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She loves me, she loves me not: On the dualistic asexual/sexual nature of dermatophyte fungi

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Abstract

Dermatophytes are ascomycetous fungi whose sexuality is greatly influenced by their ecology. Sexual reproduction is ubiquitous among soil-related geophiles and some animal-associated zoophiles. In contrast, anthropophiles are generally present as a single mating type in the population and appear to reproduce asexually. In this article, the current knowledge on the sexuality of dermatophytes including reproduction modes, mating conditions, mating type distributions and the mating type (*MAT*) locus is presented in the context of revised taxonomy and discussed from an evolutionary perspective.

Keywords

Dermatophytes; sexual reproduction; mating; mating type (*MAT*) locus

Introduction

Although costly, sexual reproduction is widespread throughout eukaryotes possible because of its counterbalancing benefits such as the selection of beneficial mutations from a deleterious background and accelerating adaptation in response to changing conditions [1, 2]. Asexuality might provide short-term advantages based on well-adapted genomic configurations, but due to the lack of a mechanism providing adaptation and because of the accumulation of deleterious mutations, asexual species are at an increased risk of extinction. Therefore, the few examples that appear to be asexual have been referred to as evolutionary scandals [3, 4].

Sexual reproduction is pervasive in the fungal kingdom, but approximately 20% of fungi have been referred to as asexual because they do not have a known sexual cycle [5]. Recent

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molecular evidence brings into question whether these species are indeed asexual based on the presence of mating- and meiosis-related genes in the genomes of these presumed “asexual fungi”. In fact, direct or indirect evidence of sexual cycles has been discovered for many of these species. One of the most notable is *Candida albicans*, in which a parasexual cycle was identified involving the fusion of 2 diploid cells to produce a tetraploid cell, which morphs into a diploid/aneuploid state via concerted chromosome loss [6, 7]. Another example is *Aspergillus fumigatus*, a species that has long been regarded as asexual. *A. fumigatus* forms cleistothecia (fruiting bodies) on oatmeal agar after extended incubation time for up to 6 months [8]. The discovery of sexual reproduction in several other *Aspergillus* and *Penicillium* species followed these findings [5, 9].

Sexual reproduction in the Pezizomycotina subphylum of Ascomycota is governed by a single mating type (*MAT*) locus [10,11]. There are 2 alleles of the *MAT* locus, termed idiomorphs, that are completely different in sequence and harbor key transcription factor genes [12]. One of the idiomorphs, *MAT1-1*, codes for an alpha domain transcription factor, while the other, *MAT1-2*, encodes a high mobility group (HMG) transcription factor. In heterothallic species, isolates harboring different idiomorphs are mating partners, while homothallic species bear both idiomorphs (linked or unlinked) in their genome, permitting self-fertility. However, there are also self-fertile species harboring only a single *MAT* idiomorph in their genome [13, 14]. This special type of homothallism is called unisexual reproduction, and has been observed in a number of species including the pathogens *Cryptococcus neoformans* and *C. albicans*, as well as in certain species of *Neurospora*, *Stemphylium*, and *Huntia* [15–19].

Dermatophytes belong to the family of Arthrodermataceae in Onygenales, an order that contains several pathogenic filamentous fungi [20]. Dermatophytes are keratinolytic fungi that live as saprobes in soil containing keratinaceous debris or as commensals on the hairy skin of animals, but these species can also cause infections in both humans and in animals [21]. They are classified into 3 groups based on their habitats: the soil-related geophiles, animal-associated zoophilic organisms, and human-associated anthropophiles [22]. Sexual reproduction is common in geophilic species and in zoophiles related to animals closely associated with soil [23]. Therefore, it has been hypothesized that the niche in which the sexual reproduction of dermatophytes occurs in nature is soil with keratin sources [24]. On the other hand, non-soil-associated dermatophytes, such as anthropophiles and some zoophiles, seem to have lost the ability to sexually reproduce [24, 25]. In addition, some of the anthropophiles such as *T. rubrum* and *T. interdigitale* appear to be present as a single mating type in the population [23, 26–29]. However, recent genomic evidence shows that these species have the necessary mating- and meiosis-related genes in their genome compared to their sexually reproducing relatives [30, 31].

Sexual reproduction of dermatophytes can be observed in the laboratory by using a variety of media. The most common and oldest of these is hair and soil plates [32–34] resembling the niche of geophiles. Other media, such as DCM agar with powdered hair, dextrose agar with powdered hair [35], 2.5 % malt extract agar [36], oatmeal salts agar [37], diluted Saboraud dextrose agar with salts [38, 39], diluted Pablum cereal agar with salts [39], and niger seeds salt agar with yeast extract [40] have also successfully been used for different

species as detailed later in the text. Because most sexually reproducing dermatophyte species are heterothallic, compatible mating partners, (+) and (–), or *A* and *a*, are inoculated on these media a couple of mm's apart [35, 36] and incubated mostly at room temperature to see the fruiting bodies [35]. These structures are called gymnothecia or cleistothecia bearing asci and ascospores enclosed by an interwoven network of peridial hyphae [36, 41]. Even the single mating type having species, for which sexual reproduction has not been seen, have been observed to demonstrate a positive response when co-cultured with compatible mating type isolates of tester strains of *Trichophyton simii* [26]. Before the molecular era, the “Stockdale test” had been very helpful in indicating the mating type of non-mating species.

The *MAT* locus structure is very similar among dermatophytes (Figure 1) [23]. For the dermatophytes where both mating type sequences are available, such as *T. benhamiae* and *N. gypsea*, the *MAT* locus boundaries can be determined [42, 43]. In addition to harboring the key transcription factor gene (*MAT1-1-1* or *MAT1-2-1*), the *MAT* locus extends to include the 3' end of the *MAT1-1-4* gene on the right and the 5' end of a gene coding for a hypothetical protein (*HYP1*) on the left. In other Pezizomycotina members, generally, *SLA2* is located on the left of the *MAT* locus and *APN2* and *COX13* are located on the right [44]; however, all three genes are linked to the right hand side of the *MAT* locus in dermatophytes.

In this review, we discuss the current knowledge on dermatophyte reproductive strategies, mating conditions, *MAT* loci and mating types based on the revised taxonomy, which defines the dermatophytes into 9 genera: *Guaromyces*, *Ctenomyces*, *Arthroderma*, *Lophophyton*, *Microsporum*, *Epidermophyton*, *Paraphyton*, *Nannizzia*, and *Trichophyton* [20].

The genera *Guaromyces*, *Ctenomyces* and *Arthroderma*

Guaromyces and *Ctenomyces* are basal genera of dermatophytes [20] (Table 1). *Guaromyces* was defined recently in the new taxonomy and is represented by one species, *Guaromyces ceretanicus* with the older name *Keratinomyces ceretanicus*, which is a soil fungus with no known sexual cycle [20, 45]. In the genus *Ctenomyces*, several species have been described. *Ctenomyces serratus* is the type species and is associated with soil and feathers [46]. It is the only species of *Ctenomyces* described with a sexual cycle. The ascomata of *C. serratus*, which can be observed on hair and soil plates, oatmeal salts agar (Medium E), and diluted Pablum cereal agar with added salts, are clearly different from that of the rest of the dermatophytes with distinct ctenoid appendages that resemble the teeth of a comb with tiny projections [46, 47]. The sexual cycle observed is heterothallic [48]. In a study analyzing the mating behavior of *C. serratus*, of the nineteen isolates analyzed, seven were found to be (–) and eleven were of (+) mating type, while one isolate was sterile with the isolates tested [47]. Four new *Ctenomyces* species, *C. indicus*, *C. albus*, *C. obovatus*, *C. peltricolor*, isolated from soil have recently been described [49, 50]. In addition, *Ctenomyces vellereus*, previously proposed to be a synonym of *C. serratus* [51, 52], was suggested to be a separate species in these studies.

According to the new taxonomic scheme, the previous teleomorphic genus name *Arthroderma* was accepted as the genus name of the species of dermatophytes harboring mostly geophilic and sexually reproducing species [20]. The genus *Arthroderma* comprises 22 species, 16 of which have the ability to reproduce sexually (Table 1). Most of these species have heterothallic sexual cycles; the only exceptions are *A. ciferrii* and *A. curreyi*, which have been described as homothallic [23, 53–56].

Arthroderma species have mainly been isolated from decaying feathers in soil near burrows or from animal fur. For example, *A. cuniculi* and *A. multifidum* were isolated from the soil of rabbit burrows and from apparently normal live rabbits [57]. Other studies reported *A. glorieae*, *A. uncinatum*, *A. phaseoliforme*, and *A. insingulare* from soil samples [58–61], *A. ciferrii* from the soil of hog pens [55], *A. melis* from badger burrows [62], *A. eboreum* from the soil of badger and rabbit burrows [63], *A. tuberculatum* from bird-related environments such as the feathers of a robin and from an owl pellet and soil [64, 65], *A. flavescens* from birds [66], *A. amazonicum* and *A. redellii* from rats [67, 68], *A. vespertilii* from bats [69], *A. silverae* from arctic fox dung from arctic regions [70], and *A. thuringiensis* from small mammals and once from a human [71, 72].

Sexual reproduction is common in *Arthroderma* and can be induced using a variety of media, such as oatmeal agar, water agar, Takashio medium with hair [73], hair and soil plates [55, 57–60, 63, 68, 74], and oatmeal salts agar (Medium E) [37, 65, 75]. Only *A. onychocola* requires special conditions: low temperature (17°C, instead of 25°C) for gymnothecia formation [73]. Ascomata are similar between the *Arthroderma* species and are called gymnothecia. Gymnothecia have with peridial walls formed by a network of interwoven hyphae composed of dumbbell-shaped cells, sometimes terminating with spiral appendages [68].

The structure of the *MAT* locus of *Arthroderma* species is not yet known. The only molecular study involved PCR amplification of *MAT1–2* from single isolates of *A. onychocola* and *A. thuringiensis*, a species with no known sexual cycle [73].

The genera *Lophophyton*, *Microsporum*, *Paraphyton*, *Epidermophyton*, and *Nannizzia*

Lophophyton

Lophophyton gallinae is the only species of the *Lophophyton* genus [20]. It is a zoophilic species that has been isolated from a squirrel, a dog, a cat, humans, and soil (Table 2) [78–81]. The sexual cycle of *L. gallinae* is heterothallic and was observed on hair and soil plates, oatmeal salts agar, diluted Sabouraud dextrose agar with salts, and diluted Pablum cereal agar with salts [39, 78]. The ascomata resemble those of the *Arthroderma*, with interwoven, branched, septate peridial hyphae and spiral appendages; however, the peridial cells have been described to be only gradually constricted at the center as opposed to the dumbbell-shaped cells of *Arthroderma* [78]. The *MAT* locus of *L. gallinae* has not been described, yet.

Microsporum

The *Microsporum* clade consists of 3 species: *M. canis*, which is zoophilic, and the anthropophilic species, *M. audouinii* and *M. ferrugineum*. Among these, only *M. canis* has a heterothallic sexual cycle that can be observed on hair and soil plates, oatmeal salts agar, and Niger seed salts agar with yeast extract (Table 2) [40, 82, 83]. Ascospores of *M. canis* consist of septate, echinulate (spiny), and usually curved peridial hyphae harboring dumbbell-shaped outer cells and spiral appendages [64]. However, almost all *M. canis* isolates are the (–) mating type [40, 84]. A total of 12 (+) mating type isolates, all from Japan, have been reported [40, 82, 83, 85]. The (+) and (–) mating type isolates currently used in phylogenetic studies, CBS495.96 (VUT-77054) and CBS496.86 (VUT-77055), respectively, are monoascospore cultures obtained from a cross of the strains VUT-73015 (+) and VUT-74001 (–), which were isolated from feline ringworm in Japan [20, 40, 82, 86]. The availability of the genome sequence of the clinical isolate CBS113480 has allowed characterization of the *M. canis* *MAT* locus, which is quite similar among the dermatophytes (Figure 1). Based on the genomic sequence, the commonly observed (–) mating type is *MAT1-1* [23, 30, 43]. Recently, sequencing of the *MAT*PCR amplicons from the two monoascospore strains indicated that CBS496.86 (–) and CBS495.96 (+) harbor the *MAT1-1* and the *MAT1-2* idiomorphs, respectively [87]. Additionally, *M. audouinii* 8 isolates and 26 *M. ferrugineum* isolates harbor the *MAT1-2* idiomorph (Table 2) [87]. Interestingly, CBS495.96, the only (+) mating type (*MAT1-2*) *M. canis* isolate analyzed, is phylogenetically more closely related to *M. audouinii* than to *M. canis* [20, 86]. Analysis of the other (+) mating type isolates from Japan would be informative to study the phylogeny of these three species. It would also be interesting to cross a super-mater *M. canis* isolate (*MAT1-1*) with *M. ferrugineum* and *M. audouinii* (*MAT1-2*) in the search for a successful cross.

Paraphyton

The genus *Paraphyton* consists of 3 species: *P. cookei*, *P. cookiella*, and *P. mirabile* [20]. *P. cookei* and *P. cookiella* are geophilic species that have mainly been isolated from soil, but *P. cookei* also has been isolated from wild animals, dogs, sheep, rats, and humans [88–91]. *P. mirabile* has been isolated from a dog, an alpine chamois, and a human and is thought to be zoophilic [92]. All 3 species are heterothallic and reproduce sexually resulting in ascospores composed of interwoven, branched, peridial hyphae (Table 2) [88, 89, 92]. Sexual reproduction was observed on hair and soil plates and oatmeal salts agar for *P. cookei* [39, 89, 90], Niger seed salts agar for *P. cookiella* [88], and Niger seeds agar for *P. mirabile* [92]. Interspecies mating assays, such as *P. mirabile* x *P. cookiella* and *P. mirabile* x *P. cookei* crosses, result in pseudoascomatal structures either without asci or without ascospores [92]. These findings indicate that *Paraphyton* species are phylogenetically close enough to stimulate the sexual reproduction pathways but, too distant to result in viable recombinant ascospores. Molecular studies have not been performed on *Paraphyton* species; therefore, their *MAT* locus structures are not known.

Epidermophyton

Epidermophyton floccosum, the only species of the genus *Epidermophyton*, is an anthropophile (Table 2) [20]. Although spiral hyphae that might represent degenerate peridial hyphae have been observed for certain isolates [93], a sexual cycle has not been described. *E. floccosum* isolates do not respond to *A. simii* tester strains, which is a useful method to determine the mating type of some dermatophytes [26]. Because its *MAT* locus has not been described and because the genome sequence is not known yet, the mating type of the isolates remains to be determined.

Nannizzia

Nannizzia harbors 4 geophilic and 2 zoophilic species with heterothallic sexual cycles and 4 species with unknown hosts and undefined sexual cycles (Table 2). Among the geophilic species, *N. incurvata*, *N. gypsea*, and *N. fulva* are commonly observed and cause occasional infections in humans and animals [94]. The heterothallic sexual reproduction of *N. incurvata* and *N. gypsea* can readily be observed on hair and soil plates, oatmeal salts agar, diluted Pabulum cereal agar with salts, DCM agar with powdered hair, and dextrose agar with powdered hair [35, 37, 39, 94]. However, *N. fulva* forms ascumata poorly on oatmeal salts agar or on diluted Pabulum cereal agar with salts [37, 39]. In addition, sterilization of the soil by autoclaving reduces the efficiency of ascumata formation suggesting either heat labile components or other viable microbes that contribute to stimulate mating [94]. The ascumata of *Nannizzia* species are similar to *Lophophyton* and *Arthroderma*, but the peridial cells are not as constricted in the dumbbell-shaped cells, and instead showing only a slight central constriction [94]. Spiral appendages are also observed. The mating type distribution of *N. incurvata*, *N. gypsea*, and *N. fulva* was determined to be nearly equal [94, 95–97]. Among *Nannizzia* species, only the *MAT* locus of *N. gypsea* has been characterized and was shown to have the typical dermatophyte *MAT* locus structure (Figure 1) [43]. Other molecular studies have included the amplification of *MAT1-1* and *MAT1-2* sequences from *N. incurvata* [43] and *N. fulva* [98]. For *N. corniculata* (the other geophilic species), sexual reproduction was observed between soil-derived strains, one isolated in Somalia and the other in Guinea. The species was determined to be heterothallic after ascospore mating analysis, with ascumata production on Niger salts agar and Sabouraud 1/10 with salts agar [99].

Among the zoophilic species, *N. persicolor* has been isolated from soil, small mammals (especially rodents), and occasionally human infections [100–104]. Sexual reproduction was observed on hair and soil plates and determined to be heterothallic [101]. Interestingly, oatmeal salts agar was not successful for the induction of ascumata production [39]. *N. nana* is the other zoophilic species and is generally associated with pigs [105], but sometimes is observed in humans as well [106]. A sexual cycle is challenging to observe, ascumata are not formed on hair and soil plates or on oatmeal salts agar [39], but could be induced on unsterilized soil with hair after a long incubation period (10–12 weeks) [34]. Mating assays with single ascospore isolates indicate that *N. nana* is heterothallic [34].

Four *Nannizzia* species have no known sexual reproduction: *N. aenigmaticum*, of which only a single human isolate has been reported [107], *N. perplicata*, a recently described

species isolated from a human tinea corporis case [108], *N. duboisii* [20], and *N. praecox*, which is likely a geophilic species and has been isolated from soil, horse hair, and humans in contact with horses [109–111].

The genus *Trichophyton*

The *Trichophyton* genus contains the highest number of anthropophilic species of the dermatophytes. Sixteen defined *Trichophyton* species are recognized in 5 different series: *T. mentagrophytes*, *T. simii*, *T. benhamiae*, *T. bullosum*, and the *T. rubrum* complex (Table 3) [20].

T. mentagrophytes series

T. mentagrophytes is a zoophilic species isolated from chinchillas, guinea pigs, cats, dogs, mice, horses, and humans [28, 112–115]. Ascomata are of the *Arthroderma*-type with constricted dumbbell-shaped peridial cells [116]. The heterothallic sexual cycle can be observed on Sabouraud 1/10 plus salts [112, 116], Niger seed agar [28], and Takashio medium [95, 117]. Mating type distribution is skewed in favor of the (+) mating type (*MAT1-2*) (80% to 95%) in different geographical locations, including Japan, India, and Germany [87, 95, 112, 118]. However, one study reported that 30% of 10 Czechoslovakian isolates were the (+) mating type [117].

T. interdigitale had been considered the anthropophilic counterpart of *T. mentagrophytes* [20, 28], but recent studies identified new genotypes of *T. mentagrophytes* as the causative agent of dermatophytosis [119–122]. Currently 10 ITS genotypes have been defined for *T. mentagrophytes* (8 genotypes) and *T. interdigitale* (2 genotypes) [121]. The Indian genotype (VIII) has come to prominence over the past several years due to the highly increased number of cases in India and the resistance of the isolates to treatment [119–122]. The genome-wide phylogeny of 20 isolates shows that the Indian isolates form a distinct clade apart from the other *T. mentagrophytes* and *T. interdigitale* genotypes [123]. In addition, three of the isolates bear both an HMG and an alpha-box gene in their genomes, while the other seventeen harbor only an HMG gene [123]. The presence of both idiomorphs might be indicative of hybridization events or an incomplete sexual cycle demonstrating the possibility of sexual reproduction, which could be important in spreading antifungal resistance properties [123]. The inflammatory nature of the isolates might be indicative of zoophilic ancestry; however, because zoophilic species are not expected to cause an epidemic like this, the Indian genotype could be in the process of evolving into an anthropophilic species. It would be interesting to test the sexual reproduction potential of these isolates with fertile *T. mentagrophytes* tester strains. Unlike the Indian genotype VIII, all known *T. interdigitale* isolates are of the (+) mating type (*MAT1-2*) [29, 112]. The genome sequence of *T. interdigitale* also indicates the *MAT1-2* locus structure [31]. The 4 Japanese isolates having the (–) mating type reported to be *T. interdigitale* by Anzawa and colleagues in 2011 with the GenBank accession numbers AB617768 and AB617769 [124] fall into other genotypes of *T. mentagrophytes* according to the 10-genotype scheme [121]. Therefore, *T. mentagrophytes* appears to be a mixture of different genotypes/species including *T. interdigitale*, and the populations of some are composed of only 1 mating type.

The other species in the *T. mentagrophytes* series are *T. equinum* and *T. tonsurans* [20]. While *T. tonsurans* is an anthropophilic species [125], *T. equinum* is zoophilic and mainly associated with horses, but it is sometimes observed in humans who interact with horses as well [126, 127]. Mating has not been observed in either species, but their mating types have been studied either by molecular analysis or by confrontation tests [26]. Sixty *T. tonsurans* isolates from Japan were reported to harbor the *MAT1-1* idiomorph implying that they all are of (–) the mating type [128]. A recent study screened 8 isolates of *T. tonsurans* composed of reference strains and clinical isolates (from Germany and of unknown origin) and found that all were *MAT1-1* [87]. The sequenced isolate of *T. tonsurans* (CBS 112818) also harbors the *MAT1-1* idiomorph (Figure 1) [30]. Other studies show that 10 isolates from India [95], as well as 15 isolates from around the world [102 and references therein], all have the (–) mating type. The same study found that 2 isolates from Kenya have the (+) mating type, but questioned the identity of these strains [129]. On the other hand, studies on the mating type of *T. equinum* are limited. Three reference strains from horses [87], and the sequenced clinical isolate (CBS127.97) [30] harbor the *MAT1-2* idiomorph (Figure 1) [(+) mating type]. Additionally, 5 isolates have been determined to be (+) mating type by confrontation assays [26]. Although their host preferences differ significantly, molecular methods have demonstrated surprisingly high similarity between *T. tonsurans* and *T. equinum* [30, 129, 130]. While there has been a debate for and against conspecificity of these species [130, 131], mating between *T. tonsurans* and *T. equinum* has not been observed.

***T. simii* series**

The *T. simii* series includes 3 species: *T. simii* and *T. quinckeanum*, which are zoophilic, and *T. schoenleinii*, which is anthropophilic [20]. *T. simii* has been isolated from monkeys, chickens, a dog, small mammals, humans, and soil [36, 132, 133]. It was reported to have a heterothallic mating system [36, 134] that can be observed on 2.5% malt extract agar, hair (horse) and soil plates, oatmeal agar, and glucose peptone agar, in addition to a variety of other media [36]. Ascomata have been observed to be the *Arthroderma* type, with interwoven, branched, peridial hyphae with cells constricted in the middle and spiral appendages [36].

The other zoophilic species in this series is *T. quinckeanum*, which is associated with small rodents and camels, and is sometimes observed in horses, cats, dogs, and humans [135, 136]. Ajello et al. [136] reported the heterothallic sexual reproduction of 2 *T. quinckeanum* isolates [TQ10 (X804) and TQ13 (X808)] among a total of 17 strains on hair and soil plates. The progeny obtained from this cross successfully mated both with other isolates of *T. quinckeanum*, as well as with *T. benhamiae* in a heterothallic mode on oatmeal agar. In this study, 2 of the isolates [TQ5 (X392) and TQ10] were found to be “A” mating type, while 3 were “a” mating type, the other isolates did not mate. Six isolates from this study and 13 new isolates of *T. quinckeanum* were evaluated in another study [137], involving mating assays with *T. simii* and *T. benhamiae*. In this study, all 19 isolates mated with *A. benhamiae* mating type A, indicating that all evaluated *T. quinckeanum* isolates were mating type a. In addition, some of the isolates also produced fertile ascomata with *T. simii* mating type A, but the ascospores had irregularities in germination or maturation resembling interspecific

crosses. However, the study by Weitzman and Padhye [137] include the isolate X392 (TQ5), previously found to be the *A* mating type [136]. The inconsistency might be due to incorrect isolate numbers and requires further clarification. In the previous study [136], a heterothallic sexual cycle was observed with an *A/a* ratio of 2/3; however, in the later study [137] all isolates were mating type *a* (inferred idiomorph: *MAT1-1*). In agreement with the study by Weitzman and Padhye [137], the *MAT1-1* idiomorph was detected in the 2 reference and 3 clinical isolates of *T. quinckeanum* [87]. Additional studies are needed to clarify the sexual reproduction properties of *T. quinckeanum*.

The only anthropophilic species in the *T. simii* series is *T. schoenleinii*, which is mainly involved in scalp infections [138]. The 16 *T. schoenleinii* isolates that have been analyzed were reported to harbor the *MAT1-2* idiomorph [87].

***T. benhamiae* series**

T. benhamiae is a zoophilic species that is generally associated with guinea pigs, but it has been isolated from other animals such as dogs, rabbits, cats, and humans [113, 114, 139–141]. Different genotypes/phenotypes have been defined for *T. benhamiae*, such as the African and American-European races [142], and the yellow and white phenotypes [143]. A recent study defined 4 ITS genotypes; genotype 1 group II (American-European race/yellow phenotype), a related genotype group I (American-European race/white phenotype), genotype 2 (the African race), and genotype 3 (a new genotype defined in the study) [144]. Compatibility is reduced when strains belonging to different genotypes/phenotypes are crossed [142], which might indicate the presence of a complex composed of closely related species. *T. benhamiae* mating has been observed on soil and hair plates [139], Sabouraud 1/10 with salts [142], and oatmeal salts agar [37] showing ascospores typical of the genus *Arthroderma* and with a reportedly heterothallic mating system [139]. The mating type distribution differs between genotypes. For example, Symoens and colleagues [143] reported the presence of both mating types, but 12 of the 14 group I (white phenotype) isolates were (+), whereas only (–) isolates were identified in the 13 genotype 1 (yellow phenotype) isolates. Similarly, 10 clinical yellow phenotype isolates of German/Swiss origin were typed as *MAT1-1*, while white isolates harbored either the *MAT1-1* (n=5) or the *MAT1-2* (n=8) idiomorph [87]. In other studies, 1 (–) and 40 (+) among 41 Czechoslovakian isolates [117], 7 (–) and 5 (+) among US and Canadian isolates [145], 2 (–) and 5 (+) among Russian isolates [146], and 8 *MAT1-1* (–) and 2 *MAT1-2* (+) among Japanese isolates [144] were detected. The (–) and (+) mating type isolates were reported to harbor the idiomorphs *MAT1-1* and *MAT1-2*, respectively [147]. The sequenced clinical isolate, strain 2354 (LAU2354) unveiled a *MAT1-2* structure and sequencing the *MAT* locus of its mating partner (CBS 809.72) showed the complete *MAT* locus of *T. benhamiae* (Figure 1) [42].

T. erinacei is a zoophilic fungus mainly isolated from hedgehogs and hedgehog nests, but sometimes from humans as well [148–150]. Stimulation by *T. simii* tester strains showed that all 21 isolates of *T. erinacei* were mating type (+) (inferred idiomorph: *MAT1-2*) [26]. Similarly, Padhye and Ajello [151] found that, 26 out of 27 *T. erinacei* isolates mated with the mating type *a* *T. benhamiae* tester strain on Pabulum cereal with salts agar and on dilute Sabouraud dextrose agar with salts, which indicates that almost all isolates analyzed in this

study were mating type *A* (inferred idiomorph: *MAT1-2*). On the other hand, Takahashi et al. reported the presence of both mating types of *T. erinacei*, 12 (+/*A*) and 6 (-/*a*), and demonstrated complete fertility of two compatible isolates [152]. Of the 6 (-/*a*) isolates studied, 5 were from Kenya and 1 was from Japan. Overall, these results indicate that, although infrequent, the (-/*a*) mating type of *T. erinacei* is found in nature and the organism is able to reproduce sexually. In addition, *T. erinacei* mates with the African race of *T. benhamiae*, but the resulting ascomata are small, with a low number of asci, suggestive of interspecific crossing [152]. A recent study involving *T. erinacei* indicates the presence of the *MAT1-2* idiomorph in the 4 reference strains [87].

T. verrucosum, another zoophilic species in the *T. benhamiae* series, is mainly implicated in cattle dermatophytosis [20, 125]. Sexual reproduction has not been observed in *T. verrucosum*. In a study of 4 isolates from the Czech Republic and 18 from Japan, all were found to harbor the *MAT1-2* idiomorph [153]. Similarly, 4 reference strains and 3 clinical strains of unknown origin were also found to be *MAT1-2* [87]. Genome sequencing of *T. verrucosum* demonstrated the presence of the whole set of genes necessary for mating and meiosis, similar to *T. benhamiae* [42]. In addition, the *MAT* locus of the sequenced strain (which is of clinical origin) appears to have the typical dermatophyte *MAT1-2* locus structure (Figure 1).

T. concentricum, an anthropophilic species in the *T. benhamiae* series has been observed in SouthEast Asia, Central and South America, and the South Pacific islands [20, 154]. The species is not known to reproduce sexually, and the only study focusing on the *MAT* locus indicated that all 13 analyzed isolates contained the *MAT1-1* idiomorph [87].

T. eriotrephon is a species in the *T. benhamiae* series that is closely related to the zoophilic species *T. verrucosum* and *T. erinacei* [20]. Very few clinical isolates of this species have been isolated [141, 155], and the only molecular study revealed the presence of *MAT1-1* in the reference strain CBS220.25 [87]. Rarity of clinical cases brings into question the presumed anthropophilic nature of the species, and it might have an as yet unknown habitat.

T. bulbosum

T. bulbosum is a rare, zoophilic dermatophyte that has been isolated from horses and donkeys and once from a human [156, 157]. No sexual cycle has been described for this species. A *MAT1-1* idiomorph sequence was amplified from the only studied isolate (CBS363.35) [87], and the potential for sexual reproduction is unknown in this species [157].

***T. rubrum* complex**

The *T. rubrum* species complex contains the most commonly observed anthropophilic dermatophyte, *T. rubrum* [158], and species closely related to it: *T. violaceum*, which causes scalp infections and *T. soudanense* [20]. A majority of *T. rubrum* isolates analyzed were the (-) mating type (inferred mating type by *T. simii* stimulation assays) and harbor the *MAT1-1* idiomorph [26, 27, 31, 43, 56]. Eleven analyzed *T. violaceum* isolates and 12 analyzed *T. soudanense* isolates also harbored the *MAT1-1* idiomorph [87]. The *MAT1-1* locus of *T.*

rubrum has the structure of the archetypal *MAT* locus of dermatophytes (Figure 1) [43]. *T. rubrum* was shown to mate with a super-mater isolate of *T. simii*, producing 1 hybrid progeny on Takashio medium (1/10 Sabouraud plus salts) [159]. In addition, genome analysis showed that *T. rubrum* has the genes necessary for mating and meiosis [30]. These findings suggest that *T. rubrum* has the ability to sexually reproduce. The only (+) mating type species in the *T. rubrum* complex is the morphotype *T. megninii* [160], which harbors the *MAT1-2* idiomorph (Figure 1) [31, 87]. *T. megninii* was found to be very similar to *T. rubrum* with the highest-diversity region in the *MAT* locus [31], suggesting that mating could be possible between the two species. However, mating assays did not result in ascospore production between *T. rubrum* and *T. megninii* using Takashio medium or Medium E [31]. However, it is possible that *T. rubrum* requires other conditions for mating.

Conclusions

Dermatophytes are keratinophilic microorganisms that are associated with soil with keratinaceous materials (geophiles), with animals (zoophiles), or with humans (anthropophiles). Sexual reproduction is common among geophiles and some zoophiles, but has not been observed among the anthropophilic dermatophytes, which are mostly found as a single mating type. In terms of evolutionary concepts, it could be advantageous in the short term for dermatophyte pathogens to proliferate asexually once they have attained the genetic composition that allows successful host invasion. However, in the long term, asexual propagation would not be advantageous based on the Red Queen hypothesis, which necessitates continual adaptation of both the host and the pathogen, [161, 162]. What we know about other fungal pathogens is that they somehow reduce their sexual activity and it is hypothesized that this is to avoid disrupting their well-functioning genomic order [163]. For example, the population of *C. neoformans* largely consists of a single mating type, but this species has retained the ability to sexually reproduce both in a heterothallic manner and through unisexual reproduction. Similarly, *C. albicans* requires specific conditions to undergo a parasexual cycle both in a heterothallic and unisexual form. Likewise, *A. fumigatus* requires stringent conditions for mating, and mating is not as ubiquitous as in its saprobic *Neosartorya* relatives [164]. It may be the case for dermatophytes that restricted mating has led to successful pathogens, but they are expected to retain some form of sexual activity. Sexual reproduction might occur between different mating types infrequently, such as between *T. rubrum* and *T. megninii* or between *T. tonsurans* and *T. equinum*, under conditions that have not yet been found. Another possibility is that the dermatophytes have developed other mechanisms that have not been detected, yet, such as unisexual reproduction, which is observed in two of the three most common fungal pathogens (*C. neoformans* and *C. albicans*). Future studies will shed light on these concepts.

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Fig 1.

The archetypal *MAT* locus structure of dermatophytes. The isolates harboring the *MAT1-1* locus are *T. benhamiae* CBS809.72 (GQ996965.1), *T. rubrum* CBS118892 (NW_003456427.1), *T. tonsurans* CBS112818 (GG698488.1), *M. canis* CBS113480 (DS995708.1), and *N. gypsea* CBS118893 (FJ798794.1). The *MAT1-2* locus bearing isolates are *T. benhamiae* strain 2354 (ABSU01000008.1), *T. equinum* CBS127.97 (DS995742.1), *T. verrucosum* HKI 0517 (NW_003315532.1), *T. megninii* CBS735.88 (KK210299.1), *T. interdigitale* MR816 (AOKY01000593.1), and *N. gypsea* ATCC48982 (the available sequence (FJ798798.1) harbors *SLA2*, *COX13*, *APN2*, *MAT1-1-4*, *MAT1-2-1*, and *HYP1*). The dashed line indicates the limits of the *MAT* locus for *T. benhamiae*.

Table 1.

Host preferences and mating characteristics of the species of the genera *Guarromyces*, *Ctenomyces* and *Arthroderma*

Genera	Species	Host	Mating	References
<i>Guarromyces</i>	<i>G. ceretanicus</i>	Geophilic?	?	[20, 45]
<i>Ctenomyces</i>	<i>C. serratus</i>	Geophilic?	Heterothallic	[46–48]
	<i>C. vellereus</i>	?	?	[49–52]
	<i>C. indicus</i>	?	?	[49]
	<i>C. albus</i>	?	?	[50]
	<i>C. obovatus</i>	?	?	[50]
	<i>C. peltricolor</i>	?	?	[50]
	<i>C. peltricolor</i>	?	?	[50]
<i>Arthroderma</i>	<i>A. amazonicum</i>	Zoophilic	Heterothallic	[54, 68]
	<i>A. ciferrii</i>	Geophilic	Homothallic	[54, 55]
	<i>A. cuniculi</i>	Geophilic	Heterothallic	[57]
	<i>A. curreyi</i>	Geophilic	Homothallic	[53, 56]
	<i>A. chiloniense</i>	?	?	[76]
	<i>A. eboreum</i>	Zoophilic	Heterothallic	[63]
	<i>A. flavescens</i>	Zoophilic	Heterothallic	[54, 66]
	<i>A. gertleri</i>	Geophilic	Heterothallic	[54, 77]
	<i>A. gloriae</i>	Geophilic	Heterothallic	[58]
	<i>A. insingulare</i>	Geophilic	Heterothallic	[54, 59]
	<i>A. lenticulare</i>	Geophilic	Heterothallic	[54, 74]
	<i>A. melis</i>	Geophilic	Heterothallic	[62]
	<i>A. multifidum</i>	Geophilic	Heterothallic	[57]
	<i>A. onychocola</i>	?	Heterothallic	[73]
	<i>A. phaseoliforme</i>	Geophilic	?	[61]
	<i>A. redellii</i>	Zoophilic	?	[67]
	<i>A. silverae</i>	?	?	[70]
	<i>A. thuringiensis</i>	Zoophilic?	?	[71–73]
	<i>A. quadrifidum</i>	Geophilic	Heterothallic	[34, 54]
	<i>A. tuberculatum</i>	Zoophilic	Heterothallic	[64, 65]
	<i>A. uncinatum</i>	Geophilic	Heterothallic	[34, 54]
	<i>A. vespertili</i>	Zoophilic	?	[69]

Table 2.

Sexual reproductive patterns and host characteristics of the genera *Lophophyton*, *Microsporum*, *Paraphyton*, *Epidermophyton*, and *Nannizzia*

Genera	Species	Host	Mating	MAT idiomorph	References
<i>Epidermophyton</i>	<i>E. floccosum</i>	Anthropophilic	?	?	[26, 93]
<i>Nannizzia</i>	<i>N. aenigmatum</i>	?	?	<i>MAT1-2</i> (single isolate)	[73, 107]
	<i>N. corniculata</i>	Geophilic	Heterothallic	Not determined	[99]
	<i>N. duboisii</i>	?	?	?	[20]
	<i>N. fulva</i>	Geophilic	Heterothallic	<i>MAT1-1</i> and <i>MAT1-2</i>	[94, 98]
	<i>N. gypsea</i>	Geophilic	Heterothallic	<i>MAT1-1</i> and <i>MAT1-2</i>	[43, 94]
	<i>N. incurvata</i>	Geophilic	Heterothallic	<i>MAT1-1</i> and <i>MAT1-2</i>	[41, 43]
	<i>N. nana</i>	Zoophilic	Heterothallic	Not determined	[34]
	<i>N. perplicata</i>	?	?	?	[108]
	<i>N. persicolor</i>	Zoophilic	Heterothallic	Not determined	[101]
	<i>N. praecox</i>	Geophilic?	?	?	[109–111]
<i>Paraphyton</i>	<i>P. cookei</i>	Geophilic	Heterothallic	?	[89, 90]
	<i>P. cookiellum</i>	Geophilic	Heterothallic	?	[88]
	<i>P. mirabile</i>	Zoophilic	Heterothallic	?	[92]
<i>Lophophyton</i>	<i>L. gallinae</i>	Zoophilic	Heterothallic	?	[78, 79]
<i>Microsporum</i>	<i>M. canis</i>	Zoophilic	Heterothallic	Predominantly <i>MAT1-1</i>	[40, 84, 85]
	<i>M. audouinii</i>	Anthropophilic	?	<i>MAT1-2</i>	[87]
	<i>M. ferrugineum</i>	Anthropophilic	?	<i>MAT1-2</i>	[87]

Table 3.*Trichophyton* species: Host preferences, reproductive patterns and mating types

Series	Species	Host	Mating	Mating type	References
<i>T. mentagrophytes</i>	<i>T. tonsurans</i>	Anthropophilic	?	<i>MAT1-1</i>	[30, 87, 95, 128, 129]
	<i>T. equinum</i>	Zoophilic	?	<i>MAT1-2</i>	[26, 30, 87]
	<i>T. interdigitale</i>	Anthropophilic	?	<i>MAT1-2</i>	[28, 29, 112]
	<i>T. mentagrophytes</i>	Zoophilic	Heterothallic	<i>MAT1-1</i> and <i>MAT1-2</i>	[116]
<i>T. simii</i>	<i>T. schoenleinii</i>	Anthropophilic	?	<i>MAT1-2</i>	[87]
	<i>T. simii</i>	Zoophilic	Heterothallic	<i>MAT1-1</i> and <i>MAT1-2</i>	[36, 134]
	<i>T. quinckeanum</i>	Zoophilic	Heterothallic	<i>MAT1-1</i> only? <i>A</i> and <i>a</i> ?	[87, 136]
<i>T. benhamiae</i>	<i>T. benhamiae</i>	Zoophilic	Heterothallic	<i>MAT1-1</i> and <i>MAT1-2</i>	[87, 117, 139, 143–147]
	<i>T. concentricum</i>	Anthropophilic	?	<i>MAT1-1</i>	[87]
	<i>T. erinacei</i>	Zoophilic	Heterothallic	<i>MAT1-2</i> (detected in four isolates) (+/ <i>A</i>) and (–/ <i>a</i>)	[26, 87, 148, 151, 152]
	<i>T. verrucosum</i>	Zoophilic	?	<i>MAT1-2</i>	[42, 87, 153]
	<i>T. eriotrephon</i>	Anthropophilic?	?	<i>MAT1-1</i> (a single isolate was studied)	[87]
<i>T. bullosum</i>	<i>T. bullosum</i>	Zoophilic	?	<i>MAT1-1</i> (a single isolate was studied)	[87, 156, 157]
<i>T. rubrum</i>	<i>T. rubrum</i>	Anthropophilic	?	<i>MAT1-1</i>	[26, 27, 31, 43, 56]
	Morphotype <i>megninii</i>	Anthropophilic	?	<i>MAT1-2</i>	[87, 160]
	<i>T. soudanense</i>	Anthropophilic	?	<i>MAT1-1</i>	[87]
	<i>T. violaceum</i>	Anthropophilic	?	<i>MAT1-1</i>	[87]