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THE BLACK YEASTS AS DISEASE AGENTS: HISTORICAL PERSPECTIVE[1]

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The black yeasts have been recognized as disease agents only in recent years. They are of interest to medical mycologists because they are potentially pathogenic to humans and are capable of causing a wide range of diseases, some of which are life threatening. Much confusion has surrounded the classification of these fungi because their diverse growth forms and means of asexual reproduction are difficult to study and interpret. This article discusses the taxonomic position and roles as disease agents of the five species: Aureobasidium pullulans, Exophiala jeanselmei, E. spinifera, E. werneckii, *and* Wangiella dermatitidis.

The bipartite term "black yeasts" merits definition before we proceed any further with this topic, since its second component is used in a very special sense. Classically, yeasts are defined as fungi that are primarily unicellular and that multiply asexually by a process of budding or partitioning.

In the context of this presentation, the black yeasts or "levaduras pretas" (*44*) are defined as dematiaceous, filamentous fungi which, in certain stages of their development or under certain environmental conditions, have a unicellular phase during which multiplication is by a budding process. The colonies at this stage are pasty with some shade of black.

The black yeasts are of interest to medical mycologists because they are potentially pathogenic to humans and are capable of causing diseases that range in severity from the mild and superficial to those that involve vital organs and hence jeopardize the life of their hosts. These fungi have proved to be difficult to classify taxonomically because their diverse growth forms and means of asexual reproduction are difficult to study and interpret.

I will discuss the most recent concepts regarding the taxonomic position of these fungi, and, briefly, their roles as disease agents. The five species of black yeasts that are of medical interest are listed in Table 1. Each species will be discussed in the sequence shown.

Aureobasidium pullulans (De Bary, 1866) Arnaud, 1910

This black yeast is probably the most widely distributed and frequently encountered of the group. It has a global distribution and occurs as a plant pathogen and an agent of decay on a wide variety of substrates (*12*). As a result, its spores are ubiquitous, and *A. pullulans* is frequently encountered as a contaminant in diagnostic laboratories. Only in recent years has pathogenicity been attributed to this fungus.

On rare occasions, *A. pullulans* has been considered to be the etiologic agent of such diseases as cheloidean blastomycosis, keratitis, onychomycosis, otomycosis, pulmonary infections, and tinea capitis (*21, 42*). However, there is a reason to suspect that in most, if not all of these cases, the isolates played the role of contaminants rather than

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Table 1. Black yeast of medical interest

Genus and species	Associated disease
Aureobasidium pullulans	Phaeohyphomycosis
Exophiala jeanselmei	Mycetoma, phaeohyphomycosis
E. spinifera	Phaeohyphomycosis
E. werneckii	Tinea nigra
Wangiella dermatitidis	Phaeohyphomycosis

pathogens. The mere isolation, even if repeated, of a fungus from a lesion or from clinical material does not per se establish the isolate as a pathogen. The investigator must find and demonstrate fungal elements in the clinical material, along with a host-tissue response that correlate with the morphological and physiological properties of the isolate.

The skin infection discovered in a wild porcupine (*Erethizon dorsatum*) and described by Salkin, Gordon, and Stone in 1976 (*42*) as being caused by *A. pullulans* was well documented and represents an excellent example of phaeohyphomycosis (*2, 3*). The tissue sections contained a mixture of dematiaceous mycelial fragments and yeast-like budding cells.

In an exhaustive monograph Cooke (*13*) compiled a list of 36 synonyms of *A. pullulans* that date back to 1866. These were classified in 18 different genera. This plethora of names stemmed from the failure of some workers to correlate their isolates with previously isolated and described fungi or from the way in which they visualized and interpreted conidium ontogeny, in their isolates. Kendrick and Carmichael (*26*) basically define the genus *Aureobasidium*, with *A. pullulans* as its type species, as producing amerospores, i.e., single-celled conidia, in slimy heads or masses from hyaline or dematiaceous mycelium. As described in detail by Cooke (*12*) the unicellular conidia are borne on papillae that are produced from the inner wall of the mycelium. These spores are hyaline and ovate and pointed at the base.

Colony expression varies widely, depending on the isolate and the growth medium used. Young colonies on Sabouraud's agar are moist, yeast-like, and cream colored. They become blackish as they grow. At this stage they are composed almost exclusively of unicellular cells that reproduce by a budding process. With age, mycelium develops that become septate and dark walled, and the colony becomes velvety and black. Thick-walled chlamydospores are commonly produced along with arthrospore-like cells and the previously described amerospores.

Exophiala jeanselmei (Langeron, 1928) McGinnis and Padhye, 1977

This commonly encountered fungus is one of the few pathogenic moulds that have two different tissue forms. It forms eumycotic black granules in one set of circumstances and dematiaceous mycelium in another. Development of these forms presumably is dependent upon the internal environment of the site invaded.

When *E. jeanselmei* enters the body through some traumatic incident, such as a thorn prick, a mycetoma may ensue in which it develops in the form of black granules. In marked contrast, when inhaled and disseminated in the lungs and other internal organs, it does not produce granules. Instead, the fungus develops and exists in the form of dark-walled mycelial filaments. Such systemic infections come well under the definition of phaeohyphomycosis.

As a saprophyte, *E. jeanselmei* is quite common in nature throughout the world. In the laboratory, it is frequently encountered as a contaminant. But it is also an opportunistic fungus with latent pathogenic properties that permit it to survive and de-

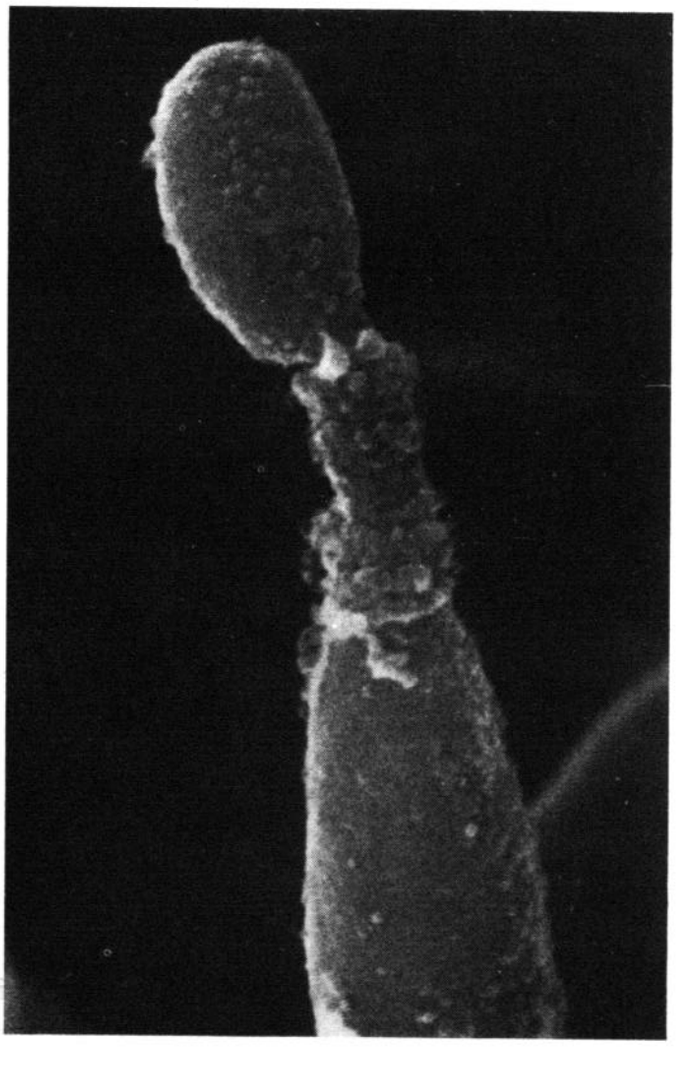
velop in a compromised host. *E. jeanselmei* has been usually referred to as *Phialophora jeanselmei*. But as McGinnis and Padhye noted in a recent publication (*34*), this fungus does not fit into the modern concept of the genus *Phialophora*. Instead, they found that it could well be placed in the genus *Exophiala,* a genus first described by Carmichael in 1966 (*10*).

The fact that *E. jeanselmei* has two different tissue forms has created diagnostic and taxonomic confusion. Infections in which the etiologic agent developed in the form of black granules have been considered to be caused by *P. jeanselmei*. When the fungus was mycelial in tissue, however, it has been variously identified as *Sporotrichum gougerotii* or *P. gougerotii*.

As McGinnis and Padhye (*34*) clearly pointed out, *P. gougerotii* (Matruchot, 1910; Borelli, 1955) started out as a variant of *Sporothrix schenckii* with Matruchot's informally proposed name of *S. gougerotii*. In 1966 an isolate from a case of "sporotrichosis," which in retrospect should be considered a case of phaeohyphomycosis, was identified as *S. gougerotii* by Young and Ulrich (*48*). This culture was studied by Borelli in 1955 (*8*) and designated as the neotype of *S. gougerotii* to replace the lost type culture. Borelli compared the neotype of *S. gougerotii* with isolates of *Hormiscium dermatitidis* and *P. jeanselmei* and concluded that all three were identical. On the basis of supposed priority, the new combination of *P. gougerotii* was formally proposed for this fungus.

The careful study of 16 isolates of "*P. jeanselmei,*" including Langeron's 1928 type, three of "*P. gougerotii,*" and other dematiaceous fungi, led McGinnis and Padhye (*34*) to conclude that "*P. gougerotii*" and "*P. jeanselmei*" were indeed conspecific but that *Hormiscium dermatitidis* was a distinct, but improperly classified species.

Their studies revealed that the conidia of "*P. jeanselmei*" did not arise from phialides with collarettes but from annellides.[3] Since *Exophiala* (Carmichael, 1966) was the only described genus of dematiaceous fungi that produced conidia from annellides, "*P. jeanselmei*" was transferred to that genus and



Electron micrograph of the conidiophore of *Exophiala jeanselmei*. The annellides in successive layers that characterize the conidiogenous cells of genus are clearly revealed below the newly formed conidium. X 21,800 (photo: courtesy of Dr. Gary T. Cole, University of Texas, Austin).

[3]Kendrick (*25*) defines an annellide "as a conidiogenous cell which produces a single blastic conidium from the apex of each of a succession of percurrent vegetative proliferations (annellations) involving the half septum remaining after secession of the previous conidium."

named *E. jeanselmei*. "*P. gougerotii*" in Borelli's sense becomes a synonym for *E. jeanselmei,* and, as we shall see later, *H. dermatitidis* emerges as a valid species within a new genus.

Most isolates of *E. jeanselmei,* at first, produce moist, soft, black, yeast-like colonies. As they age, aerial mycelium develops that becomes greyish black.

The young colonies are frequently completely composed of blastospores, but, in time, septate dark-walled mycelium develops. These hyphae eventually give rise to simple conidiophores from lateral or terminal positions. They are elongate, tapered structures from whose extremities unicellular, subglobose to ellipsoidal conidia are produced. They are smooth and hyaline. These spores tend to aggregate at the tip of the conidiophore and then slip down its side and on down to the side of the hyphae.

E. jeanselmei can be considered to be a trimorphic fungus. In vitro it is a spore-forming mould with a transient yeast-like form. In vivo it either forms black granules (*35, 36, 38*) or develops dematiaceous mycelium (*14, 17, 31, 48*). As a granule-producing pathogen, it causes mycetomas. In its mycelial tissue form, it causes phaeohyphomycosis.

Petriellidium boydii and certain dermatophytes can also be said to be trimorphic in the sense just described. In systemic infections, *P. boydii* forms hyaline, septate mycelium (*29, 41*), but it produces white granules in mycetomas (*1, 47*). In culture, it is, of course, mycelial and produces amerospores and ascospores. Four species of dermatophytes: *Microsporum canis* (*16*), *M. ferrugineum* (*7*), *Trichophyton mentagrophytes* (*16*), and *T. verrucosum* (*9*) have been found to produce mycetomas of the scalp in which granules were formed.

E. jeanselmei is thus not unique in the diversity of its tissue expression. Until this became known, however, each tissue form had been attributed to a different fungus species.

E. spinifera (Nielsen and Conant, 1968) McGinnis 1977

In 1968 Nielsen and Conant (*37*) isolated and described a new pathogenic fungus from a nasal lesion in an elderly woman. Histological sections revealed a minimal amount of dematiaceous hyphae and numerous ovoid, budding cells—characteristics that permit the infection to be classified as phaeohyphomycosis.

Nielson and Conant described and illustrated the formation of phialides with collarettes as well as attenuated conidiophores that resembled those of *E. jeanselmei*. On the basis of these observations, the fungus was classified in the genus *Phialophora* and it was described as a new species: *P. spinifera.*

In 1977 McGinnis published the results of his study of the only known human isolate of *P. spinifera* (*32*). He found that its conidiophores were annellides, and he did not observe any *Phialophore*-type conidiophores. For these reasons, the fungus was transferred to the genus *Exophiala.*

Young colonies of *E. spinifera* are mucoid and black. At maturity they become velvety and greenish black. The mycelium is septate and dematiaceous, and the conidiophore-bearing hyphae are generally differentiated from the purely vegetative ones. Conidiogenous cells are elongated and closely annellated. The conidia or annelloconidia are nonseptate, subglobose, ellipsoidal to cylindrical. They are smooth, hyaline, and average 1.7 x 2.5 μ. These spores tend to aggregate in masses around the conidiophore tips and slide down and settle along the sides of the mycelium.

In 1973 Mackinnon and his coworkers (*30*) reported on their studies of five cultures of *E. spinifera* that had been isolated from a variety of natural substrates in Uruguay. These investigators found that their isolates as well as Nielsen and Conant's produced mucoid colonies on Czapek's agar that slid down the agar slope. Microscope

examination of this growth revealed that it was made up of yeast-like cells. Surprisingly, these were surrounded by a clear-cut capsule that was up to 5 μ thick. India ink preparations were used to make the capsules readily visible not only with this species but with an isolate of *E. jeanselmei* and young isolates of *A. pullulans.*

E. werneckii (Horta, 1921) Arx, 1970

E. werneckii has been classified as a *Cladosporium* species ever since Horta first described it in 1921 (*19*). It is well known as the etiologic agent of the superficial mycotic disease called tinea nigra. In this infection, which is common in tropical climates but not unknown in temperate zones, the fungus develops in the stratum corneum in the form of septate, dematiaceous mycelium.

It has never been clear to me why this fungus was ever classified in the genus *Cladosporium* in the first place. Certainly conidiophores of the type that characterize that genus have never been described or clearly depicted. In 1970 (*4*) Arx transferred *C. werneckii* to the genus *Exophiala* without comment, but in a personal letter to Dr. Michael McGinnis he told of having observed annellides in the isolates studied. Previously, in 1952, Vries (*46*) had stated that "this species—has nothing to do with *Cladosporium,*" and because he thought that it had great similarity to *Pullularia pullulans,* he transferred it to that genus as *P. werneckii.*

A definitive description of conidium ontogeny for *E. werneckii* cannot be found in the literature. In one United States medical mycological textbook, sporulation (*40*) is described as being "typical of the genus *Cladosporium;*" another (*15*) stated that "sporulation on arborescent conidiophores of the *Cladosporium* type may be found." Even though misinterpreted, however, the conidiophores of *E. werneckii* have been fairly well depicted in recent publications (*11, 43*). From those illustrations and personal experience with isolates of *E. werneckii,* we can describe this fungus as follows: early growth on a variety of media is black, moist, shiny, and altogether yeast-like. Microscopic examination at this time will reveal that the growth is made up of unicellular cells that bud. As development proceeds, submerged hyphae begin to appear at the periphery of the colonies. Mycelium continues to be produced and, eventually, the colony becomes velvety and greenish black.

Examination of the mycelial form will show that the filaments are dematiaceous and septate. In addition, simple, elongated conidiophores, with tapered tips, develop. The conidia that they bear are, in the main, unicellular, but two-celled conidia, with a conspicuous dark cross wall are also produced. As the conidia are produced from the generative apex of the conidiophore, they are cut off by the formation of a cross wall. Successive budding gives rise to a series of superimposed rings. Thus, the conidiophore of *E. werneckii* is an annellophore and not a phialide and certainly not the branched, tree-like conidiophore that typifies the genus *Cladosporium* (*6*). The development of annellides precludes any affinity to the genus *Aureobasidium.* In that genus, conidia arise from short denticles that develop on vegetative hyphae.

Bud formation in the yeast form of *E. werneckii* was studied with light and electron microscopy by Gustafson, Hardcastle, and Szaniszlo in 1975 (*18*). They found that successive budding results in the formation of collars around the tip of the conidiophore. These investigators stated that these collars resembled "the annellations found in the annellophores of certain Hyphomycetes." The isolated blastospores thus are really annellides.

In summary, spore formation in *E. werneckii* is fundamentally different from that which occurs in the *Cladosporium* species. In the latter genus, conidia are formed in acropetalous succession as blown-out ends of

branching conidiophores. From each branchlet, a branched chain of blastospores develops. In Barron's (*6*) classification scheme, the genus *Cladosporium* falls into the Blastosporae series, and *Exophiala* would be in the Annellosporae series.

In 1976 Volcan and his coworkers (*45*) reported that an isolate of "*C. werneckii*" developed fruiting bodies that resembled perithecia when grown on enriched corn meal agar. On the basis of their description of these bodies and their photomicrographs, these structures can better be described as pycnidia. The development of pycnidia remains to be confirmed in other isolates of the agent of tinea nigra.

Wangiella dermatitidis (Kano, 1934) McGinnis 1977

In 1934 Kano (*23, 24*) isolated and described a dematiaceous mould that he had isolated from a chronic lesion on a woman's face. Skin scrappings and histological sections revealed the presence of short chains of thick-walled, dark brown spores, 6-10 μD. Although Kano designated the infection to be chromoblastomycosis, he was aware that it was atypical and went on to say that the case was a special kind of chromoblastomycosis. As I stated in a previous paper (*2*), Kano's case should properly be classified as phaeohyphomycosis rather than chromoblastomycosis. Such a classification is strongly supported by the tissue forms of *W. dermatitidis* described in subsequent cases from various parts of the world and in experimentally infected animals (*22*).

In his extensive study of the type culture of Kano's isolates of *Hormiscium dermatitidis* as well as eight other human isolates and one soil isolate, McGinnis (*33*) confirmed the findings of Oujezdsky and Szaniszlo (*39*) that the conidiophores produced by this fungus were phialides without collarettes. Since members of the genus *Phialophora* produce their spores from phialides with a constricted neck and a terminal collarette and the *Exophiala* species produce annellides, Kano's fungus could not be classified in these two genera. Accordingly, the new genus *Wangiella* was created to accommodate this black yeast.

Most young colonies of *W. dermatitidis* initially are yeast-like, being pasty, smooth, and black. A black diffusable pigment is produced that discolors the agar and spreads beyond the periphery of the colony. Microscopic study of the growth at this stage reveals unicellular yeast cells that bud. In shape, the cells range from ovoid to elliptical. Some may be greatly enlarged and irregular in form. Young cells are hyaline and thin walled, but the mature ones are dematiaceous and thick walled.

As growth progresses mycelium is developed and the colonies become mould-like. At this stage flask-shaped conidiophores designated as phialides without collarettes are produced. The phialoconidia are smooth, nonseptate, obclavate, and pale brown. These spores accumulate as globose heads at the tip of the phialides or slide down its sides.

The synonymy of *W. dermatitidis* is relatively short. Previous to McGinnis' study it had been classified in four different genera, starting with *Hormiscium* by Kano in 1934 and subsequent transfers to *Fonsecaea* in 1950, *Hormodendrum* in 1954 and *Phialophora* in 1963 by Carrion, Conant, and Emmons, respectively (*33*).

SUMMARY

The black yeasts came to be recognized as disease agents only in recent years. *A. pullulans*, of limited, if not dubious, pathogenicity, was first implicated as a possible disease agent in 1921 by Ashikaga (*5*), although it was first identified as a new fungus species 55 years previously, in 1866,

by De Bary (*13*). *E. jeanselmei* was concurrently described as a disease agent and a new species in 1928 by Langeron (*28*). *E. spinifera* is the most recently described of the five black yeast species under discussion. It was first encountered as a disease agent and recognized as a new species in 1968 (*37*). Soil isolates were later reported by Mackinnon, et al. from Uruguay in 1973 (*30*). The other *Exophiala* species, *E. werneckii,* was also first encountered in 1921 as a disease agent (*19*). This fungus apparently was first isolated from soil (beach sand) in 1969 on the island of Oahu, Hawaii, by Kishimoto and Baker (*27*). *W. dermatitidis* is another of the quintet of "leveduras pretas" that was first encountered as a pathogen. Kano described his isolates as a new species in 1934 (*23*). Although *W. dermatitidis* undoubtedly exists in nature as a saprophyte or plant pathogen, there are no published records of its isolation from soil or plant material.

The synonymy that these moulds have accumulated in a comparatively short period is a reflection of the problems various investigators have encountered in observing and interpreting their microscopic morphology. Only through the adoption of the new approach to the classification of the Fungi Imperfecti, as developed by Hughes (*20*), has most, if not all, of the confusion surrounding the classification of these fungi been resolved. Doubt, however, has already been expressed by Mackinnon, et al. (*30*) as to whether *E. spinifera* is really distinct from *E. jeanselmei.* As more investigators study conidium ontogeny among the black yeasts and related fungi, a clearer understanding of the taxonomy of these fungi of medical importance will be obtained.

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