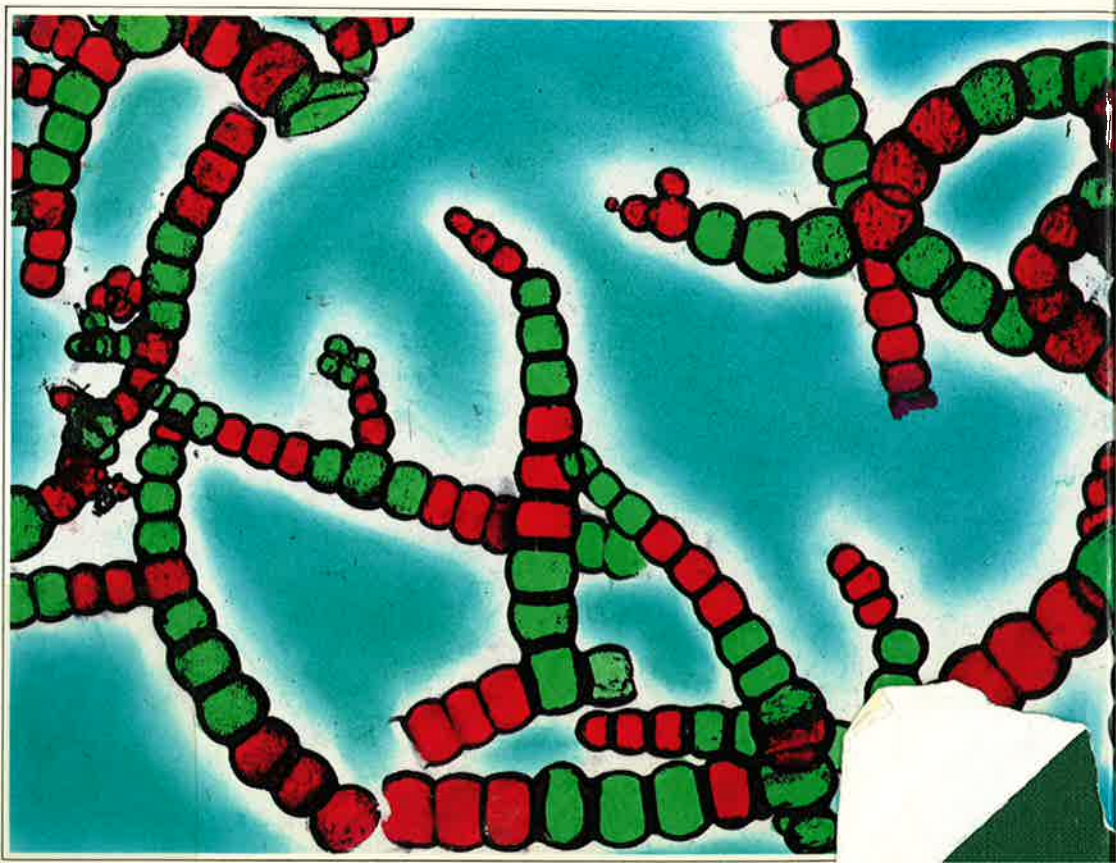


# Pleomorphic Fungi

## The Diversity and Its Taxonomic Implications

Edited by

Junta Sugiyama



## CHAPTER 10

# Pleomorphy in Holobasidiomycetes

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### 10.1 INTRODUCTION

When considering pleomorphy it is necessary to define the structures under discussion. In the following pages, definitions and a general survey are given of the various types of basidiomycetous anamorphs, in which most anamorphic genera are mentioned (for a detailed survey see Kendrick and Watling, 1979). Subsequently, some examples of pleoanamorphy are discussed as well as some problems of classification, (1) when various phases in the development of a single propagule would be classified differently, (2) when the development stops before the completion of the "typical" ontogenetic processes or (3) when a certain stage in the ontogeny remains poorly expressed or is missing completely. Comparisons are made between anamorphic and teleomorphic structures and nomenclatural problems connected with haploid apomixis are discussed.

### 10.2 VARIOUS TYPES OF ANAMORPHS

The term "anamorph", reintroduced by Hennebert and Weresub (1977), is used here in a broad sense to include any asexual morph. It has been adopted as such in the International Code of Botanical Nomenclature. In the Holobasidiomycetes it is applied not only to conidial forms of sporulation, but also to hyphal differentiations. Several types can be distinguished:

#### 10.2.1. *Modified sterile hyphae*

This is a purely hyphal type based on the characters of a single hypha, not on interactions of several hyphae. The best known example is probably *Rhizoctonia* DC., which in its broadest sense contains anamorphs of *Aquathanatephorus* Tu & Kimbrough, *Athelia* Pers., *Botryobasidium* Donk, *Ceratobasidium* Rogers, *Helicobasidium* Pat., *Thanatephorus* Donk, *Tulasnella* Schröt. and *Waitea* Warcup & Talbot.

Within *Rhizoctonia* several distinct groups can be distinguished. The type species, *R. crocorum* DC., has multinucleate cells, the colonies are purplish and its teleomorph, *Helicobasidium purpureum*, belongs to the Auriculariales. The second group, known as the *R. solani* complex, contains the multinucleate species of *Thanatephorus* and *Aquathanatephorus*, which also often produce sclerotia. A separate generic name is available for this group: *Moniliopsis* Ruhland. A third group contains several multinucleate species with orange hyphae and sclerotia. The teleomorph of one of these species belongs to *Waitea*. The fourth group contains binucleate and generally white species with teleomorphs in *Ceratobasidium* and *Athelia*. Many are known as mycorrhiza symbionts of orchids and also as the causal agents of web blight in various phanerogams. The *Athelia* anamorphs of this group often have some septa with clamp connections and some straight "runner hyphae", but not all have clamps. "Runner hyphae" are sometimes also found in *Ceratobasidium* anamorphs. An anamorph name proposed for this group is *Orcheomyces* Burgeff (Donk, 1962).

Another well-known hyphal anamorph is the genus *Ozonium* Link: Fr. with teleomorphs in *Coprinus* Pers.: Fr. subsectio *Domestici* Sing. (Watling, 1979).

### 10.2.2 Hyphal strands or rhizomorphs

The simplest types of anamorph resulting from hyphal aggregation are hyphal strands and rhizomorphs. Rhizomorphs have a distinct outer layer (cortex), with rather narrow and often anastomosing and encrusted hyphae distinct from the hyphae of the inner layer (medulla), which are thin-walled, broad and straight. Hyphal strands do not show this differentiation, but intermediates do occur. Well-known examples of rhizomorphic genera are *Rhizomorpha* Roth (teleomorph *Armillaria* Kummer), *Rhizostroma* Fr. (teleomorphs in *Phallus* Hadr. Junius: Pers. and *Oudemansiella* Speg.) and *Anthina* Fr. (? teleomorph in *Phanerochaete* P. Karst.).

### 10.2.3 Carpophoroids

Rhizomorphs can be confused with sterile stipes or stipes with a delayed pileus formation as may occur, for example in species of *Collybia* Kummer or *Marasmius* Fr. (Singer, 1975). Such structures, which are known as carpophoroids (Singer, 1975), occur also in more fleshy species and have sometimes received anamorph names as *Acurtis* Fr. (teleomorph: *Entoloma abortivum* (Berk. & Curt.) Donk) or *Digitellus* Paulet for species of the interrelated genera *Lentinus* Fr., *Pleurotus* (Fr.) Quél. and *Polyporus* Mich.: Fr., which developed in the dark. *Himantia* Pers. is used for sterile resupinate mycelia of, e.g., *Athelia* and *Serpula* Pers. A special case is

*Rhacophyllus lilacinus* Berk. & Broome, the anamorph of *Coprinus clastophyllus* Maniotis, where groups of thick-walled cells occur in the gills. This phenomenon has been called *bulbillosis* by Singer (1975). Watling (1979) found all intermediates between a typical fertile *Coprinus* basidiome and a completely sterile form and consequently considered the thick-walled cells sclerobasidia.

#### 10.2.4. *Bulbils and sclerotia*

Weresub and LeClair (1971) rejected the indiscriminate use of the term "bulbil" for a compact and sometimes intricate branching of a single cell as done by Nobles (1948, 1965) and Stalpers (1978), and defined it according to Hotson (1912) as comprising sclerotoid bodies originating from intricately branched hyphae consisting of swollen, more or less hyaline, thin-walled cells. Such species are classified in *Burgoa* Goid. (teleomorph: *Sistotrema* Fr.), for example *B. verzuoleana* Goid. (Fig. 10.1 d-e).

To complicate matters, the propagules produced by species of *Mini-medusa* Weresub & LeClair (an older name for it is *Myriococcum* Fr.), were also considered bulbils by Weresub & LeClair. The bulbils of this genus originate from several undifferentiated hyphae, which later form somewhat swollen cells at the periphery of the structure (Fig. 10.1 f-h). Similar ontogeny is found in *Myriococcum praecox* Fr. (teleomorph: *Athelia coprophila* (Wakef.) Jülich), *Sclerotium hydrophilum* Sacc. (teleomorph unknown, probably in *Athelia*) and *S. rolfsii* Sacc. (teleomorph: *Athelia rolfsii* (Curzi) Tu & Kimbrough). In some of these species, some fluid may be formed around the sclerotia which in drying forms a cortical outer layer, with the result that the surface of the distinctly swollen cells becomes uniformly smoothed (Fig. 10.1 h). It seems impossible to distinguish this type of sclerotium on the generic level from a typical sclerotium as found in *Typhula* Fr. (the teleomorph of the type specimen of *Sclerotium* Tode: Fr. is *Typhula gyrans* Fr. *vide* Donk, 1962). In these species there are often even more swellings (e.g., *Typhula incarnata* Lasch: Fr., Fig. 10.1 i-k). For that reason I suggest to restrict the term "bulbil" to *Aegerita* Pers.: Fr. (teleomorphs in *Bulbillomyces* Jülich and *Subulicystidium* Parm.) with a very regular, restricted, centripetal development and the *Sistotrema* anamorphs, which have swollen cells from the start of development, and to call the compact structures of *Athelia* sclerotia. Another genus with small sclerotia is *Akenomyces* Arnaud ex Hornby having fusiform sclerotia covered with peculiar spiny hyphae. All sclerotial genera mentioned so far have small sclerotia, although in species such as *Sclerotium delphinii* Welch many initials may fuse to form a single, relatively large sclerotium. Typical sclerotia are also found in the Agaricales (e.g., *Agrocybe* Fayod, *Collybia*, *Coprinus*).

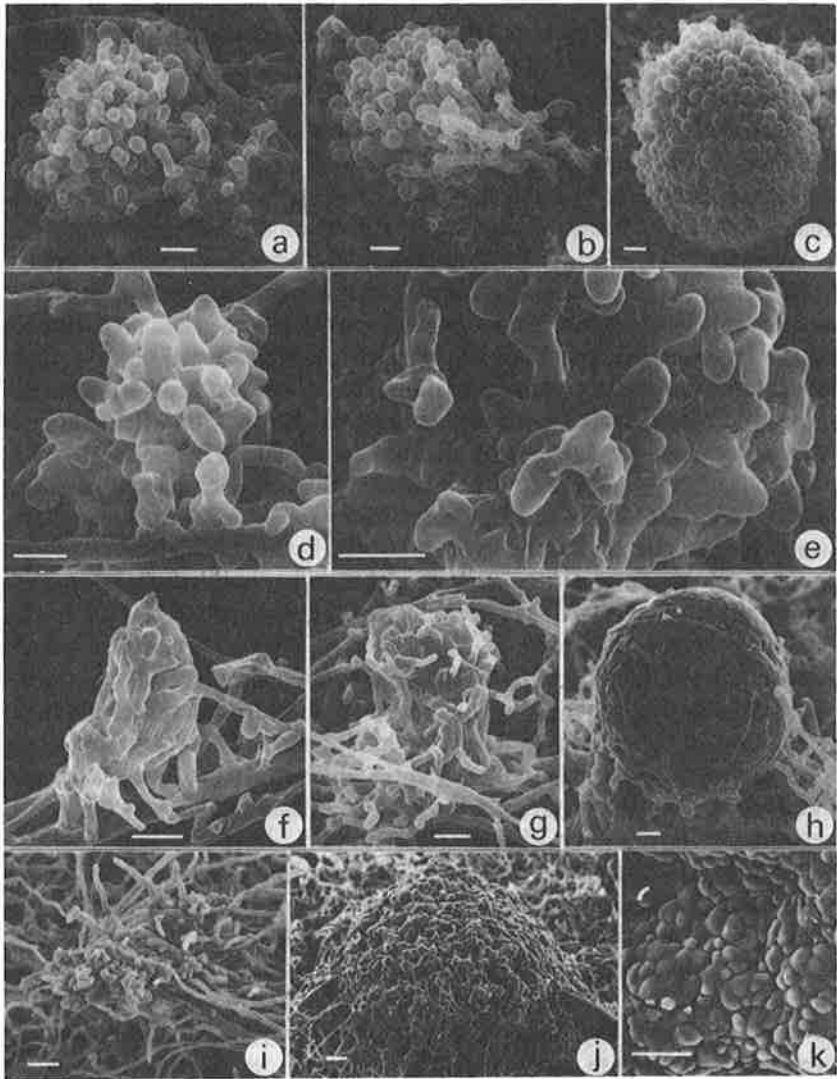


Fig. 10.1. Sclerotium development in some Aphylophorales.  
 a-c. *Aegerita candida*, CBS 320.63. d, e. *Burgoa verzuoleana*, CBS 197.76.  
 f-h. *Minimedusa polyspora*, CBS 671.75. i-k. *Typhula incarnata*, CBS 571.82.  
 Bar = 10  $\mu$ m.

Large sclerotia are found in *Wolfiporia extensa* (Peck) Ginns (= *Poria cocos* Wolf; anamorph: *Pachyma* Fr.) and the related genera *Polyporus* (anamorphs: *Mylitta* Fr., *Pietraia* Fr.), *Lentinus* (anamorph: *Scleroma* Fr.) and *Pleurotus*. They are often called pseudosclerotia because they may include sand grains or stone fragments and have no distinct cortex; however, there are intermediates towards more typical sclerotia and I doubt that this character has any taxonomic value here, as Pegler (1984) described both types from species of *Lentinus* (*L. tuber-regium* (Fr.: Fr.) Fr., with true sclerotia and those such as *L. velutinus* Fr. and *L. connatus* Berk. with pseudosclerotia).

#### 10.2.5. Chlamydo spores

Hughes (1953) and Barron (1968) defined a chlamydo spore as a "thick-walled resting spore, frequently intercalary, which is formed by modification of a pre-existing cell". This is mainly a functional definition, and it is not limited to spores with thallic ontogeny, as Kendrick and Watling (1979) have pointed out. It simply says that any cell can become a chlamydo spore, provided that it is or becomes thick-walled and is capable of germinating. Such a definition is more useful than that adopted at Kan-anaskis-I (Kendrick, 1971), where the functional element is lacking and a chlamydo spore is defined as "a thick-walled, thallic, terminal or intercalary spore". The term "chlamydo spore" is only useful when it is considered a functional term irrespective of ontogeny and thus not in competition with any ontogenetic term.

As mentioned earlier, cells becoming chlamydo spores can have widely differing origins, as demonstrated by the following examples:

- a) An undifferentiated mycelial cell swells, the cytoplasm contracts, and a new interior wall is laid down. This is the most common type of chlamydo spore in cultures of Aphylophorales (Stalpers, 1978), and it is found, for example, in *Fomitopsis* P. Karst., *Phlebia* Fr. and *Trametes* Fr.
- b) Arthroconidia may become chlamydo spores: in *Punctularia strigosozonata* (Schw.) Talbot the arthroconidia remain thin-walled and nearly cylindrical, but in *P. atropurpurascens* (Berk. & Broome) Petch they round off and become thick-walled. Thus they can be considered chlamydo spores, as has been done by Kendrick and Watling (1979).
- c) Blastoconidia may become chlamydo spores as well: in *Sporotrichum aurantiacum* (Bull.: Fr.) Fr. (teleomorph: *Pycnoporellus metamorphosus* (Fuckel) Stalpers) the conidia may become conspicuously thick-walled after dehiscence and thus function as chlamydo spores; of course they are still blastoconidia.
- d) The basidiospores of *Jaapia argillacea* Bres. are thin-walled at first, but after liberation the protoplasm withdraws from the ends of the spores and

develops a new secondary wall; they have become chlamydo-spores.

e) A basidiole may also become thick-walled and thus function as a chlamydo-spore. This happens for example in sclerobasidia, found in various members of the Tricholomataceae, but also the "bulbils" of *Rhacophyllus lilacinus* show structures which can be considered as such. Also the chlamydo-spores of *Fistulina* Bull.: Fr. and *Michenera* Berk. & Curt. are derived from basidioles; this will be discussed later.

#### 10.2.6. *Arthroconidia*

Arthroconidia are formed by fragmentation of hyphae, and the fragmenting conidiogenous cells change only after delimitation by a septum. They are most often found in pure culture and may occur in monokaryotic strains only or also in di- or polykaryotic strains of a species.

In the rhexolytic type, two new septa are formed within a pre-existing cell, thus forming arthroconidia separated by empty cells. Clamp connections, when present in the fragmenting hypha, are never a part of the mature conidium. This occurs, for example, in *Coniophora* DC. and many dark-spored agarics (Kühner, 1977). Typical members of *Ptychogaster* Corda (teleomorphs in *Tyromyces* P. Karst.) also belong here.

In other cases, a terminal hyphal part may disarticulate completely by splitting septa (schizolytic). When the fragmenting part is limited to the terminal cell, the conidia never show remnants of a clamp (e.g., *Phlebia*, *Flammulina* P. Karst.), but if the conidiogenous region includes primary clamped septa, remnants of these clamps will be recognizable, especially directly after separation of the conidia, for example, *Osteomorpha fragilis* Arnaud ex Watling & Kendrick, the anamorph of *Trechispora farinacea* (Pers.: Fr.) Libert and *Pleurotus dryinus* (Pers.: Fr.) Kummer.

Normally the conidiogenous hyphae are not differentiated, but in some species synnemata are formed, terminating with a conidiogenous head, for example, *Antromyopsis* Pat. & Trabut (Fig. 10.2 a; teleomorphs in *Pleurotus*), *Tilachlidiopsis* Keissler (= *Sclerostilbum* Povah, teleomorph in *Collybia*) and *Nothoclavulina* Sing. (teleomorph in *Arthrosporella* Sing.). The conidia in these genera generally show remnants of a clamp connection, but not always. Sometimes a secondary septum is produced, which may also split. Thus, in the same fungus, cells separated by a dolipore septum and by a simple septum can be liberated schizolytically (Moore, 1977).

#### 10.2.7. *Blastoconidia*

Blastoconidia usually obtain their final shape before a septum separates them from the conidiogenous cell. Several types can be distinguished:

a) The conidia are formed on denticles and are forcibly discharged. They

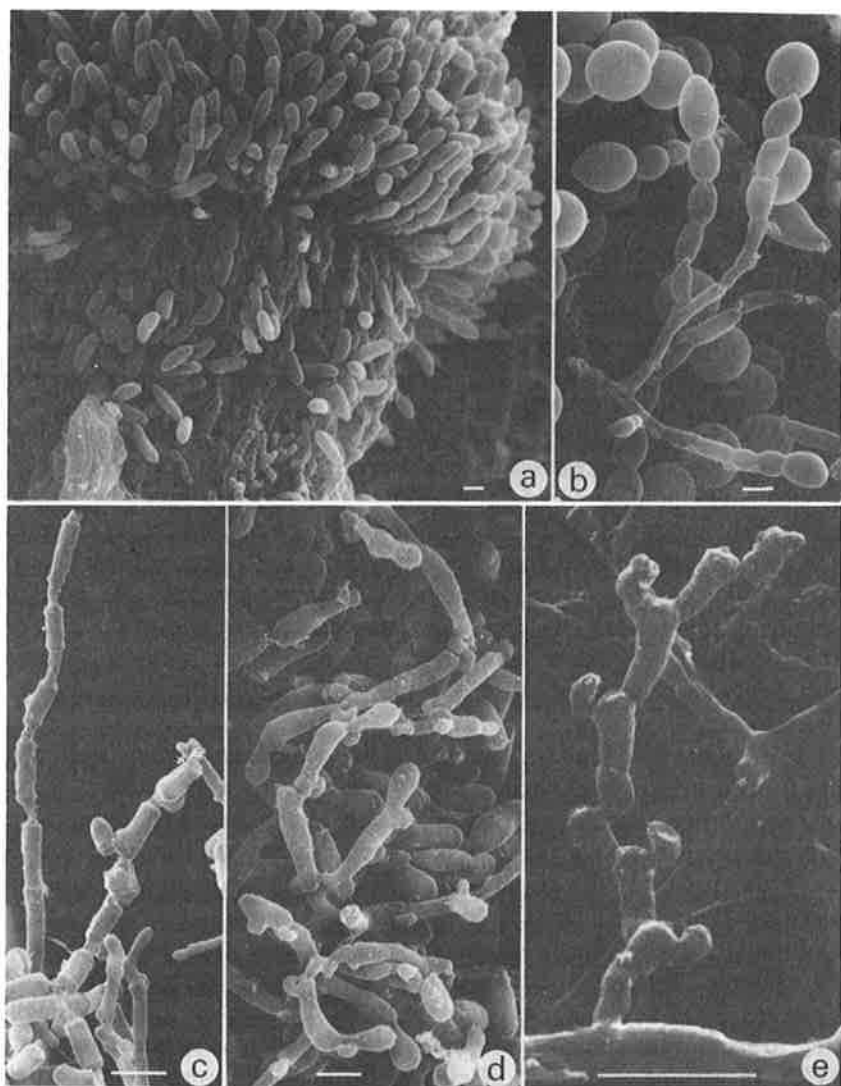


Fig. 10.2. a. *Pleurotus cystidiosus*, CBS 297.35. b. *Pleurotus dryinus*, CBS 449.77. c. *Punctularia strigoso-zonata*, CBS 308.78. d. *Punctularia atropurpurascens*, CBS 388.66. e. old conidiophore of *Taeniospora* sp., CBS 615.83. Bar = 5  $\mu$ m.

are then either the product of haploid fruiting (known from, e.g., *Agrocybe aegerita* (Brig.) Sing., *Schizophyllum commune* Fr.: Fr. or *Athelia rolfsii*) or they originate directly from a basidiospore as secondary spore, known from, e.g., *Ceratobasidium*, *Thanatephorus* or *Tremella* Pers.: Fr. b) The conidia are formed on denticles, are not forcibly discharged, and originate from undifferentiated hyphae. Such species may belong to the nematode trapping genus *Nematoctonus* Drechsler (teleomorphs in *Pleurotus* and *Hohenbuehelia* Schulz.) or to *Hapalopilus* P. Karst. or *Galzinia* Bourd.

c) The conidia are formed on denticles, on distinct conidiophores, on which the conidia originate simultaneously and are not forcibly discharged. They are found in *Dexhowardia* J. J. Taylor, *Jacobia* Arnaud and *Spiniger* Stalpers, the latter genus with teleomorphs in *Bondarzewia* Sing., *Dichostereum* Pilat, *Heterobasidion* Bref., *Hyphoderma* Wallr. (*Mutatoderma* (Parm.) C. Gómez), *Laurilia* Pouzar, and *Resinicium* Parm. (Stalpers, 1974). *Dichostereum* was segregated from *Vararia* P. Karst. on the presence of globose to ellipsoid, amyloid basidiospores and the presence of a *Spiniger* anamorph Lanquetin, 1973). *Scytinostroma arachnoideum* (Peck) Gilbertson can be distinguished from the other species of *Scytinostroma* Donk by the same characters that distinguish *Dichostereum* from the species belonging to *Vararia* s. str., but *S. arachnoideum* is not known in culture. If it produces a *Spiniger* anamorph, the distinction between *Vararia* and *Scytinostroma* based on the presence of dichohyphidia should be re-evaluated.

d) In *Haplotrichum* Link (teleomorph in *Botryobasidium*) hyphal swellings are formed in acropetal chains; these swellings may either form conidia on short, broad denticles or function directly as conidia. In the latter case, they are comparable with the conidia produced by some species classified in *Ptychogaster* s.l., for example, *P. effusus* Pat. (teleomorph: *Oxyporus obducens* (Pers.: Fr.) Donk).

e) Broadly attached blastoconidia may also be produced sympodially as, for example, *Sistotrema raduloides* (P. Karst.) Donk, several species of *Calocera* (Fr.) Fr., and *Typhula* (Berthier, 1976). From this it is but a small step to percurrent conidia, which are also found in *Typhula* (Berthier, 1976). In various cases it is difficult to distinguish between a sympodial and a random pattern. In *Sporotrichum* Link: Fr. (teleomorphs in *Laetiporus* Murrill, *Phanerochaete*, and *Pycnoporellus* Murrill), where the distance between the conidia is generally considerable, some conidiophores exhibit perfect sympodial development, while in others the pattern can only be considered random, although a sympodial tendency may still be recognizable (Stalpers, 1984). In *Glutinoaggar* Sivanesan & Watling and *Confistulina hepatica* (Sacc.) Stalpers (teleomorph: *Fistulina hepatica*

(Schaeff.: Fr.) Fr.) a similar pattern exists, but here the conidiogenous loci are condensed (Stalpers and Vlug, 1983). *Ellula* Nag Raj, *Fibulocoela* Nag Raj and *Michenera* display thick-walled conidia with a sterile apical appendage. Stauroconidia are found in *Riessia* Fres. and aquatic basidiomycetes as *Dendrosporomyces* Nawawi et al., *Ingoldiella* D. Shaw (teleomorph: *Sistotrema*) and in *Taeniospora* Marvanová (Fig. 10.2e, teleomorph in *Fibulomyces* Jülich).

### 10.3 MYCOPARASITES MIMICKING ANAMORPHS

Eriksson and Hjortstam (1969) report phialides in *Hyphodontia alutacea* (Fr.) John Erikss. var. *mamillaecrinis* John Erikss. & Hjortst. and later Eriksson and Ryvarden (1976) mention them for *H. floccosa* (Bourd. & Galzin) John Erikss. In Belgium, material of *H. crustosa* (Fr.) John Erikss. and *H. floccosa* was collected on which conidia were found. All isolates derived from these specimens yielded species of *Acremonium* Link: Fr. and *Verticillium* Nees, which are known as parasites of higher Basidiomycetes, and the conidia of these species agreed with those found on the natural substrate. Even when reexamined, it was often impossible to recognize the point where the phialides grew out of the basidiomycete; however, cultural work provided evidence that the conidia belong to a parasite.

There are more examples of these parasites that have been described even recently as parts of basidiomycetes, e.g., the conidia formed on the elongations of the flagella of *Flagelloscypha abruptiflagellata* Agerer (Agerer, 1975), and the spiny elements of *Trechispora stellulata* (Bourd. & Galz.) Liberta (J. Eriksson, pers. comm.) as described by Liberta (1973). The problem with parasites is not only that they add structural elements to the fungus under consideration that may be taken as parts of the host fungus, but also that the host reacts to the presence of the parasite by modifying or adding structures, which may be considered taxonomically important. An example of this is the genus *Syzygospora* Martin inducing the production of galls by *Collybia dryophila* (Bull.: Fr.) Kummer.

### 10.4 PLEOANAMORPHY

Many of the above mentioned types of anamorphs occur in combination. Even if we restrict the discussion to conidial anamorphs, there are many examples. Some of these examples deal with completely different anamorphs. Others deal with related anamorphs and then intermediates are often found. This second type of pleoanamorphy is especially useful in the understanding of relationships.

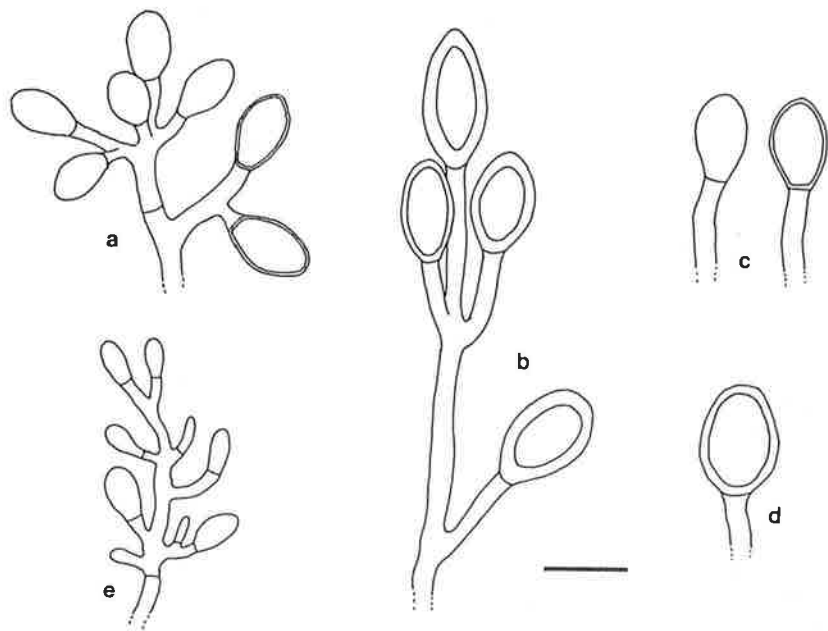


Fig. 10.3. Various types of conidia and transitions between them in *Sporotrichum*.  
 a-d. Blastoconidia to chlamydoconidia. e. Blastoconidia to arthroconidia.  
 Bar = 10  $\mu\text{m}$ .

Both arthroconidia and intercalary chlamydoconidia arising from undifferentiated hyphal cells occur throughout the holobasidiomycetes. Their occurrence is often not constant within strains of a species and they often can be induced (e.g., chlamydoconidia by growing strains in unfavourable conditions). Degenerated strains more often produce arthroconidia than do fresh isolates, and monospore cultures more often than dikaryotic strains. Combinations of chlamydoconidia and arthroconidia on undifferentiated conidiophores occur rather frequently in trametoid genera like *Dichomitus* Reid, *Lenzites* Fr., *Pycnoporus* P. Karst. and *Trametes* (Stalpers, 1978), but are also found in *Coprinus cinereus* (Schaeff.: Fr.) S. F. Gray.

The genus *Punctularia* Pat. presents a very clear case of transition between arthroconidia and chlamydoconidia. *P. strigoso-zonata* (Fig. 10.2 c) develops cylindrical arthroconidia that are separated by empty cells. Even after dehiscence, the conidia remain cylindrical or rounded off only at the ends. In *Punctularia atropurpurascens* (Fig. 10.2 d) the conidia are also separated by a sterile cell, but some swelling occurs in the early stages. These conidia, which are arthric in origin, become ellipsoid and somewhat

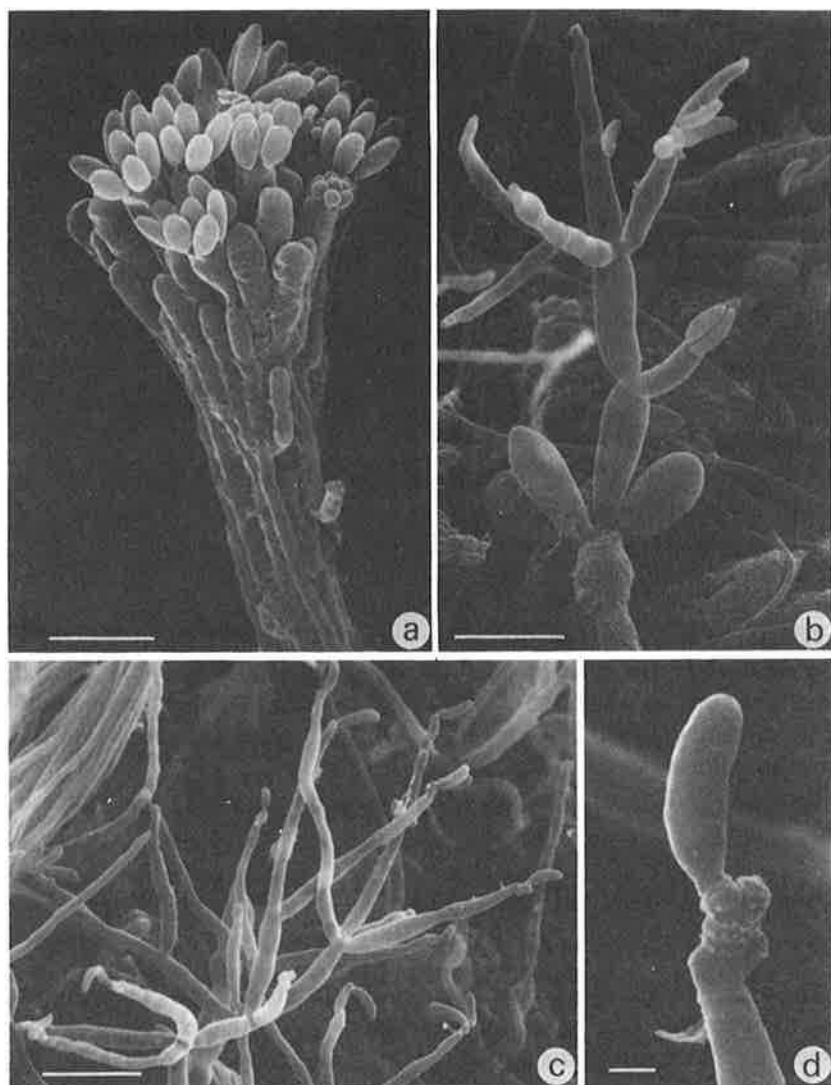


Fig. 10.4. *Pachnocybe* sp., CBS 564.83.

a. Synnema with apical layer of conidiogenous cells. b. Branched chain of swollen cells. c. *Sporothrix*-like conidiophores. d. Detail of conidiogenous cell with both sympodial and percurrent conidiogenesis. Bar represents 10  $\mu$ m for a-c; 1  $\mu$ m for d.

thick-walled after dehiscence and are described as chlamydospores (Sen, 1973) or blastoconidia (von Arx, 1973).

*Sporotrichum* also displays a good example of transitions (Stalpers, 1984). Fresh isolates of *S. pruinosum* Gilman & Abbott produce blastoconidia, cylindrical arthroconidia, and large chlamydospores. The blastoconidia often become thick-walled after or sometimes before dehiscence and then function as chlamydospores. Figure 10.3 illustrates these spores, typical chlamydospores, which are formed terminally on supporting hyphae, and intermediates. Older strains often develop less swollen blastoconidia, and sometimes they do not or hardly swell before a septum is laid down and thus are terminal arthroconidia; moreover they remain thin-walled (Fig. 10.3). Typical arthroconidia may, on the contrary, become ellipsoid and thick-walled and are then indistinguishable from mature blastoconidia.

A very peculiar case of pleoanamorphy is found in a species that is tentatively identified as *Pachnocybe* sp. It shows four types of conidia. The first type consists of synnemata with an apical layer of conidiogenous cells on which up to 10 blastoconidia are formed synchronously on small denticles (Fig. 10.4 a). The second type consists of branched chains of swollen cells that fall apart and function as diaspores (Fig. 10.4 b), and finally there is a *Sporothrix*-like type of conidiogenous cell (which may be derived from type two) on which the conidia may be formed either sympodially or percurrently (annellidic, Fig. 10.4 c-d). Both types are present on the same conidiogenous cell (Fig. 10.4 d).

Berthier (1976) described both sympodial and percurrent conidiogenesis for *Typhula*.

## 10.5 HOMOLOGIES BETWEEN ANAMORPHIC AND TELEOMORPHIC STRUCTURES

The basidiolate, the subglobose to narrowly clavate cell, which may function as precursor of a basidium, is probably (with the exception of the hyphal tip) the most plastic structure in the basidiomycetes. Normally, its nucleus undergoes a meiotic division, but if this does not occur, the following patterns of development are known:

- a) The development of the cell ceases without further modifications: it is then a cystidiolate, morphologically indistinguishable from a young basidium.
- b) Some morphological changes (*e.g.*, elongation, differentiation of the apex, swelling) take place and the cell becomes a cystidium.
- c) The cell becomes an acanthocephidium, which is covered with hyphal pegs; it varies from nearly hyphoid (*e.g.*, *Stereum* Pers.: Fr. s.str.) to

broadly clavate (e.g., *Aleurodiscus penicillatus* Burt, *Mycena* spp.). In some species all transitions between acanthohyphidia and fertile basidia are known, for example, *Aleurodiscus delicatus* Wakef. (Oberwinkler, 1965) and *A. penicillatus* (Lemke, 1964).

d) The cell becomes a dendrohyphidium, which is densely branched apically. Here also a continuum exists between hyphoid (e.g., *Peniophora* Cooke, *Vuilleminia* Maire) and clavate (e.g., *Pulcherricium* Parm.). There are transitions between acanthohyphidia and dendrohyphidia (e.g., *Aleurodiscus botryosus* Burt) and also between dendrohyphidia and fertile basidia, (e.g., *Pulcherricium coeruleum* (Lamarck: Fr.) Parm., Jülich, 1974).

e) There are indications, that a basidiole may also become a dextrinoid, dichotomously branched dichohyphidium as known in the Lachnocladiaceae (cf. Boidin *et al.*, 1980, for *Vararia abortiphysa* Boid. & Lanquetin).

f) The basidiole may be liberated and function as a conidium.

#### 10.5.1. Homology of conidia with basidia

Several observations support the hypothesis that conidia may be homologous with basidia. Examples of such a homology are found in species with broadly attached blastoconidia, for example, *Allescheriella* Henn., *Confistulina* Stalpers, and *Sporotrichum*.

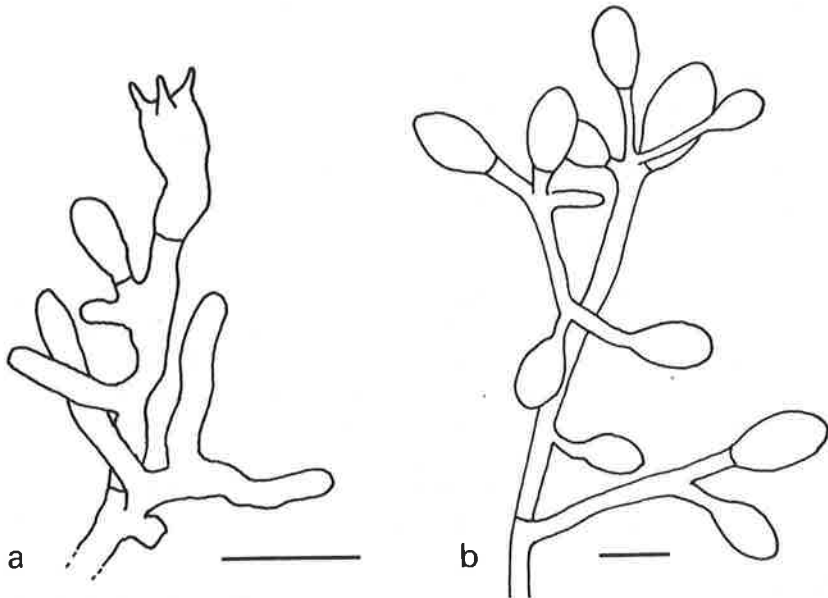


Fig. 10.5. Branching patterns.

a. Basidiogenous hypha of *Phanerochaete chrysosporium*. b. Conidiogenous hypha of *Sporotrichum aurantiacum*. Bars = 10  $\mu$ m.

a) The branching of basidiogenous and conidiogenous hyphae is similar. This is demonstrated by the branching pattern of these structures in, for example, *Sporotrichum pruinosum* and its teleomorph *Phanerochaete chryosporium* Burdsall (Stalpers, 1984; Fig. 10.5), in *Allescheriella crocea* (Mont.) Hughes and its teleomorph *Botryobasidium croceum* Lentz (Lentz, 1967), and in *Michenera artocreas* Berk. & Curt. and its teleomorph *Licrostroma subgiganteum* (Berk.) Lemke. Hughes (1951) illustrated a species of *Botryobasidium* (as *Pellicularia pruinata* (Bres.) Rogers) with basidia and *Haplotrichum*-conidia at the same hypha.

b) The shape of immature basidia and conidia is comparable. Both are subglobose in *Botryobasidium croceum* and *Allescheria crocea*; the basidioles of *Pycnoporellus metamorphosus* (Fuckel) Stalpers and the conidia of its anamorph *Sporotrichum aurantiacum* are ellipsoid to subclavate.

c) The maximum number of nuclei in the blastoconidia of *Sporotrichum* is eight and that number is only found in mature conidia. In young basidia (before the sterigmata are fully developed) eight nuclei can also be found.

#### 10.5.2. Homology of conidia with basidiospores

Many observations justify the hypothesis that conidia can be homologous with basidiospores. The best known example is found in the genus *Spiniger*. Conidiogenesis can be compared with sporogenesis along four stages:

##### A. Conidiophore versus basidium

Corner (1948) distinguished seven stages in the development of the basidium, viz., 1) inception (the preliminary hyphal stage), 2) charging (the filling with dense cytoplasm), 3) condensation of storage material, 4) initial vacuolation of the full-sized basidium, 5) development of sterigmata, 6) development of spores, and 7) discharge of spores and collapse of the basidium.

The first three stages (inception, charging, and initial vacuolation) are quite similar in normal holobasidia (e.g., *Oudemansiella*, *Coprinus*, *Schizophyllum* Fr.) and some types of conidiophores (e.g., *Spiniger*). Even if inception also is considered to comprise the insertion of the young basidium between pre-existing basidia, then this is also found in conidial specimens of, e.g., *Laurilia sulcata* (Burt) Pouzar and *Heterobasidion*. At the apex of young basidia and conidiophores there is a concentration of membrane-bound vesicles. The amount of lipids and/or glycogen increases.

##### B. Denticles versus sterigmata

There are some differences in the development of the sterigmata compared with the denticles of *Spiniger*, as the position of the sterigmata is more or

less fixed at a similar distance from each other and from the centre of the apex, while that of the conidiogenous denticles seems to be random. There are several reports, however, of a more random development of sterigmata, both in the Hymenomycetes, for example, basidia with supernumerary sterigmata in *Phanerochaete chrysosporium* (Stalpers, 1984) and more commonly in the Gasteromycetes (e.g., *Crucibulum* Tul.), where even more than eight spores may be produced on a single basidium. The irregularly spaced sterigmata of *Exobasidium* Woronin were often interpreted as conidiogenous denticles.

The development of sterigmata seems to be similar in most major groups of the Basidiomycetes: when the basidium has reached its full size, small conical initials are formed, after which the two inner wall layers break through the outer wall layers and form a tube-like structure. Sterigmata are thus endogenous structures and the sterigmal wall is thinner than that of the basidium. The original basidial wall consists of 4 layers, the wall of the young sterigma of 2 layers. This has been reported for *Thanatephorus cucumeris* (Frank) Donk (Tu *et al.*, 1977), *Auricularia fuscusuccinia* (McLaughlin, 1980), *Tulasnella* sp. (McLaughlin, 1980), and *Ustilago maydis* (DC.) Corda (Ramberg and McLaughlin, 1980). McLaughlin (1982) and Yoon and McLaughlin (1984) found no rupture in *Coprinus cinereus* and *Boletus rubinellus* Peck, respectively, but did report a gradual attenuation of the outer layer(s).

The descriptions given by Cook (1977) and Hanlin (1982) of the formation of conidial denticles in *Spiniger meineckellus* (Olson) Stalpers (teleomorph: *Heterobasidion annosum* (Fr.) Bref.) agree in detail with the development of sterigmata in *Thanatephorus cucumeris*. The initial is four-layered, but the two outermost layers become thin and rupture. The denticles are two-layered and have a thinner wall than the conidiophore.

### C. Dehiscence

In the Holobasidiomycetes two types of basidiospore dehiscence are generally recognized: active liberation when the spores are shot off (ballistospores) and passive liberation when the spores fall off (statismospores). The first type is generally found in the Agaricales and the Aphyllophorales and the second type is seen in the Gasteromycetes. In the Aphyllophorales, however, specimens are occasionally found with deviating basidia in which the spores are not actively discharged; in such cases the sterigmata are underdeveloped or nearly lacking and the whole structure can be (and has been) mistaken for a *Spiniger* anamorph.

Actively discharged conidia also occur in the holobasidiomycetes, but only as "secondary spores" arising from basidiospores; they are not known from basidium-like conidiophores (except in the case of haploid

apomixis). In *Spiniger* and related anamorphs the discharge is always passive, that is, the conidia fall off.

The development of sterigmata has been the subject of several studies, those with an active discharge (*e.g.*, Wells, 1965; Oláh and Reisinger, 1974; McLaughlin, 1977) as well as those with a passive discharge (*e.g.*, Perreau, 1977). The ontogeny is quite similar up to the development of the hilar appendage in the ballistospores, which leads to the asymmetrical position on the sterigma. The spores are separated from the sterigma by a solid double septum. The development of the conidial denticles in *Spiniger* seems to be comparable to that of the sterigmata of passively discharged basidiospores as far as can be concluded from the TEM micrographs of Cook (1977) and Hanlin (1982).

#### D. Conidia versus basidiospores

Basidiospores, as well as conidia of the *Spiniger*-type, develop synchronously and the nuclei inside the basidium or conidiophore migrate simultaneously into the sterigmata or denticles.

The wall structure of the basidiospores of *Heterobasidion annosum* is completely comparable with that of the *Spiniger* conidia. In Keller's photographs (Keller, 1973) four layers can be distinguished in the basidiospore wall: an innermost electron transparent layer (corium, endosporium), followed by a granular to nearly lamellar thicker layer (coriotunica, episporium); the next layer ("ligne c", perisporium) is electron transparent and displays thickenings, which form the ornamentation, and the outer layer (tunica, ectosporium) is electron dense and often somewhat thickened at the apices of the ornamentation. Often a sporothecium is present, which generally is not continuous and may consist of the remnants of the old sterigmal wall. TEM photographs of the conidia of *Spiniger meineckellus* were published by Cook (1977) and Hanlin (1982) and they show layers similar to those of the basidiospores.

The shape of the conidia of a *Spiniger* anamorph is nearly identical with that of the teleomorph basidiospores. The conidia are more symmetrical, because the point of attachment is on the longitudinal axis contrary to the asymmetrical apiculus of the basidiospores. Conidia also tend to be slightly more elongated and narrowed towards the base than the respective basidiospores. For example, *Bondarzewia montana* (Quél.) Sing has globose conidia and basidiospores (Keller, 1979): in several species of *Dichostereum* (*Vararia* s.l.) the basidiospores are globose and the conidia globose to broadly pyriform; *Heterobasidion annosum* has broadly ellipsoid spores and ovoid to pyriform conidia; the basidiospores of *Laurilia sulcata* are subglobose, while its conidia are ovoid to narrowly pyriform; and both

the conidia and the basidiospores of *Hyphoderma mutatum* (Peck) Donk are cylindrical.

The ornamentation of the conidia is comparable to that of the basidiospores, but as a rule is less pronounced in the former. The basidiospores of *Bondarzewia berkeleyi* (Fr.) Bond. & Sing. have distinct ridges, but the conidia are warted or have low ridges; the basidiospores of *Laurilia sulcata* are echinulate (Eriksson and Ryvarden, 1976), but the conidia are warted. The basidiospores of *Heterobasidion annosum* are warted, but the conidia are smooth when examined with the light microscope; the electron microscope, however, reveals a minute ornamentation (Cooke, 1977; Hanlin, 1982).

The reaction of the basidiospores with Melzer's reagent is comparable to that of the conidia, but when positive it is stronger in the basidiospores. The intensity of the amyloid reaction seems to be correlated with the degree of ornamentation. The wall layer responsible for the ornamentation is the perisporium, which is very thin in smooth spores or conidia. The basidiospores of *Bondarzewia* and *Laurilia* are strongly amyloid, as are the conidia of *Bondarzewia berkeleyi*, but those of *Laurilia sulcata* are only weakly amyloid. The basidiospores of *Heterobasidion annosum* are very weakly amyloid (Stalpers, 1979) and the conidia do not react at all.

## 10.6 HAPLOID APOMIXIS

A special kind of anamorph occurs in fungi with haploid apomixis, also known as haploid fruiting. Here basidia are formed, which in all respects resemble normal basidia except that no sexual processes take place. The spores are thus mitospores (conidia) and not meiospores. The phenomenon is well known in higher basidiomycetes such as *Schizophyllum commune*, *Athelia rolfsii* and *Flammulina velutipes* (Curt.: Fr.) Sing. (Prillinger, 1982).

Besides haploid apomixis, which is a mitotic process, also autogamy may occur with an ensuing meiosis.

## 10.7 CONCLUDING REMARKS

The term anamorph is here used for discrete vegetative modifications or asexual sporulating structures of a fungus that can occur independently from other structures. Whether such a morph should be named separately, cannot be ruled by the Code. The experienced mycologist has to decide whether the heuristic advantages outweigh the burden of an increasing number of names.

In the past sterile morphs, for example, rhizomorphs or abortive basidiomata, have been named and subsequently forgotten. When such structures are unequivocally connected with a particular teleomorph and no suitable taxa exist to classify the anamorph (e.g., *Acurtis gigantea* (Schw.: Fr.) Fr. with *Entoloma abortivum*) then a separate naming is meaningless.

However, changing taxonomy may also change such a supposed connection. For example *Rhizomorpha fragilis* Roth: Fr. has generally been considered as an anamorph of *Armillaria mellea*. However, this is proven to be a species aggregate consisting of at least five species, and the status of *R. fragilis* is no longer unequivocal; thus now there may be reasons to use the anamorph name, especially at the generic level. Conversely, the genus *Rhizostroma*, used for hyphal strands of either *Phallus* or *Oudemansiella*, is of little use as the fungi in question cannot be recognized reliably by these structures.

The situation is completely different in cases of haploid apomixis. Fertile "fruitbodies" strongly resemble the teleomorphic basidiomata, only differing sometimes in the lack of clamp connections and more variable numbers of sterigmata. Generally these fruitbodies can be identified with keys to the teleomorphs and can be provided with teleomorphic names, at least at the generic level. Thus, although they are anamorphs, there is no need to classify such species in an anamorphic system.

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