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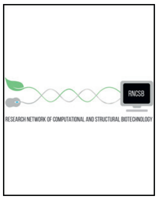

Taxonomy and evolution of *Aspergillus*, *Penicillium* and *Talaromyces* in the omics era – Past, present and future

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ABSTRACT

Aspergillus, *Penicillium* and *Talaromyces* are diverse, phenotypically polythetic genera encompassing species important to the environment, economy, biotechnology and medicine, causing significant social impacts. Taxonomic studies on these fungi are essential since they could provide invaluable information on their evolutionary relationships and define criteria for species recognition. With the advancement of various biological, biochemical and computational technologies, different approaches have been adopted for the taxonomy of *Aspergillus*, *Penicillium* and *Talaromyces*; for example, from traditional morphotyping, phenotyping to chemotyping (e.g. lipotyping, proteotypingand metabolotyping) and then mitogenotyping and/or phylotyping. Since different taxonomic approaches focus on different sets of characters of the organisms, various classification and identification schemes would result. In view of this, the consolidated species concept, which takes into account different types of characters, is recently accepted for taxonomic purposes and, together with the lately implemented 'One Fungus – One Name' policy, is expected to bring a more stable taxonomy for *Aspergillus*, *Penicillium* and *Talaromyces*, which could facilitate their evolutionary studies. The most significant taxonomic change for the three genera was the transfer of *Penicillium* subgenus *Biverticillium* to *Talaromyces* (e.g. the medically important thermally dimorphic '*P. marneffei*' endemic in Southeast Asia is now named *T. marneffei*), leaving both *Penicillium* and *Talaromyces* as monophyletic genera. Several distantly related *Aspergillus*-like fungi were also segregated from *Aspergillus*, making this genus, containing members of both sexual and asexual morphs, monophyletic as well. In the current omics era, application of various state-of-the-art omics technologies is likely to provide comprehensive information on the evolution of *Aspergillus*, *Penicillium* and *Talaromyces* and a stable taxonomy will hopefully be achieved.

1. Introduction

Aspergillus, *Penicillium* and *Talaromyces* are diverse genera which belong to the Order *Eurotiales* and contain a large number of species possessing a worldwide distribution and a huge range of ecological habitats. They are ubiquitous and can be found in the air, soil, vegetation and indoor environments [1,2]. Some members are able to grow in extreme environments such as those with high/low temperatures, high salt/sugar concentrations, low acidities or low oxygen levels [3,4]. Species of the three genera are mainly environmental saprobes [3,4] and the primary contribution of these microorganisms to nature is the decomposition of organic materials [1].

Many *Aspergillus*, *Penicillium* and *Talaromyces* species are economically, biotechnologically and medically important with huge social impacts. For example, these species are vital to the food industry and quite a number of them are exploited to produce fermented food such as cheeses (e.g. *P. roqueforti*), sausages (e.g. *P. nalgiovense*) and soy sauce (e.g. *A. oryzae* and *A. sojae*). These fungi are also important biotechnologically for their strong degradative abilities which have been utilised for the production of enzymes [5,6]. In addition, they are robust producers of a diverse spectrum of secondary metabolites (or extrolites) some of which could be used as drugs and antibiotics or as the lead compounds of potential drug candidates with pharmaceutical or biological activities [7]. On the other hand, many of these species, such as *A. chevalieri*, *A. flavipes*, *P. citreonigrum* and *T. macrosporus*, are food spoiling decomposers which cause pre- and post-harvest devastation of food crops; and many of these food-spoiling species are also mycotoxin-producers [8]. Even worse, some of them are infectious agents and cause diseases in humans and animals. The most notorious

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pathogenic species on a global sense is *A. fumigatus* [9], which is the aetiological agent for the majority of aspergillosis cases [10]. Other commonly encountered pathogenic *Aspergillus* species include *A. flavus*, *A. nidulans*, *A. niger* and *A. terrus*. Although *Penicillium* and *Talaromyces* species are less commonly associated with human or veterinary infections, the thermally dimorphic fungus *T. marneffei*, previously known as *P. marneffei*, is an exception. This notorious fungus is endemic in Southeast Asia and it is able to cause systemic infections particularly in immunocompromised individuals such as HIV-positive patients [11] or patients with impaired cell-mediated immunity [12].

Aspergillus, *Penicillium* and *Talaromyces* were traditionally classified according to their morphologies. As technologies capable of characterising biological macromolecules advanced, various approaches focusing on the profiles of different cellular constituents such as lipids, proteins and exometabolites have emerged to supplement the taxonomy of these fungi. The availability of DNA sequencing technology in the past two-to-three decades has generated an enormous amount of DNA sequence data, allowing fungal taxonomy through phylogenetics, including genealogical concordance. The currently accepted consolidated species concept [13], or informally known as the 'polyphasic taxonomic approach', has revolutionised fungal taxonomy, and the classification scheme for a vast number of fungi has been revised. In particular, significant changes have been made to reclassify *Aspergillus*, *Penicillium* and *Talaromyces* species in the past seven years. Such revision on the classification of these fungi results in redefined species concepts for *Aspergillus*, *Penicillium* and *Talaromyces*, providing new insights on the evolution of these important filamentous fungi. In this article, the development of various taxonomic approaches as well as species recognition and identification schemes for *Aspergillus*, *Penicillium* and *Talaromyces* is reviewed. These include the traditional morphological/phenotypic approach, the supplementary lipidomic, proteomic and metabolomic approaches, as well as the currently widely used phylogenetic/consolidated approach. The clinical implications of this evolving taxonomy are also discussed.

2. Classification and nomenclature: a brief history and recent development

The name *Aspergillus* was first introduced by Micheli in 1729 to describe asexual fungi whose conidiophores resembled an aspergillum, a device used to sprinkle holy water [14] (Fig. 1a–f). Later in 1768 von Haller validated the genus [15] and in 1832 Fries sanctioned the generic name [16]. Similarly, the genus *Penicillium* was erected by Link in 1809 [17] to accommodate asexual fungi which bore penicillum (painter's brush)-like fruiting bodies (Fig. 1g–l).

Although both *Aspergillus* and *Penicillium* were originally described as anamorphic (asexual), some species of the two genera were subsequently found to be ascocarp-forming (Fig. 1c, f and l). For example, the sexual genus *Eurotium* was first firmly connected to *Aspergillus* by de Bary in 1854 [18] whereas the ascomycetous genus *Eupenicillium* has been used to describe *Penicillium* species capable of producing sclerotoid cleistothecia from as early as 1892 [19]. Since the discovery of the various sexual states of *Aspergillus* and *Penicillium* species, it has been controversial as to whether separate sexual generic names should be used to describe species able to produce ascospores. In spite of the fact that several sexual genera had already been established to accommodate the sexual morphs of some *Aspergillus* and *Penicillium* species, Thom, Church, Raper and Fennell, in their monographic masterpieces on the taxonomy of these two genera, neglected the use of sexual names. This was because, in their opinions, this would cause unnecessary nomenclatural confusion, especially for strains which were in sexual stages at first and then lost their ascospore-forming ability under laboratory maintenance. In addition, this would also lead to the fragmentation of the large and obviously cohesive *Aspergillus*/*Penicillium* groups [20–25]. Nevertheless, in order to abide by the then *International Code of Botanical Nomenclature* (*Stockholm Code*), where the first valid names of the 'perfect states' (sexual morphs) of fungi took precedence [26], Benjamin assigned *Aspergillus* species which possess sexual life cycles into the sexual genera *Eurotium*, *Emericella* and *Sartorya* [27]. In addition, he transferred *Penicillium* species with sexual life cycles to the ascomycetous genus *Carpenteles* (later synonym of *Eupenicillium*) [27,28]. During his assignment, Benjamin also established the novel genus *Talaromyces* to describe *Penicillium* species which, in their sexual life cycles, possessed soft ascocarps exhibiting indeterminate growth and whose walls were composed of interwoven hyphae [27] (Fig. 1m–o).

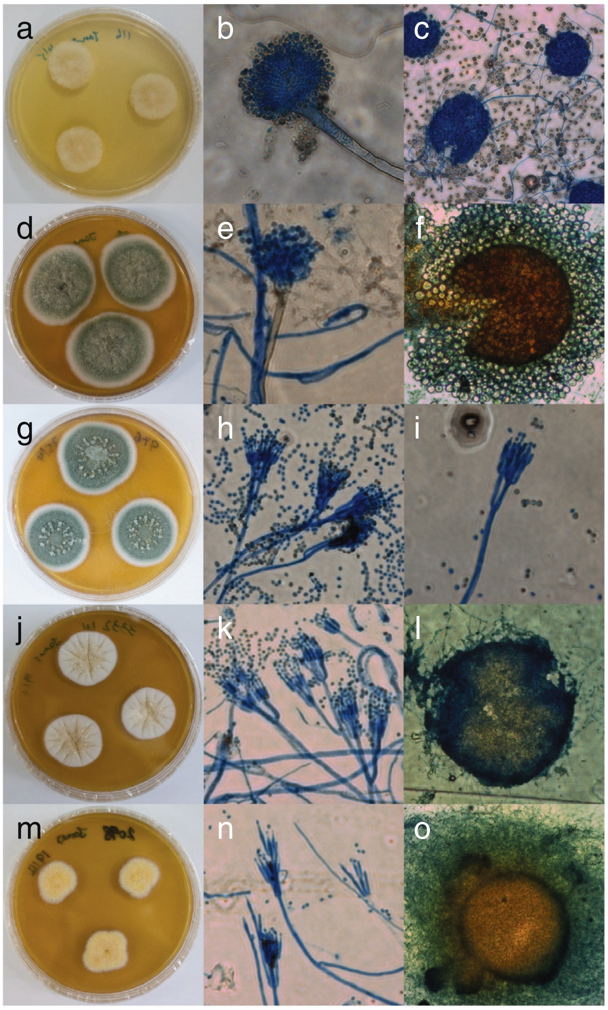

Fig. 1. Morphological features of *Aspergillus*, *Penicillium* and *Talaromyces* species. (a) Colony morphology after 7 days of incubation on dichloran 18% glycerol agar, (b) a conidiophore (magnification 400×) and (c) ascomata (*Eurotium*-like sexual stage, magnification 200×) of *A. glaucus* NRRL 116^T. (d) Colony morphology after 7 days of incubation on malt extract agar (MEA), (e) a conidiophore (magnification 400×) and (f) an ascocarp (*Emericella*-like sexual stage, magnification 100×) of *A. nidulans* NRRL 187^T. (g) Colony morphology after 7 days of incubation on MEA and (h and i) conidiophores (magnification 400×) of *P. expansum* NRRL 976^T. (j) Colony morphology after 7 days of incubation on MEA, (k) conidiophores (magnification 400×) and (l) an ascocarp (*Eupenicillium*-like sexual stage, magnification 100×) of *P. kewense* NRRL 3332^T. (m) Colony morphology after 7 days of incubation on MEA, (n) conidiophores (magnification 400×) and (o) an ascocarp (magnification 100×) of *T. flavus* NRRL 2098^T.

As the number of species of the genera *Aspergillus*, *Penicillium* and *Talaromyces* increased, closely related species were grouped into subgroups [29–32]. Such infrageneric classification system underwent vigorous changes since different authors focused on different morphological features when establishing their subgrouping schemes (Table 1). For example, Blochwitz as well as Thom and his co-workers were the first to divide *Aspergillus* species into seven and 18 subgeneric 'groups', respectively, based on their phenotypes [21,24,30,31]. The