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Phylogenetic and ecological reevaluation of the order Onygenales

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34 **Abstract**

35 The order Onygenales is classified in the class Eurotiomycetes of the subphylum Pezizomycotina.

36 Families in this order have classically been isolated from soil and dung, and two lineages contain

37 causative agents of superficial, cutaneous, and systemic infections in mammals. The ecology and

38 habitat choices of the species are driven mainly by abilities of keratin- and cellulose-degradation. The

39 present study aimed to investigate whether the ecological trends of the members of the Onygenales can

40 be interpreted in an evolutionary sense, linking phylogenetic parameters with habitat preferences, to

41 achieve polyphasic definitions of the main taxonomic groups. Evolutionary processes were estimated

42 by multiple gene genealogies and divergence time analysis. Previously described families namely,

43 Arthrodermataceae, Ajellomycetaceae, Ascosphaeraceae, Eremascaceae, Gymnoascaceae,

44 Onygenaceae and Spiromastigaceae were accepted in the Onygenales, and two new families,

45 Auxarthraceae and Neogymnomycetaceae were introduced. A number of species could not be assigned

46 to any of the defined families. Our study provides a revised overview of the main lines of taxonomy of

the Onygenales, supported by multilocus analyses of ITS, LSU, *TUB*, *TEF1*, *TEF3*, *RPB1*, *RPB2*, and ribosomal protein 60S L10 (L1) (*RP60S*) sequences, combined with available data on ecology, physiology, morphology, and genomics.

Key words

• Ancestral reconstruction • Evolution • Onygenales • Taxonomy

Introduction

Phylogenetic studies using barcoding genes (Chen et al. 2015), as well as corroborated by whole-genome sequence data (Wang et al. 2009; Li et al. 2021), have demonstrated that the order Onygenales is one of the derived clades of the fungal Kingdom, experiencing recent diversification. Among the main drivers of evolution is keratin degradation, a unique ability that has shaped large clades within the order. Several families show a pronounced adaptation to mammalian hosts, which are evolutionarily recent (Sharpton et al. 2009; Muñoz et al. 2018). This has culminated in the emergence of anthropophilic species, i.e., those adapted to *Homo sapiens*, one of the most recent vertebrates.

The orders Eurotiales and Onygenales, together with some unclassified taxa, constitute the subclass Eurotiomycetidae (Schoch et al. 2020). Members of the Onygenales show pronounced sexual state morphology, with mostly gymnothecial fruitbodies, frequently elaborate hyphal extensions, as well as some well-differentiated asexual forms of sporulation (Currah et al. 1985; Hubka et al. 2013). This has enabled the classification of genera and families on the basis of morphology. However, in the absence of sexual states and macroconidia, phylogenetically remote microconidial species are morphologically similar, which has led to highly polyphyletic genera such as *Chrysosporium*. Such groups require taxonomic revision based on modern criteria. A major problem is the absence of interpretable type specimens for numerous taxa in this order. Therefore, one of the aims of the present

paper is to redefine higher taxa and essential species, with the deposition of neotypes or epitypes where necessary.

Several groups within the Onygenales have long been recognized by their pronounced ecological preference, e.g., association with bees in Ascosphaeraceae, systemic infections of mammals in Ajellomycetaceae, and superficial infections of mammals in Arthrodermataceae. In the present article, we will investigate the extent to which ecological parameters can assist in defining groups at the genetic or familial levels. Given these ecologies, the revised order might provide a model for a polyphasic approach to a taxonomy that includes parameters that play a role in the course and speed of evolution, in contrast to the present taxonomy that is largely phylogenetic and using anonymous markers. The ultimate aim is to define taxa as entities of evolution, rather than by solely applying phylogenetic history.

Materials and methods

Strains

Strains were selected based on the species which have been described in the order Onygenales according to NCBI taxonomy (<http://www.ncbi.nlm.nih.gov/taxonomy>) and Index Fungorum (www.indexfungorum.org). In total, sequences belong to 95 genera, 370 species and 537 strains were analyzed in this study. Genera and species that have been described after December 2019 were not included in the analyses (Table 1, Suppl Table 1). Available strains were obtained from Centraalbureau voor Schimmelcultures reference collection (housed at Westerdijk Fungal Biodiversity Institute, Utrecht, The Netherlands) and inoculated on Sabouraud's Glucose Agar (SGA, BD Difco™). Cultures were incubated at 24°C for 14–21 days. Sequences of remaining strains and for the largest subunit of RNA polymerase II (*RPB1*), the second largest subunit of RNA polymerase II (*RPB2*) and translation elongation factor 1-alpha (*TEF1*) were retrieved from the NCBI nucleotide databank. Whole genome data for 53 strains (Suppl. Table 1) was obtained from NCBI Genome and Joint Genome Institute MycoCosm (<https://mycocosm.jgi.doe.gov/mycocosm>) databases and added to

phylogenetic tree analyses. Ecology and ascomata morphology for the type species were retrieved from the original articles where the species were described for the first time.

DNA extraction, PCR and sequencing

DNA extraction was performed using the cetyltrimethylammonium bromide protocol (Su et al. 2019) and MasterPure™ Yeast DNA Purification Kit (Epicentre, Madison, WI, U.S.A.). The quantity and quality of the isolated DNA were evaluated using a NanoDrop ND-1000 spectrophotometer with the ND-1000 v3.3.0 software (Coleman Technologies, Wilmington, NC, U.S.A.). Five gene regions; the rDNA internal transcribed spacer (ITS), D1-D2 region of large subunit (LSU), partial β -tubulin (*TUB*), translation elongation factor 3 (*TEF3*) and ribosomal protein 60S L10 (L1) (*RP60S*) were amplified using the primers ITS4-ITS5, LR0R-LR5, TUB2Fd-TUB4Fd, EF3-3185F / EF3-3538R and 60S-908R / 60S506F, respectively (de Hoog et al. 2017; Dukik et al. 2017). PCRs were carried out as described by Stielow et al. (2015). PCR products were visualized on 1.5% agarose gels and cycle-sequenced using Applied Biosystems BigDye Terminator version 3.1 (Thermo Fisher Scientific) after purification. Bidirectional sequencing was performed using a capillary electrophoresis system (3730×1 DNA analyzer; Life Technologies, Carlsbad, CA, U.S.A.). Obtained sequences were manually inspected and stored in a BIOLOMICS database.

Phylogenetic analyses

Alignments were generated using PASTA (Mirarab et al. 2015) and MAFFT v7 with default settings, and trimmed using ClipKIT with smart-gap function (Steenwyk et al. 2020). Percentages similarity between strains were determined using BIOEDIT v7.2 (Hall 1999). ModelFinder (Kalyaanamoorthy et al. 2017) on IQ-TREE software (Nguyen et al. 2015) was used to find the best-fitting model for each gene according to the Bayesian Information Criterion (BIC). Phylogenetic trees were constructed using the maximum likelihood methods implemented on IQ-TREE software and MEGA v6 (Minh et al. 2020b; Tamura et al. 2013). Branch support values were measured using both ultrafast bootstraps and SH-like approximate likelihood ratio test (Guindon et al. 2010; Minh et al. 2020a). Additionally, RAxML v8.0.0 with GTRCAT model (Stamatakis 2014) with 1000 bootstrap iterations and

MRBAYES v3.2.7a-dev (Ronquist and Huelsenbeck 2003) with default settings on the CIPRES portal (<http://www.phylo.org/>) were used for ITS and LSU phylogeny. *Aspergillus fumigatus* strain Af293 (Aspergillaceae, Eurotiales) was used as an outgroup to define families. Single-locus analyses for ITS and LSU were performed in two groups: Group I containing type species with additional strains from each species and Group II containing only type species. Strains which had more data for eight loci were selected for each species and used for the multilocus phylogenetic analyses. To determine the phylogeny of the genera, family-based ITS analyses were performed. The characteristics of the trees were analyzed using AMAS (Alignment Manipulation And Summary) tool (Borowiec 2016) with a Python package. Command files were prepared on Alignment Transformation Environment (ALTER) (<http://www.sing-group.org/ALTER/>) for the maximum likelihood phylogeny analyses and with MESQUITE v2.75 (Maddison and Maddison 2007) for the Bayesian inference analyses. TREEVIEW v1.6.6, MEGA v6 (Tamura et al. 2013) and iTOL v6 (Letunic and Bork 2019) were used to visualize and edit trees. Branches composing the backbone starting with >1 species with bootstrap values $\geq 80\%$ were collapsed and considered as “supported clades”. Branches formed in the supported clades with >1 species with bootstrap values $\geq 80\%$ were considered as “groups”. The ratio of supported/unsupported clades with low number of branches outside of the clades were taken as parameters to define tree quality.

In order to increase the robustness of the ML topologies observed in concatenated dataset, gene concordance factor (gCF) and the site concordance factor (sCF) implemented in the IQTREE2 software were also shown together with ultrafast bootstrap (UFBoot) and SH-like approximate likelihood ratio (SH-aLRT) values (Minh et al. 2020a; Hoang et al. 2018; Guindon et al. 2010). For every clade in the multilocus Onygenales tree, gCF is defined as the percentage of conclusive gene trees containing that partition. On the other hand, sCF is stated as the percentage of decisive alignments sites (SNPs) supporting the branch of a family or a clade in the ML tree. The alignment was deposited in TREEBASE under accession number 28949.

Relative Divergence Time Estimation

The absolute time of divergence, relative orders of the taxa and spacing of speciation events within the Onygenales were estimated based on RelTime method implemented in MEGA 7 (Tamura et al. 2012; Kumar et al. 2016) using highly reliable calibration fossils available for Ascomycota (Samarakoon et al. 2019). In addition to *Arachnomyces* spp. (Arachnomycetales) and *Aspergillus fumigatus* (Eurotiales); *Arthrobotrys oligospora* (Orbiliales, Orbiliomycetes), *Ascobolus immersus* (Pezizales, Pezizomycetes), *Botrytis cinerea* (Helotiales, Leotiomycetes), *Cladonia grayi* (Lecanorales, Lecanoromycetes), *Colletotrichum simmondsii* (Glomerellales, Sordariomycetes), *Dactylellina haptotyla* (Orbiliales, Orbiliomycetes), *Microthyrium microscopicum* (Microthyriales, Dothideomycetes), *Piedraia hortae* (Capnodiales, Dothideomycetes), *Pyronema omphalodes* (Pezizales, Pezizomycetes), *Sclerophora sanguinea* (Coniocybales, Coniocybomycetes) and *Usnea florida* (Lecanorales, Lecanoromycetes) were used as representers of the main lineages of the Ascomycota. *Candida tropicalis* and *Saccharomyces cerevisiae* (Saccharomycetales, Saccharomycetes) were used as outgroups for the analysis.

Results

In the current study, a total of 1667 sequences for LSU ($n = 421$), ITS ($n = 503$), *TUB* ($n = 189$), *RP60S* ($n = 123$), *TEF1* ($n = 119$), *TEF3* ($n = 144$), *RPB1* ($n = 71$) and *RPB2* ($n = 97$) were examined. Among these sequences, 860 of them [ITS, $n = 324$; LSU, $n = 270$; *TUB*, $n = 122$; *RP60S*, $n = 73$; *RPB1*, $n = 25$ and *RPB2*, $n = 46$] represented the type strains. A combined tree consisted of eight loci data of 342 strains. This dataset was found to be 7014 bp in length and contained 3706 parsimony-informative sites. A summary of the tree characteristics for each locus is given in Table 2. On the basis of defined parameters above, the quality of the trees constructed with IQ-TREE-ML for ITS, LSU and multilocus sequences was found better than those created by MrBayes and RAxML tools separately. On the other hand, for the family-based ITS analyses, MrBayes on the CIPRES portal and ML method on the MEGA6 gave better resolution among the genera for Gymnoascaceae and, Ascosphaeraceae and Spiromastigaceae, respectively.

The best-fit model for LSU data evaluation was Transition model (TIM3)+I+G4+F. The results of the LSU phylogeny of 409 strains (Group I LSU analysis) showed one unsupported and 13 supported clade branches (bootstrap support $\geq 80\%$). The ultimate clade of Arthrodermataceae was followed by Onygenaceae, Gymnoascaceae, Ascosphaeraceae, and Spiromastigaceae, with Ajellomycetaceae in the ancestral position (Suppl. Fig. 1). In this phylogeny, members formerly classified in Gymnoascaceae were found in two supported clades. Onygenaceae formed three clades (A–C), the first of which included the type species of *Auxarthronopsis*, *Canomyces*, *Currahmyces*, *Neogymnomycetes* and *Renispora*; the second one (Clade B) was formed by *Auxarthron* and *Malbranchea* species, and the last one (Clade C) included the types of *Amauroascus*, *Aphanoascella*, *Aphanoascus*, *Ascocalvatia*, *Byssoonygena*, *Coccidioides*, *Keratinophyton*, *Nannizziopsis*, *Onygena*, *Ophidiomyces*, *Paranannizziopsis*, *Pectinotrichum* and *Emydomyces*. The family Ajellomycetaceae was subdivided into two clades, while members of the Eremascaceae were found within Ajellomycetaceae. Meanwhile, Group II LSU analysis ($n = 269$) revealed 13 supported and three unsupported clades, and Gymnoascaceae members were subdivided into one unsupported and three supported clades (Suppl. Fig. 2).

Phylogenetic evaluation of ITS data was performed with General time-reversible model (GTR)+I+G4+F as the best-fit tree model. Phylogenetic analysis using only ITS locus sequences of 488 strains (Group I ITS analysis) revealed 15 clades with bootstrap support values of $\geq 80\%$ (Suppl. Fig. 3). The genus *Sigleria*, a purported member of Spiromastigaceae, was found far from the remaining members of the family, and members of Nannizziopsiaceae (correct name according to the Index Fungorum database: Nannizziopsidaceae) were placed far apart from other members of Onygenaceae Group C. Species attributed to Onygenaceae were scattered over four supported clades along with species previously described as *incertae sedis*. The classical family Gymnoascaceae was found with 72/94% support, with a basal clade formed by *Kraurogymnocarpa trochleospora* (CBS 591.71) and *Diploospora rosea* (DAOM 250100). Eremascaceae was found to be a separate supported clade. The tree topology revealed the soilborne and halophilic genera *Spiromastigoides* to be positioned at the base of the tree, while the family Arthrodermataceae with mammal-associated

species was placed in the most derived position, followed by Gymnoascaceae; Onygenaceae; Eremascaceae; the bee- and pollen-associated genus *Ascosphaera*; and Ajellomycetaceae including members causing systemic infections in mammals. Using the ITS sequences of 323 strains (Group II) yielded 12 supported and three unsupported clades. In addition, the genus *Paranannizziopsis* was found distant from the members of *Nannizziopsis* (Suppl. Fig. 4) in ITS Group II phylogeny.

Similar to the ITS data, the best-fit tree model for the multilocus analysis was found to be GTR+I+G4+F. Results of the combined analysis of eight loci using 342 sequences yielded 14 clades with $\geq 80\%$ bootstrap support. Families, based on their type genera and type species, were resolved as Ajellomycetaceae, Arthrodermataceae, Ascosphaeraceae, Eremascaceae, Gymnoascaceae, Onygenaceae and Spiromastigaceae (Fig. 1). Onygenaceae were found to be polyphyletic, breaking up into three supported clades (A–C), as in the LSU analyses. Arthrodermataceae were again found in the ultimate position, and Ascosphaeraceae were at the base, with Eremascaceae. Other clades below Arthrodermataceae were placed as follows: Onygenaceae clade C, Onygenaceae clade B, Onygenaceae clade A, Gymnoascaceae, Ajellomycetaceae and Spiromastigaceae. Strains belonging to Arachnomycetaceae were included in the analyses but were found outside the order Onygenales in all phylogenetic trees.

The highest rate of supported/unsupported clade value among the ITS, LSU and multilocus trees was found in the ITS Group I phylogeny (15/0), followed by multilocus phylogeny. However, members of Onygenaceae and Spiromastigaceae were divided into more groups in the ITS phylogeny than in the multilocus analyses. In addition, clades were supported with higher bootstrap values in the multilocus analysis. Therefore, multilocus phylogeny was chosen to demonstrate the combined ecology, physiology and phylogeny data (Fig. 2).

Among the phylogenies of the other loci, Eremascaceae were not represented in the *TUB*, *TEF3* or *RP60S* analyses. Further, no *TEF3*, *RPB1*, *RPB2* or *RP60S* records were found for the members of Neogymnomycetaceae, while Ascosphaeraceae could not be included in the *RP60S* analysis. The most variable results were obtained for the Onygenaceae family, changing from one to five clades. The highest supported/unsupported ratio was found in the *RP60S* analysis (11/0) because

the family Arthrodermataceae was divided into three supported clades. In addition, Ascospaeraceae were found in a doubtful position, close to Arthrodermataceae. In contrast, the lowest ratio was found in the *TEF3* analysis (11/2) with four Onygenaceae and two Arthrodermataceae clades. Both *RPB1* and *RPB2* phylogenies revealed similar topologies to multilocus phylogeny (Fig. 3). A comparison of all the phylogenetic trees is summarized in Table 3.

The ecological preferences of species can be classified as soil/oligotrophic, soil/keratinophilic, dung/agricultural, skin/nail, hair/feather, insect/pollen, halophilic/osmophilic, systemic, plant and other/unknown (Fig. 4). Four main ascomata morphology types were noted as cleistothecium, gymnothecium, spore cyst and naked fruitbody (Fig. 2). Fruitbodies on a stipe structure reported in *Onygena corvina*, *Onygena equina* and *Narasimhella poonensis* were classified as “other”.

Although 21 families have been introduced in the Onygenales between 1833 and 2014, descriptions of these families were mostly based on their ascomata and peridium morphology, however, most of them are currently obsolete because they were not supported in later studies (Table 1). Judging from the multilocus phylogeny, ecology and reconstruction data, the order Onygenales can be described with the core families Arthrodermataceae, Ajellomycetaceae, Ascospaeraceae, Eremascaceae, Gymnoascaceae, Onygenaceae, and Spiromastigaceae. The family Nannizziopsidaceae clustered amidst members of Onygenaceae and therefore, Nannizziopsidaceae are preliminarily considered as a group within Onygenaceae rather than a separate family. Clades supported by high bootstrap values but lacking a type of described family are indicated as *incertae sedis*. Meanwhile, two clades with type species supported by high bootstrap values were reintroduced or newly introduced as Auxarthraceae and Neogymnomycetaceae, respectively. Relationships between genera within each family were determined by ITS phylogeny, because of the higher variability of this marker enabling the comparison of more closely related entities for more recent speciation events (Berbee and Taylor 2001; Stielow et al. 2015) and the number of available sequences in public databases being larger than that of other loci. Branches formed by *Harorepupu aotearoa*, *Pectinotrichum llanense* and *Testudomyces verrucosus* were found to be relatively long in multilocus analyses (Fig. 1). The first species was found outside of defined families in all phylogeny analyses; therefore, it was regarded as

incertae sedis. The other two species were found to be related to Onygenaceae (Fig. 1; Suppl. Figs 3 and 4). Using these species as outgroups did not change the topology of the multilocus tree, while the supported/unsupported ratio was found to be lower, i.e., 12/1 for *H. aotearoa* and *T. verrucosus* and 12/2 for *P. llanense* (Table 3).

Results from phylogenetic analyses (Fig. 1) can be summarized as follows. **Clade 1** comprises members of the family Arthrodermataceae including the keratinophilic genera *Arthroderma*, *Ctenomyces*, *Epidermophyton*, *Guarromyces*, *Lophophyton*, *Microsporum*, *Nannizzia*, *Paraphyton* and *Trichophyton*. Ecology of the species was found mainly invading fur, skin and nails (73/120), followed by soil (37/120). Most geophilic species cluster in basal positions in the family, while anthropophilic species were in derived positions and zoophiles were located in the middle of the tree (Fig. 1).

Members of **Clades 2, 3 and 4** have previously been described in Arthrodermataceae, Onygenaceae, or were regarded as *incertae sedis* (Kubátová et al. 2017; Wijayawardene et al. 2017). Since morphology and ecology among the Onygenaceae members are variable, Clades 2 and 3 could be related to Onygenaceae. However, the present study determined the families based on the phylogenetic position of the type species, and Clades 2, 3 and 4 are found remote from the type of the Onygenaceae (Fig. 1). Additionally, Clade 2 was found closer to Arthrodermataceae than Onygenaceae. Ecological preferences of members of the clades showed a large diversity: all categories are represented, except for association with systemic diseases and insects or pollen. Keratinophilic species as well as cellulolytic species isolated from plant debris were included in these clades. **Clade 2** included the type species of *Shanorella* (CBS 305.56) and *Chrysosporium vallenarense* (CBS 627.83); **Clade 3** (with 68% bootstrap support) included the type species *Myotisia cremea* (CBS 141864) and *Leucothecium emdenii* (CBS 576.73); **Clade 4** (100% bootstrap support) contained the types of *Arachnotheca* (type species *A. glomerata*, CBS 348.71), *Apinisia* (type species *A. graminicola*, CBS 721.68), and *Myriodontium* (type species *M. keratinophilum*, CBS 947.73).

Clade 5 contains the members of the family Onygenaceae. Five groups are distinguishable in this clade (Fig. 1): Group 5-I was represented by the oligotrophic species of *Keratinophyton* (type

species *K. terreum*, CBS 342.64); Group 5-II contained species of *Aphanoascus* (type species *A. fulvescens*, UAMH 4114). Compared to Group 5-I, isolates of Group 5-II showed association with nutrient-rich soil, dung and keratinous substrates (Fig. 1; Suppl. Table 1). Group 5-III contained *Amauroascus* (type species *A. niger*, CBS 114.61), *Brunneospora* (type species *B. reticulata* UAMH 5704), *Byssoonygena ceratinophila* (type strain UAMH 5669) and *Coccidioides* (type species *C. immitis*, CBS 120936). Members of the latter genus are dimorphic fungi and they cause systemic mycosis in mammals via the inhalation of environmental propagules leading to endospore forming spherule formation and hematogenous dissemination in the host (Van Dyke et al. 2019). Group 5-IV included mainly reptile-associated species of *Nannizziopsis* (type species *N. vriesii*, CBS 407.71) and *Paranannizziopsis* (type species *P. australasiensis*, UAMH 11645) which have been classified in the separate family Nannizziopsidaceae by Stchigel et al. (2013d). Group 5-V included *Onygena equina* (neotype strain CBS 947.70), which is the type species of the family and of the entire order. In addition, *Ascocalvatia alveolata* (type strain CBS 777.70) from carnivore dung and another reptile-related fungus, *Ophidiomyces ophidiicola* (type strain CBS 122913) and soil-borne fungus *Pseudoamauroascus* (type species *P. australiensis* UAMH 8392) were included in this group. Additionally, *Aphanoascella* (type species *A. galapagosensis* CBS 132345), *Emydomyces* (type species *E. testavorans* ATCC TSD 145), which were described from infections in turtles (Woodburn et al. 2019; Sutton et al. 2013) and another keratinophilic genus, *Pectinotrichum* (type species *P. llanense* CBS 882.71) were also found in Onygenaceae.

Members of **Clade 6** (100% BI) belong to the genera *Auxarthron* (type species *A. californiensis*, CBS 129.62) and *Malbranchea* (type species *M. pulchella*, CBS 202.38) (Fig. 1). Keratinolytic activity varies among different *Auxarthron* species. The majority of strains analyzed had been isolated from eutrophic soil and dung (Suppl. Table 1; Fig. 4). Although *A. ostraviense* and *A. umbrinum* were occasionally reported from onychomycosis cases (Orr et al. 1963a; Hubka et al. 2013), *A. zuffianum* was once isolated from the lung of a dog (Emmons 1954) and *A. filamentosum* from a skin of snake (Sigler et al. 2002a), these species were not proven to be pathogenic (Bowman et al. 1996). Combining the previously described morphological characters (Solé et al. 2002a; Sarrocco

et al. 2015; Zhang et al. 2021) and ecology of the strains with current phylogeny results, Clade 4 was considered as a separate family and the name Auxarthraceae was chosen as proposed by Locquin (1984).

Clade 7, with 98% BI support in the ML tree (Fig. 1) included *Auxarthronopsis bandhavgarhensis* (type strain CBS 134524), *Canomyces reticulatus* (type strain MCC 1486), *Currahmyces indicus* (type strain MCC 1548), *Neogymnomyces demonbreunii* (type strain CBS 427.70) and *Renispora flavissima* (type strain CBS 708.79). Except for the type species of *Auxarthronopsis* from India, all species of this genus were recorded from karst caves in China (Suppl. Table 1). All type strains of described species were found to be keratinophilic. In consideration of a stable phylogenetic position supported with different loci analyses, as well as a consistent habitat of the species, the new family name Neogymnomycetaceae is proposed for this clade.

Clade 8 was classified as *incertae sedis* and formed by type of *Amauroascus aureus* (CBS 593.71) and xerophilic *Diploospora rosea* (epitype, DAOM 250100).

Members of Gymnoascaceae are placed in **Clade 9** (83% BI support in ML) (Fig. 1) with the type species of the genera *Arachniotus* (*A. ruber*, type strain CBS 352.90), *Gymnascella* (*G. aurantiaca*, neotype strain UAMH 3138), *Gymnoascoideus* (*G. petalosporus*, type strain UAMH 1665), *Gymnoascus* (*G. reessii*, type strain CBS 392.64) which is also the type genus of the family and *Narasimhella* (*N. poonensis* type strain CBS 393.71). Ecological key words of the clade were dominantly oligotrophic and soil (33/79), followed by dung (20/79). The clade also contains halophilic species (*Sphaerosporium equinum* and *Sporendonema casei*) isolated from cheese, which is a unique habitat in the order.

Clade 10 included the members of the family Spiromastigaceae; genera *Sigleria* (*S. carmichaelii* CBS 138264), *Spiromastigoides* (type *Sp. warcupii* CBS 576.63) which is type of the family and *Pseudospiromastix* (type *P. tentaculata* CBS 184.92) (Fig. 1). Members of this clade show xerophilic characteristics, and keratinolytic and cellulolytic activity is variable among the members

(Currah 1994; Hirooka et al. 2016). So far, only two species *Sp. asexualis* and *Sp. albida* were reported as causative agents of deep infections in mammals (Rizzo et al. 2014; Stchigel et al. 2017).

Clade 11 was classified as *incertae sedis* and formed by type of *Polytolypa* (*P. hystiricis* UAMH 7299) and *Amaurascopsis* (type species *A. perforata* FMR 3882) along with *Chrysosporium chiropterorum* (type species MUCL 45495) and *C. lobatum* (type species CBS 666.78) (Fig. 1).

Clade 12 contained the family Ajellomycetaceae with 100% support in the ML tree (Fig. 1). Ajellomycetaceae includes the genera *Blastomyces* (type species *B. dermatitidis*, CBS 674.68), *Emergomyces* (type species *E. pasteurianus*, CBS 101426), *Helicocarpus* (type species *H. griseus*, CBS 128.88), *Histoplasma* (type species *H. capsulatum*, CBS 536.84), *Lacazia* (type species *L. loboi*, BPI 792295) and *Paracoccidioides* (type species *P. brasiliensis* Pb18 = B17). The genus *Emmonsia* has been reduced to synonymy of *Blastomyces* (Jiang et al. 2018), while the remaining species were transferred to *Emergomyces* (Jiang et al. 2020). The geophilic genus *Emmonsiiellopsis* (type species *E. terrestris*, CBS 273.77) was described in Ajellomycetaceae as an ancestral position based on ML analyses of ITS, LSU, *RPB2*, *TEF3* and *TUB2* genes (Jiang et al. 2018).

Clade 13 comprises Ascospaeraceae species (100% bootstrap support in all trees) and is represented by *Ascospaera apis* (neotype strain CBS 534.69), which is the type species of the family. All members of the clade are associated with bee habitats including nests, pollen and larvae; they can be saprophytic or pathogenic for bees (Wynns 2015).

The last clade, **Clade 14** was formed by members of Eremascaceae including the insect-related fungus *Dactylodendron pinicola* (formerly known as *Arthrographis pinicola*; type strain CBS 653.89) and the osmophilic species *Eremascus albus* (neotype strain CBS 975.69). Both LSU Group I and Group II analysis were not compatible with the other phylogenetic results, such that Eremascaceae were embedded in Ajellomycetaceae (Suppl. Figs. 1, 2).

Simply structured, thallic microconidia are produced throughout the order Onygenales. Species with enteroarthric conidia are generally classified under *Malbranchea* and species with holoarthric conidiation, under *Chrysosporium*. Both genera were already described in the 19th century

and have been neotypified with *Malbranchea pulchella*, neotype strain CBS 202.38 and *Chrysosporium merdarium*, neotype strain CBS 388.68, respectively (Saccardo 1882; Corda 1833; Carmichael 1962; van Oorschot 1980). Numerous described species are phylogenetically remote from these types, clustering within or outside the order Onygenales and require reclassification. For example, in all phylogenetic analyses, the type species of the asexual genus *Malbranchea*, *M. pulchella*, CBS 202.38, was found in the same clade as that of the sexual genus *Auxarthron*, *Auxarthron californiense*, CBS 129.62. Similarly, the *Chrysosporium* species in the families Arthrodermataceae, Onygenaceae and Spiromastigaceae were reclassified when neotypes were available; otherwise, names were maintained according to their first description.

Taxonomy

Onygenales Cif. ex Benny & Kimbr. - Mycotaxon 12(1): 8, 1980

Type family: Onygenaceae Burnett - Outl. Bot. (London): 159, 1833; type genus: *Onygena* Pers. - Observ. Mycol. (Lipsiae) 2: 71, 1800; type species: *Onygena equina* (Willd.) Pers.

Neotype designated here: CBS-H 15271, on cow hoof, The Netherlands, 1970, H.A. van der Aa. Culture derived from the type CBS 947.70 = ATCC 22731 = IFO 31785.

The order Onygenales was first described by Ciferri (*nomen nudum*, Atti Ist. Bot. Univ. Pavia, Ser. 5, 14: 239. 1957: without Latin diagnosis; Art. 36 ICBN). Later Benny and Kimbrough (1980) redefined the order and distinguished three families: Dendrosphaeraceae, Gymnoascaceae, and Onygenaceae. The order includes frequently keratinophilic species with sessile or stipitate ascocarps, with or without appendages, or sessile, composed of loose, interwoven hyphae (gymnothecium), or naked asci, fruitbodies being absent; asci ovoidal or subclavate, evanescent, containing eight spores; ascospores hyaline or brightly colored; microconidia homo- or enterothallic, lateral or intercalary; additional septate macroconidia may be present.

The type species of the Onygenales was first described by Willdenow (1787) as *Lycoperdon equinum* from hooves of horses. Later, Persoon reported that *L. equinum* is different from other *Lycoperdon* species which are now known as a basidiomycetous sac fungus, and consequently introduced the genus *Onygena*, with type species *Onygena equina* (Persoon, 1800 [1799]), commonly known as the horn stalkball. Type material is not known to be preserved. A culture of the neotype specimen is available as CBS 947.70. This culture stabilizes the nomenclature of the order Onygenales.

When Currah reviewed the order Onygenales in 1985, he included cellulolytic species in the family Myxotrichaceae (Currah 1985). However, later studies questioned its assignment and at present the family has been excluded from the order (Currah 1994, Hambleton 1998, Leclerc et al. 1994, Sugiyama et al. 1999). Later, Wang et al. (2006) confirmed that Myxotrichaceae is a family of Leotiomycetes. Similarly, the taxonomic position of Arachnomycetaceae was doubtful for a long time. The generic type *Arachnomyces* was first described in Onygenaceae by Malloch and Cain (1970). Abbott et al. (1996) suggested to reclassify the genus within Gymnoascaceae based on ascospore structure and inability to degrade keratin, even though many members of the family have an apparent affinity to keratinous substrates (Ulfig et al. 1998; Scott and Untereiner 2004). *Arachnomyces* differs morphologically from Gymnoascaceae by its conidial type and by the presence of cleistothecia rather than gymnothecia. Multilocus studies of conserved genes and combined with morphological and molecular characteristics (Gibas et al. 2002a; Sun et al. 2019) suggested that Arachnomycetaceae deserve the status of a separate order as Arachnomycetales. Results of the current study also confirmed that members of Arachnomycetaceae cannot be classified in the order Onygenales (Fig. 1; Suppl. Figs 1–4).

Phylogenetic, morphological and ecological and characteristics of recognized families in the order Onygenales are summarized below.

Clade 1

Arthrodermataceae Locq. ex Currah

Type genus: *Arthroderma* Curr. - Outl. Brit. Fung. (London): 357, 1860; type species: *Arthroderma curreyi* Berkeley. Epitype CBS 353.66, from dune soil, UK, A.E. Apinis, 1966 (de Hoog et al. 2017).

Ancestral members of this family generally have white, pale yellow or yellowish brown, globose ascomata with appendages; thin-walled, transparent, subglobose to globose asci; hyaline to pale yellow, smooth, minute, oblate to oblate-discoid or oblate-convex ascospores (Currah 1985). They often produce large, multiseptate macroconidia in addition to one-celled, sessile microconidia of the chrysosporium-like (except genus *Ctenomyces*) (Currah 1985). In the derived, mostly human-associated species (genus *Trichophyton*), sexuality tends to be lost, the mating types each evolving as separate clones (Gräser et al. 2006; Kandemir et al. 2020). The family comprises the genera *Arthroderma*, *Ctenomyces*, *Epidermophyton*, *Guarromyces*, *Keratinophyton*, *Lophophyton*, *Microsporum*, *Nannizzia*, *Paraphyton* and *Trichophyton* (de Hoog et al. 2017) (Fig. 5). Phylogenetic results showed that type strains of several described *Chrysosporium* species, and that of *Pectinotrichum chinense* (type strain LC5811) clustered in the family among species of *Arthroderma* (Figs 1, 5). Additionally, *Shanorella spirotricha* (type strain CBS 305.56) and *Leucothecium emdenii* (type strain CBS 576.73) were found close to Arthrodermataceae (Fig. 1). Available molecular and morphological data for the last two species were combined and they are judged as *incertae sedis*, discussed in related sections below.

Members of Arthrodermataceae are characteristically mammal-associated fungi with keratinolytic abilities. Otčenášek and Dvořák (1975) classified them as geophilic, zoophilic and anthropophilic, depending on the part of the life cycle that is environmental or closer to the mammalian or human host. De Hoog et al. (2018), used transmissibility as a criterion to distinguish environmental pathogens from zoophilic pathogens, with infection taking place either via environmental propagules or by direct host-to-host transmission. This concept matches geophilic *versus* anthropophilic species, with zoophilic taxa being intermediate, as they are carried for prolonged periods in the fur of the host animal. However, determination of the natural habitat of a species may not always be easy. Geophilic, zoophilic and anthropophilic occurrences are statistical trends rather than diagnostic parameters. In humans, anthropophilic species have evolved toward chronic but mild

infection, while infections of humans by zoophilic species tend to be acute and inflammatory and those by geophiles are often self-limited and quickly resolved.

The above phylogenetic and ecological trends are also approximately reflected in sexuality, clonality and loss of specialized reproduction (de Hoog et al. 2017; Persinoti et al. 2018). Anthropophilic species are necessarily at the top of phylogenetic trees, given that *Homo sapiens* is the most recent host (Gräser et al. 2000; Fig. 1). Transmission occurs by skin flakes loaded with amorphous fungal cells, associated with significant morphological reduction compared to the elaborate environmental sexual forms commonly observed in geophiles (Li et al. 2010). Zoophilic species lie between these two edges by mostly sporulating and showing sexual reproduction upon mating (Metin and Heitman 2017).

Changes in habitat and host preference at the species level are usually accompanied by slight differences in phenotypic and physiological characteristics (Kandemir et al. 2020; Su et al. 2019). Clonal offshoots may become distinct species (Gräser et al. 2006; Kano et al. 2014). Understanding the biology of dermatophytes using polyphasic approaches has led to the delimitation of closely related siblings within species complexes, which are clinically relevant because of differences in predilection for the human body, such as in the *Trichophyton rubrum*/*T. violaceum* complex (Su et al. 2019; Zhan et al. 2018) and the *T. tonsurans*/*T. equinum* complex (Kandemir et al. 2020). The *T. mentagrophytes*/*T. interdigitale* complex deserves attention because of clones with increased levels of virulence and antifungal drug resistance (Singh et al. 2019; Nenoff et al. 2019; Chowdhary et al. 2019; Tang et al. 2021).

Since the derived species potentially infecting human skin and nails (dermatophytes) are among the well-studied groups in the order Onygenales in terms of laboratory identification, antifungal resistance and taxonomy (Monod 2019; Gupta et al. 2017; de Hoog et al. 2017; Khurana et al. 2019; Martinez-Rossi et al. 2018; Baert et al. 2020; l'Ollivier and Ranque 2017; Dukik et al. 2019; Su et al. 2019; Zhan et al. 2018), we summarize currently available data for remaining family members below.

During phylogenetic analyses, several GenBank records were encountered with other generic names than the ones above but which clustered in Arthrodermataceae. Two strains deposited as *Onygena corvina* CBS 225.60 and CBS 281.48 (LSU MH869510 and FJ358287, respectively), were misidentified. Both strains showed 100% LSU identity with *Arthroderma crocatum*, type strain IHEM 5251, KT155108 (Hainsworth et al. 2021). This was confirmed by CBS 225.60 having 99.6% ITS identity with *A. crocatum* CBS 130.70 (AJ877223).

Corda (1833) introduced the genus *Chrysosporium*, with *Chrysosporium corii* as a type species. The original material leather, dating back to 1833 from herbarium in Prague (PR), Czechoslovakia, is preserved at the Canadian National Mycological Herbarium with a slide of the type as DAOM 55541 (personal communication with Jennifer Wilkinson). To stabilize the current nomenclature, van Oorschot (1980) proposed *C. merdarium* as a type species of the genus, using slide DAOM 43321 as a reference. However, this material is not interpretable either, and the status of the species remains uncertain. Numerous species have been described in *Chrysosporium* based on morphology, which according to modern criteria, are non-diagnostic. Described *Chrysosporium* species appear highly polyphyletic. Given this polyphyly, and the fact that no interpretable type material exists, we regard *Chrysosporium* as *nomen confusum*.

The type strain of *Chrysosporium kuzurovianum*, CBS 667.78 has been recorded as a synonym (van Oorschot 1980) of *C. keratinophilum* (type strain CBS 104.62). However, it differs by its colony color, larger conidia, the presence of multiple conidial shapes and the absence of arthroconidia (Scharapov 1974; van Oorschot 1980). This is confirmed by phylogeny (Figs 1, 5) showing affinity to *Arthroderma multifidum* (99.7% LSU to KT155237, 97% ITS to KT155892). Therefore, the following new combination is proposed:

Arthroderma kuzurovianum (Scharapov) Kandemir & de Hoog, **comb. nov.** – MycoBank XXX.

Basionym: *Chrysosporium kuzurovianum* Scharapov - Nov. Sist. Niz. Rast. 11: 266, 1974; type strain CBS 667.78 = UAMH 4322 = VKM F-2119, from black soil, Russia.

495 Van Oorschot (1980) examined CBS 277.77 and proposed a new combination *Chrysosporium*
 496 *pannicola* (Corda) v. Oorschot & Stalpers. The holotype herbarium specimen in National Museum,
 497 Prague, Czech Republic (PRM), on cloth, is not interpretable; therefore, the following **epitype strain**
 498 **is designated here:** CBS 277.77, from unknown source, G.F. Orr, 1961. Current results show that this
 499 strain clusters in Arthrodermataceae. Note that Labuda et al. (2021) reclassified the species in
 500 *Keratinophyton*, but this was based on supposed synonymy with the type strain CBS 116.63 of
 501 *Keratinophyton evolceanui* above. The following combination is required for the strain CBS 277.77:
 502 ***Arthroderma pannicola* (Corda) Kandemir & de Hoog, **comb. nov.** – MycoBank XXXX.**

503 Basionym: *Capillaria pannicola* Corda - Icon. Fung. 1: 10. 1837 $\equiv$ *Sporotrichum pannicola* (Corda)
 504 Rabenhorst - Deutschl. KryptFl. 1: 78, 1844 $\equiv$ *Chrysosporium pannicola* (Corda) van Oorschot &
 505 Stalpers - Stud. Mycol. 20: 43, 1980 $\equiv$ *Keratinophyton pannicola* (Corda) Labuda et al. – IMA Fungus
 506 12(1):17, 2021. Type strain: CBS 277.77 = UAMH 1125 = Orr O-736 from unknown source, isolated
 507 by G.F. Orr, in 1961.

508 The soil-borne genus *Pectinotrichum* (type species: *P. llanense*, CBS 882.71) is morphologically
 509 similar to *Arthroderma* in having gymnothecia with characteristically arched hyphae with short and
 510 long appendages that are usually slightly curved or bent at the apices (Varsavsky and Orr, 1971). The
 511 GenBank record AJ390391 for the ITS locus of the type species was found to be different from that of
 512 MH860394, NR119467 and LR136983. Phylogenetic results with the first one showed *P. llanense* in
 513 Arthrodermataceae together with *Pectinotrichum chinense*, while the results with the other records
 514 placed the species in Onygenaceae. Molecular analyses based on small subunit (SSU) and LSU
 515 showed that generic type species *P. llanense* clusters in the family Onygenaceae (Sugiyama et al.
 516 1999; Sugiyama and Mikawa 1999), while *P. chinense* is amidst species of *Arthroderma* (Fig. 5).
 517 Consequently, the following combination is proposed:

518 ***Arthroderma chinense* (Zhang & Cai) Kandemir & de Hoog, **comb. nov.** – MycoBank XXXX.**

519 Basionym: *Pectinotrichum chinense* Zhang & Cai - Persoonia 39: 21, 2017; type strain: LC5811, from
 520 soil from a karst cave, China, isolated by Z.F. Zhang & S.Y. Cai.

521

522 *Ctenomyces* Eidam - Beitr. Biol. Pfl. 3: 274, 1880; type species: *Ctenomyces serratus* Eidam. Type
523 (Orr and Kuehn 1963a): CBS 187.61 = ATCC 15504 = IMI 86199 = NRRL A-11176, from soil,
524 Australia. Herb. No: CBS H-14818.

525 *Ctenomyces serratus* was originally thought to be a resting or sclerotial phase of *Arthroderma curreyi*
526 bearing comb-like appendages. Since the original material is lost, Benjamin (1956) described *C.*
527 *serratus* as a separate species and Orr and Kuehn (1963) indicated a neotype, IMI 86199. The genus
528 *Ctenomyces* was described as having orange-brown cleistothecia, a peridium composed of a thin layer
529 of densely interwoven hyphae, and ctenoid appendages consisting of thick-walled, asperulate cells.
530 Conidia are verrucose, thick-walled, lightly pigmented, commonly with ampulliform swelling
531 (Benjamin 1956; Zhang et al. 2019). The habitat of *Ctenomyces* species is soil enriched with bird
532 feathers (Currah 1985; Zhang et al. 2019); no animal pathology is known. Isolation of known
533 *Ctenomyces* species involves hair baiting techniques using chicken feathers and human hair, and hence
534 species are probably keratinophilic like other members of the family. Gymnothecia of *Ctenomyces*
535 species bear characteristic comb-like appendages on the peridia, which Currah (1985) suggested to
536 enhance the adaptation of the fungus to be transported via avian feathers. In addition, ascospores in
537 *Ctenomyces* are large (mostly > 8 µm in length; Currah 1985; Zhang et al. 2019). Currently, *C. albus*,
538 *C. indicus*, *C. serratus*, *C. peltricolor*, *C. obovatus* and *C. vellereus* have been included in the genus.
539 Zhang et al. (2019) referred to the identification key for *Ctenomyces* species.

540 Van Oorschot (1980) introduced *Ctenomyces* as a sexual morph of *Myceliophthora*, which
541 was later confirmed by phylogenetic analysis of *M. vellerea* (van den Brink et al. 2012). In the same
542 study, *M. vellerea* was found phylogenetically (ITS, *TEF1-α* and *RPB2*) remote from the type species
543 of the genus, *M. lutea* and was renamed in *Ctenomyces*.

544 *Ctenomyces vellereus* (Sacc. & Speg.) Kirk - Index Fungorum 120: 1, 2014 ≡ *Sporotrichum vellereum*
545 Sacc. & Speg. - Michelia 2 (7): 287, 1881 ≡ *Myceliophthora vellerea* (Sacc. & Speg.) van Oorschot -

Stud. Mycol. 20: 47, 1980. **Neotype designed here:** CBS 479.76, dried culture from soil, Egypt, isolated by H.M. Yusef.

Ctenomyces bossae Milochevich (1935) (GenBank MH855761, ITS and GenBank MH867274, LSU) was described with type strain CBS 176.36. However, phylogenetic results showed that this species is remote from type of the genus (Zhang et al. 2019), clustering with *Trichophyton tonsurans* and *T. equinum* (Fig. 4), which is in agreement with human skin as source of its isolation.

Vanbreuseghem (1952) introduced the genus *Keratinomyces*, typified by *K. ajelloi*, to include dermatophytes with fusiform, smooth-walled macroconidia and lacking microconidia. Molecular studies showed that *K. ajelloi* is a synonym of *Arthroderma uncinatum* (de Hoog et al. 2017), while a second species, *K. longifusus* had been reclassified as *Nannizzia fulva* (de Hoog et al. 2017). *Keratinomyces ceretanicus* was the only species left in the genus, and as it was phylogenetically remote from *A. uncinatum*, the genus *Guarromyces* was erected (de Hoog et al. 2017). The type strain FFBA 328 was described from the forest soil in Catalunya (Punsola and Guarro, 1984), but the only available record is CBS 269.89 = FMR 3063 = UAMH 6412, an isolate from soil in Chile deposited by J. Guarro in 1988; this isolate was used as a neotype (de Hoog et al. 2017).

The genus *Thallomicrosporon* was introduced with the type species *Thallomicrosporon kuehnii*, type strain CBS 119.64 (Benedek 1964). Benedek (1969) suggested that this species may have derived from another dermatophyte as a stable mutant. Molecular analyses in the current study showed that the type strain is identical to CBS 258.61, type of *Nannizzia gypsea* (99.7% LSU identity to NG064029 and 100% ITS identity to NR131271) and is therefore regarded as a synonym.

Clade 2–4 *Incertae sedis*

The genus *Shanorella* contains a single species, *S. spirotricha* with characteristic peridial hyphae with coiled appendages (Benjamin 1956) and it can be differentiated from *Ctenomyces* by its spiral rather than ctenoid appendages on the peridium (Benjamin 1956). The habitat choice of bird feathers is similar in both genera (Currah 1985; Zhang et al. 2019; Benjamin 1956) and the specialized peridial

hyphae probably enhance attachment to feathers. In the current study, *S. spirotricha* clustered in Clade 2 with the type of *Chrysosporium vallenarense* (CBS 627.83) in both ITS (with 93% similarity) and LSU analyses (with 97% similarity). Based on phylogenetic results, they formed a separate clade basal to the Arthrodermataceae (Fig. 1, Suppl. Figs 1–4). In the current study, *Shanorella* was maintained as *incertae sedis*; *Chrysosporium vallenarense* requires nomenclatural revision.

Clades 3 and 4 contain several generic type species, i.e., *Leucothecium emdenii* (CBS 576.73), *Myotisia cremea* (CBS 141864 = CCF 5407), *Arachnotheca glomerata* (CBS 348.71 = ATCC 22733 = UAMH 3551), *Arthrospis hispanica* (CBS 351.92 = FMR 4058), *Apinisa graminicola* (CBS 721.68 = ATCC 18745 = IMI 126422 = Orr O-1125), *Kuehniella racovitzae* (CBS 156.77 = ATCC 28557 = NRRL 6154), and *Myriodontium keratinophilum* (CBS 947.73) (Fig. 1). Clade 3 was found the only unsupported clade with <80% bootstrap values based on ML analysis.

The genus *Myotisia* was introduced with the type species *Myotisia cremea* (CBS 141864) from bat droppings (Kubátová et al. 2017) and classified in Onygenaceae based on morphology (gymnothecium with globose, smooth-walled and hyaline ascospores, malbranchea-like conidial morph). The genus *Arthrographis* Cochet ex Sigler & Carmich. (1976), represented by the type species *Arthrographis kalrae* (type strain CBS 693.77) is found phylogenetically to belong to Eremomycetaceae in Dothideomycetes (Giraldo et al. 2014). However, ITS, LSU and ML phylogeny data showed a cluster containing *Arthrographis alba* (type strain CBS 370.92, from marine sediment, Spain) and *Leucothecium emdenii*, the generic type species (type strain CBS 576.73, from agricultural soil, The Netherlands), in a basal position to Arthrodermataceae with different levels of support (Fig. 1; Suppl. Figs 1–4). Giraldo et al. (2014) applied sequences of ITS and D1/D2 domains of the 28S rRNA and underlined that *A. alba* is the asexual morph of *L. emdenii*. The species was published to be weakly keratinolytic and does not grow at 40°C (Gené et al. 1996).

Arthrospis hispanica and *Arachnotheca glomerata* grouped together and ITS and LSU similarities between the two species were found to be 88% and 97%, respectively. In addition, in both

species, conidia are formed by fragmentation of hyphal branches (von Arx 1971; Ulfig et al. 1995). Since the type species of the genus *Arthrospis* (*A. truncata* UAMH 4430), is classified in Sordariomycetes (Giraldo et al. 2014) a nomenclatural revision is required for *A. hispanica*.

Myriodontium keratinophilum was described from keratinous substrates in Italy (Samson and Polonelli 1978) and as a cause of infections in humans in two reports (Maran et al. 1985; Kochhar et al. 2018). The identification of the fungi in these reports was based on colony and microscopic morphology only. Cano et al. (1997) described *M. keratinophilum* as anamorph of *Neoarachnotheca keratinophila* (type strain FMR 4016, from marine sediments, Spain; Herb. IMI 351982 is stored in the Kew Herbarium, U.K.). The other strains, *Arachniotus albicans* (type CBS 151.65 = ATCC 22478 = IHEM 4423 = IMI 100875), *Chrysosporium carmichaelii* (type CBS 643.79), *C. georgiae* CBS 625.79, *C. pallidum* (type CGMCC 319575) and *C. undulatum* (type CBS 964.97 = FMR 6101) need revision since they are remote from the type species of their genera based on both LSU and ITS analyses.

Clade 5 Onygenaceae Berk.

Type genus: *Onygena* Pers. - Observ. Mycol. (Lipsiae) 2: 71, 1800; type species: *Onygena equina* (Willd.) Pers. $\equiv$ *Lycoperdon equinum* Willd. - Fl. Berol. Prodr.: 412, 1787. **Neotype designated here:** Herb. No: CBS H-15271, from cow hoof, Germany, H.A. van der Aa, 1970. Culture derived from type: CBS 947.70 = ATCC 22731 = IFO 31785.

The family Onygenaceae is one of the largest groups in the order Onygenales (Figs 1, 6). Genera are morphologically and ecologically diverse, the family includes dimorphic pathogens next to environmental saprobes (Fig. 1). The majority of the species are found on keratinous substrates and in soil (Fig. 4). Sexual states are described with pseudoparenchymatous cleistothecia or elaborate gymnothecia, and chrysosporium-like or malbranchea-like conidia are produced (Currah 1985).

In ML analyses, Clade 5 was shown as the main clade of Onygenaceae (with 100% bootstrap support). Six groups were individualized: Group 5-I (100% support), Group 5-II (96% support), Group

5-III (87% support), Group 5-IV (95% support), Group 5-V (95% support) and 5-VI (98% support) (Fig. 1). Additionally, sequences of the type of *Chrysosporium europae* (CBS 321.86 = UAMH 4587), from soil, Spain) and *Pectinotrichum llanense* (CBS 882.71 = ATCC 18921 = IHEM 4440 = IMI 155644, from Savannah soil, Venezuela) also clustered in Clade 5, as separate unresolved branches (Fig. 1). *Uncinocarpus reesii* (type species CBS 121.77 = ATCC 34533 = IMI 211204 = UAMH 3880, from feather, Australia) was also found as an unresolved branch in the clade according to LSU phylogeny (Suppl. Figs 1, 2). This soilborne species has often been regarded to be closely related to the environmental pathogens in *Coccidioides*, which was confirmed by genome comparisons (Sharpton et al. 2009), but at a relatively large distance and with other taxa in between (Untereiner et al. 2002), similar to our data.

Group 5-I *Keratinophyton* Randhawa & Sandhu

Type species: *Keratinophyton terreum* Randhawa & Sandhu - Sabouraudia 3: 253, 1964; type strain: CBS 342.64 = IFO 31781 = IMI 108689 = ATCC 16413 = UAMH 4066, from lawn soil, India.

Members of *Keratinophyton* and *Aphanoascus* share cleistothecia with a pseudoparenchymatic peridium, and they can be found on keratinous substrates and dung (Cano et al. 2002a; Sutton et al., 2013) (Suppl. Table 1). The two groups are distinguished by their ascospore morphology and differences in the ITS locus (Sutton et al. 2013; Sharma and Shouche 2017) (Fig. 6). Both genera have been shown to be separate according to ITS sequences in previous studies (Sutton et al. 2013; Sharma and Shouche 2017; Labuda et al. 2021). In the current study, differences in the LSU locus also confirmed the differentiation of *Aphanoascus* and *Keratinophyton* species (Suppl. Figs 1, 2). The *Keratinophyton* group includes several species described in *Chrysosporium*, an ancient genus that has been regarded as having a doubtful identity. Labuda et al. (2021) reclassified the following recently described species in *Keratinophyton*: *C. clavisporum* (type strain G801), *C. echinulatum* (type strain CBS 141178), *C. evolceanui* (type strain CBS 116.63), *C. fluviale* (type strain CBS 100809), *C. qinghaiense* (type strain GZUIFR-11), *C. hubeiense* (type strain EM66601), *C. linfenense* (type strain

650 GZAC-H31), *C. minutisporum* (type strain CBS 101577), *C. submersum* (type strain CBS 101575),
651 and *C. siglerae* (type strain UAMH 6541). Results of all phylogenetic analyses in the current study
652 confirmed these changes with following additional combinations:

653 ***Keratinophyton alvearium*** (Liu & Cai) Kandemir & de Hoog, **comb. nov.** – MycoBank XXXX.
654 Basionym: *Chrysosporium alvearium* Liu & Cai - Mycosphere 9(6): 1096, 2018; holotype HMAS
655 247780, ex-holotype culture CGMCC 3.18783 = LC 11684 = LF1882 isolated from hive-stored pollen
656 collected in the Italian honey bee colonies in the flowering season of *Brassica campestris*, by Y.Z.
657 Zhao, 2016.

658 ***Keratinophyton indicum*** (Garg) Kandemir & de Hoog, **comb. nov.** – MycoBank XXXX. Basionym:
659 *Chrysosporium indicum* (Randhawa & Sandhu) Garg - Sabouraudia 4(4): 262, 1966 ≡ *Trichophyton*
660 *indicum* Randhawa & Sandhu - Mycopath. Mycol. Appl. 20: 227, 1963; type strain CBS 117.63 =
661 ATCC 22401 = UAMH 1274, Herb. IMI 147544, isolated from soil, India, by H.S. Randhawa, 1960.

662 *Trichophyton evolceanui* was described with type strain CBS 116.63 by Randhawa and Sandhu (1963)
663 from Indian soil. However, since the morphological structures originally described as macroconidia
664 appeared to be lost in subcultures, with only hyaline, aseptate echinulate thalloconidia remaining, it
665 was renamed *Chrysosporium evolceanui* by Garg (1966). In the present study, the type strain of *C.*
666 *evolceanui* (CBS 116.63) was found in Clade 5 within the *Keratinophyton* Group (Fig. 6) and the
667 following new combination is proposed:

668 ***Keratinophyton evolceanui*** (Randhawa & Sandhu) Kandemir & de Hoog, **comb. nov.** – MycoBank
669 XXXX. Basionym: *Trichophyton evolceanui* Randhawa & Sandhu - Mycopath. Mycol. Appl. 20: 232,
670 1963 ≡ *Chrysosporium evolceanui* (Randhawa & Sandhu) Garg - Sabouraudia 4(4): 262, 1966; type
671 strain: CBS 116.63 (van Oorschot 1980), Herb. IMI 147545, isolated by R.S. Sandhu from soil, India,
672 1961.

673

674 **Group 5-II *Aphanoascus* (Cooke) Apinis**

675 Type: *Aphanoascus fulvescens* (Cooke) Apinis - Mycopath. Mycol. Appl. 35: 99, 1968 $\equiv$ *Badhamia*
 676 *fulvescens* Cooke - Grevillea 4(30): 69, 1875 $\equiv$ *Eurotium fulvescens* (Cooke) Cooke - Grevillea 8 (45):
 677 11, 1879 $\equiv$ *Pyrobolus fulvescens* (Cooke) Kuntze - Revis. Gen. Pl. (Leipzig) 2: 868, 1891 $\equiv$ *Anixiopsis*
 678 *fulvescens* (Cooke) de Vries - Mykosen 12: 120, 1969. Cooke described the species on an old sacking
 679 from U.K., but this material is not known to be preserved. **Neotype designated here:** UAMH 4114 =
 680 IMI 74750, from soil, U.K., P.M. Stockdale, 1958.

 681 = *Castanedomyces australiensis* Cano, Pitarch & Guarro - Stud. Mycol. 47: 167, 2002; type strain IMI
 682 370017 = FMR 5484, from soil, Australia.

 683 The deposition of a neotype stabilizes the current concept of *Aphanoascus* as described recently by
 684 Labuda et al. (2021). However, the nomenclatural history of this genus is confusing. In 1875, Cooke
 685 published what he thought was a myxomycete and named it *Badhamia fulvescens*. One year later,
 686 Hansen (1877) introduced *Eurotium stercorarium*, isolated from old fox manure. Based on Hansen's
 687 description, Cooke re-examined *B. fulvescens* and renamed it *Eurotium fulvescens* (1879). Zukal
 688 recognized that *E. stercorarium* Hansen differs from other *Eurotium* species and he described
 689 *Aphanoascus cinnabarinus*, isolated from crocodile dung, from his collection in Vienna. After this
 690 description, Hansen re-examined the type specimen of *E. stercorarium* and proposed a new genus
 691 *Anixiopsis* with the type species *Anixiopsis stercoraria*. De Vries (1964) accepted *Aphanoascus*
 692 *cinnabarinus* Zukal as a synonym of *Anixiopsis stercoraria* Hansen. To resolve this confusion, Apinis
 693 (1968) examined the type specimens, except the type specimen for Zukal's *A. cinnabarinus*, which
 694 was not available, and found that the strains from Hansen and Cook's specimens were identical
 695 (1967). Apinis combined the generic name priority (Zukal's, in 1890 against Hansen's in 1897) with
 696 specific epithet priority (Cooke's in 1875 against Zukal's, in 1890) and proposed a new combination
 697 *Aphanoascus fulvescens*, instead of *Aphanoascus cinnabarinus*, which should be a type species
 698 (Apinis 1968). Meanwhile, since the original material of *A. cinnabarinus* Zukal was lost, Udagawa
 699 and Takada designated a neotype ATCC 26215 (CBS 267.72) from pepper soil in Japan in 1973.
 700 However, this neotype was later shown to have a deviating conidial state, named *Paecilomyces*
 701 *cinnabarinus* (Jong and Davis 1975), and decades after the introduction of the neotype, *A.*

cinnabarinus was moved to the genus *Talaromyces* (Yilmaz et al. 2014). *Aphanoascus* was synonymized with *Anixiopsis* Hansen (1897), even though they were considered two different genera by several researchers based on their cleistothecia differences in color and size, late or early closure of their peridial walls and ascospore morphology (de Vries 1969; Guého and de Vroey 1986). In the current study, the neotype was chosen as *Aphanoascus fulvescens* UAMH 4114 for several reasons. First, the generic name *Aphanoascus* was described prior to *Anixiopsis*. Second, the material for UAMH 4114 was described in the U.K. similar to Cooke's original material (Cooke 1875).

Another keratinophilic fungus, *Castanedomyces australiensis* (Cano et al. 2002b; type strain FMR 5484), was described with the same morphological characteristics as *A. fulvescens* (i.e., ascomata with membranous peridium and lenticular ascospores with an equatorial crest and polar thickenings), but the two species were distinguished by a difference of 15 nucleotides in the 18S region (Cano et al. 2002b). According to the results of the ITS analysis in the current study (Fig. 6), *C. australiensis* can be considered a synonym of *A. fulvescens* (99.8% ITS identity to KT155718).

Chrysosporium tropicum (Carmichael 1962; type strain CBS 171.62, from woolen overcoat, Solomon Islands) showed a 100% identical ITS and LSU profile with the type of the keratinophilic species *Aphanoascus verrucosus* (Cano and Guarro 1990; type strain CBS 468.88 from arable soil, Spain). Therefore, *C. tropicum* is considered a synonym of *A. verrucosus*. Similarly, the type of *C. shanxiense* (GZAC EB1601M.1) was synonymized with *A. verrucosus* (99% ITS identity to NR131309) and *C. articulatum* was synonymized with *A. reticulisporus* (100% ITS identity to MH859002). Another *Chrysosporium* species, *C. jingzhouense* (Zhang et al. 2017a; type: EB1303M) was found in the same cluster with the types of *A. reticulispora* and *A. keratinophilus* (with 97% and 94% ITS identity, respectively). Similarly, *C. crassitunicatum* (Kushwaha and Agrawal 1977; type strain CBS 167.78) was found close to the type of *A. pinarensis* (CBS 113874) with 96% ITS identity. Therefore, following combinations were proposed for these two species:

Aphanoascus jingzhouense (Zhang, Han & Liang) Kandemir & de Hoog, **comb. nov.** – MycoBank XXXX. Basionym: *Chrysosporium jingzhouense* Zhang, Han & Liang - Phytotaxa 303(2): 175, 2017; type strain GZUIFR-EB1303M, from farmland soil, China.

729 *Aphanoascus crassitunicatum* (Kushwaha & Agarwal) Kandemir & de Hoog, **comb. nov.** –
 730 MycoBank XXXX. Basionym: *Chrysosporium crassitunicatum* Kushwaha & Agarwal - Trans. Br.
 731 Mycol. Soc. 68(3): 464, 1977; type strain CBS 167.78, Herb. IMI 185320, from buried human hair,
 732 India.

733 CBS 783.70 is the type strain of *Xynophila mephitalis* (Malloch & Cain 1971), defining this genus. As
 734 shown earlier by Cano and Guarro (1990), this genus is not significantly different from *Aphanoascus*
 735 and should be regarded as a synonym. Similarly, the type species of *Neoxenophila*, *N. foetida* (Apinis
 736 & Clark 1974; type strain CBS 453.75) is found amidst *Aphanoascus* species; the genus is considered
 737 a synonym, confirming Cano and Guarro (1990). *Chrysosporium lucknowense* (Garg 1966; type strain
 738 CBS 143.77) and *C. mephiticum* (Sigler et al. 1986; type strain CBS 320.86) clustered with
 739 *Aphanoascus foetidus* (Cano et al. 2002a; type strain 453.75) in all trees. Cano et al. (2002) reported
 740 *C. lucknowense* to be an asexual state and *C. mephiticum* a synonym of *A. foetidus*. In the current
 741 study, ITS similarity of *C. lucknowense*, *C. mephiticum* and *A. foetidus* was found to be above 98%
 742 (NR145206, NR145207 and KT55907, respectively) and LSU similarity above 99% (NG063936,
 743 MH873650 and AB040693, respectively). Additionally, *C. guizhouiense* (type EM14.2002) also
 744 placed in this cluster with 98% ITS identity to the type of *A. foetidus* (NR158324 vs. KT55907). For
 745 precise species resolution, multilocus studies of a larger number of strains is required.

746

747 **Group 5-III *Amauroascus* Schröt.**

748 Type: *Amauroascus niger* Schröt. - Krypt.-Fl. Schlesien (Breslau) 3.2(1–2): 211, 1893 ≡ *Arachniotus*
 749 *niger* (Schröt.) Kuehn, Orr & Varsavsky - Mycopath. Mycol. Appl. 25: 106, 1965; type strain CBS
 750 114.61 = ATCC 22339 = IFO 32599 = NRRL A-10697, from soil, U.S.A., G.F. Orr.

751 In addition to type of *Amauroascus*, the group included the type species of *Brunneospora* (*B.*
 752 *reticulata* UAMH 5704 = FMR 784 = IMI 315744 from arable soil, Spain), *Byssoonnygena* (*B.*
 753 *ceratinophila* ATCC 64724 from soil, Spain), *Coccidioides* (*C. immitis*, CBS 120936 from human,
 754 U.S.A) and *Uncinocarpus* (*U. reesii*, CBS 121.77) (Fig. 6).

The genus *Amauroascus* was found to be polyphyletic (Fig. 1; Suppl. Figs 1–4). Nomenclatural confusion about this genus goes back to 1893, when Schroeter described two new genera, *Amauroascus* and *Arachniotus* at the same time (Schroeter 1893). In *Amauroascus*, he included Eidam's *Gymnoascus verrucosus* (Eidam 1886; from moldy leather boots) and his own new species *Amauroascus niger* (Schroeter 1893; from old badger dung). The only criterion to differentiate between these two genera was the color of the ascospores. Since this is unfit for generic distinction, some researchers considered these two genera as congeneric (Benjamin 1956, Kuehn 1958, Orr et al. 1965), whereas von Arx (1971) recognized *Amauroascus* as a separate genus and indicated *A. verrucosus* as a type species, albeit without an explanation. However, *A. niger* was already cited as the lectotype of the genus earlier (Clements and Shear; Benjamin 1956) and it was suggested to follow this choice according to article 8.1 (ICBN) (Currah 1985).

Rammeloo (1982) compared the type specimens of *Onygena mutata* Quélet (1875; from the hoofs of an ox) and *A. verrucosus* (Eidam) Schroeter (1893; from moldy leather boots) and reported that the two species were identical, confirming the conclusions of Orr et al. (1965). However, he chose to change the name *O. mutata* to *Amauroascus mutatus* for the combined species. Since *A. verrucosus* was described earlier, it had priority over *A. mutatus*. Therefore, the following **epitype is designated here** for *Amauroascus verrucosus*: CBS 181.70, from soil, U.S.A., G.F. Orr. This strain has an alternative collection number ATCC 22395.

Apinisia queenslandica (CBS 280.77 = IMI 121675 = IFM 47370) was described from bird feathers in Australia by Apinis and Rees (1976). The species was subsequently placed in *Uncinocarpus* based on microscopic morphology (Sigler et al. 1998) and then moved to *Amauroascus* based on a higher ITS sequence similarity compared to *Uncinocarpus reesii* (Solè et al. 2002a). Solè et al. (2002a) synonymized *Brunneospora reticulata* (Guarro et al. 1987b; FMR 784, from arable soil, Spain) and *Orromyces spiralis* (Ghosh and Sur, 1985; GS-191, from soil, India) with *U. queenslandica*. These species are all keratinophilic and possess gymnothecia, helical peridial appendages, pigmented ascospores and chrysosporium-like anamorphs. The only difference mentioned in description of the species was in terms of ascospore shape, i.e., globose in *Apinisia*, ellipsoidal in *Brunneospora*, oval in *Orromyces* and ovoid to globose in *Uncinocarpus* (Apinis and Rees 1976;

Ghosh and Sur, 1985; Guarro et al. 1987b; Solè et al. 2002a). In the current study, *Amauroascus verrucosus* and *Amauroascus niger* grouped with *U. reesii*, whereas *A. queenslandica* and *B. reticulata* formed a separate, supported branch in this group (Figs 1, 6). The similarity between *A. queenslandica* (CBS 280.77) and *B. reticulata* (UAMH 5704) was found to be 99%, while the similarity of *Apinisia queenslandica* (AJ390394) with *U. reesii* (NR111092) and with *A. niger* (NR159639) was 81%. Although the fungus was first described as *Apinisia*, it was found to be placed far from the generic type, *Apinisia graminicola* (La Touche, 1968; type strain CBS 721.68 on rotting Poaceae, UK). For *Orromyces*, type (GS-191) and isotype cultures (GS-141) of *O. spiralis* were reportedly deposited in the fungal herbarium of the Botany Laboratory, Department of Sciences, Regional College of Education, Bhubaneswar, Orissa (Ghosh and Sur 1985). However, we did not receive any response from the herbarium regarding the presence of this species and no related information is available from other collections. Therefore, *Orromyces spiralis* is considered doubtful and has been abandoned. The following combination is proposed for *A. queenslandica*:

Brunneospora queenslandica (Apinis & Rees) Kandemir & de Hoog, **comb. nov.** – MycoBank XXXX. Basionym: *Apinisia queenslandica* Apinis & Rees - Trans. Br. Mycol. Soc. 67(3): 524, 1976 = *Uncinocarpus queenslandicus* (Apinis & Rees) Sigler - Can. J. Bot. 76(9): 1632, 1999; type strain CBS 280.77 = IMI 121675 from feathers of domestic fowl, Australia, Apinis and Rees, 1965.

The type strain of *Byssoonygena ceratinophila* (ATCC 64724 = FMR 785 = IMI 316057 = UAMH 5669) was also found in Group III and clustered with *Brunneospora queenslandica* (CBS 280.77) and *B. reticulata* (UAMH 5704) (Fig. 6), which are keratinophilic, possess gymnothecia and brown ascospores, whereas *Byssoonygena* lacks peridial appendages and has a malbranchea-like anamorph (Guarro et al. 1987a).

The genus *Coccidioides* (Stiles 1896) is represented by two species: the generic type *Coccidioides immitis* (type strain CBS 120936) and *Coccidioides posadasii* (Fisher et al. 2002; type strain CBS 113859). *Coccidioides* is a unique genus in Onygenaceae, having an environmental asexual life cycle, and a pathogenic phase with spherules and endospores in mammalian hosts. The genus combines keratinophily and systemic dimorphism with xerotolerance, being able to grow in soils with low pH levels and temperatures between –6.5°C and 60.6°C, and tolerating up to 8% NaCl (del Rocío

Reyes-Montes et al. 2016; de Hoog et al. 2005; Barker 2018). Previously, some arthroconidial fungi isolated from soil were described as the *Malbranchea* state of *C. immitis* and named as *Malbranchea dendritica* and *Malbranchea gypsea* (Sigler and Carmichael 1976); however, despite their morphological resemblance with *C. immitis*, they were not shown to form endosporulating spherules in tissue (Orr 1972). *Malbranchea gypsea* was found to be cellulolytic (Sigler and Carmichael 1976). Phylogeny also supported that *Malbranchea* and *Coccidioides* are two different genera; consequently, *M. gypsea* was transferred to *Spiromastigoides* (Fig. 1).

Group 5-IV *Nannizziopsis* Currah

Type species: *Nannizziopsis vriesii* (Apinis) Currah - Mycotaxon 24: 164, 1985 $\equiv$ *Rollandina vriesii* Apinis - Trans. Br. Mycol. Soc. 55(3): 501, 1970; type strain: CBS 407.71 = CMI 149994, from *Ameiva* skin and lung, the Netherlands, collected by A.E. Apinis, isolated by G.A. de Vries.

The type of *Nannizziopsis vriesii* was first described as *Rollandina vriesii* (Apinis 1970) based on the description of the type species of the genus, namely *Rollandina capitata* (Patouillard 1905; type specimen from green waste, Vietnam, in Herb. FH). However, re-examination of the type specimen yielded different descriptions by different researchers (Benjamin 1956; Apinis 1970). Von Arx (1971) considered the genus *Rollandina* to be doubtful because the type species is not known in pure culture. Currah (1985) followed Von Arx, indicating *Rollandina* as a *nomen confusum* and proposed a new genus *Nannizziopsis* which was classified in Onygenaceae. In the National Institute of Technology and Evaluation Culture Collection, Japan, the isolate CBS 115.54 = ATCC 15314 = NRRL 2850 = NBRC 9194, from a buried cable, in U.S.A., was recorded as the type of *R. capitata* (based on the ex-type culture of *Pseudoarachniotus marginosporus*; Kuehn and Orr 1962). Another species, *Rollandina hyalinospora* (Roy et al. 1978) was described with the basionym *Pseudoarachniotus hyalinosporus* (Kuehn et al. 1960; type strain CBS 548.72 = IHEM 3416 = IMI 099725 = NRRL 2881, from guinea pig dung, India). In the current study, both species clustered in Gymnoascaceae (Figs 1, 7).

Stchigel et al. (2013d) combined the physiology, morphology and multilocus phylogeny of *Nannizziopsis* and a number of chrysosporium-like strains, mostly isolated from reptile habitats, and proposed a new family, Nannizziopsidaceae. The predominant reptile-associated ecology, combined with discrete, spherical ascomata with a peridium of loosely interwoven, hyaline hyphae; eight-spored, spherical asci; and thick-walled, smooth, hyaline ascospores (Stchigel et al. 2013d), was suggestive of an independent evolutionary course. In the larger phylogeny of the Onygenales, this family does not clearly from an individual entity separate from Onygenaceae (Fig. 6). The reptile-associated fungus *Ophidiomyces ophiodiicola* (type strain CBS 122913) (Sigler 2013), isolated from a granuloma of a black rat snake, was found to be remote from *Nannizziopsis* and *Paranannizziopsis* in Onygenaceae (Figs 1, 6).

Group 5-V *Onygena* Pers.

Type species: See above.

According to the Index Fungorum database, the genus *Onygena* contains 12 species excluding the varieties. Among these species, *O. lycoperdon* was recorded as *nomen nudum* (MycoBank.org), *O. mougeotii* was recorded as synonym of *O. equina* and *Onygena mutata* was re-named as *Amauroascus mutatus* (Rammeloo 1982) (see the section Group 5-III, *Amauroascus*). There are no known type specimens or isolates for the *O. apus* (Berkeley and Broome 1851; from decaying bones in U.K.), *O. bommerae* (Saccardo 1913; on feathers and bones of birds), *O. caprina* (Fuckel 1870; from a sheep horn), *O. hypsipus* (Ditmar 1813; on Marten excretion mixed with mouse bones), *O. piligena* (Fries 1829; from sheep's wool and murine fur) and *O. ungulina* (Rostrup 1894; on horse hooves). Therefore, they have been considered as doubtful. Only the specimens that were identified as *O. equina*, which is the type species of the family Onygenaceae determining the order Onygenales, and *O. corvina* are represented by herbarium specimens in collections. Since the original type materials are not known to be preserved for both of the species, neotypes are indicated in the present study.

861 *Onygena corvina* Alb. & Schwein. - Consp. Fung. (Leipzig): 113, 1805. **Neotype designed herewith:**
862 Herb. No: CBS H-15266, on rotting bird remains, The Netherlands, H.A. van der Aa, 1972. Culture
863 derived from type: CBS 152.73.

864

865 The additional species *Aphanoascella galapagosensis* (type strain CBS 132345, isolated from a
866 Galápagos tortoise *Chelonoidis nigra*), and another reptile-associated member, *Emydomyces*
867 *testavorans* (type ATCC TSD-145) (Woodburn et al. 2019), also cluster in Onygenaceae (Figs 1, 6).
868 Even though they formed a monophyletic group based on ML analyses, mutual distances and distances
869 to other reptile related members of the clade are considerable in ITS and LSU analyses (Suppl. Figs 1,
870 2, 4).

871

872 **Clade 6 Auxarthraceae** Locq.

873 Type genus: *Auxarthron* Orr & Kuehn - Can. J. Bot. 41: 1439, 1963; type species: *Auxarthron*
874 *californiense* Orr & Kuehn; type strain: CBS 129.62 = ATCC 15600 = IHEM 4422 = IMI 099590 =
875 NRRL A-1122, from dung of pack rat, by G.F. Orr, U.S.A.

876 The members of the genera *Auxarthron* and *Malbranchea* were placed in Clade 6 with 100% support
877 in all phylogenetic analyses, but formed an unsupported clade (40% bootstrap support) in ITS Group II
878 analysis (Suppl. Fig. 4). The genus *Auxarthron* has been described with mesh-like gymnothecia, well-
879 differentiated thick-walled peridial hyphae with knuckle-joint septal enlargements (usually in 1–3
880 septa) (except *A. concentricum* which lacks both knuckle-joints and peridial appendages), punctate
881 ascospores and an asexual morph in *Malbranchea* (Orr and Kuehn 1963b; Currah 1985; Sigler et al.
882 2002a; Sarrocco et al. 2015). The genus was classified as a monophyletic group in Onygenaceae
883 (Currah 1985; Sarrocco et al. 2015; Rodríguez-Andrade et al. 2021). However, in the present study,
884 the group was considered as a separate family Auxarthraceae, because this monophyletic group was
885 found to be distant from the type species of Onygenaceae (Fig. 7). In addition, during the course of the
886 present study, Rodríguez-Andrade et al. (2021) synonymized *Auxarthron* with *Malbranchea* based on

887 the phylogenetic analysis of the concatenated ITS-LSU sequences. Members of the family can be
888 found in eutrophic environments enriched by dung, such as in cave soil, or on animal dung.
889 Rodríguez-Andrade et al. (2021) referred to the identification key for the species classified in
890 Auxarthraceae.

891

892 **Clade 7 Neogymnomycetaceae** Kandemir & de Hoog, **fam. nov.** MycoBank XXXXX

893 **Type genus:** *Neogymnomyces* Orr - Can. J. Bot. 48(6): 1065, 1970; type species: *Neogymnomyces*
894 *demonbreunii* (Ajello & Cheng, 1968) Orr - Can. J. Bot. 48(6): 1065, 1970 $\equiv$ *Gymnoascus*
895 *demonbreunii* Ajello & Cheng - Mycologia 59(4): 692, 1967; type strain: CBS 427.70 = ATCC 18394
896 = O-3200 = M19, from soil, U.S.A., J. Brandsberg. Herb. No: CBS H-7197, provided by G.F. Orr,
897 1970.

898 The clade was formed by species mainly isolated from dung and soil (Fig. 4) and supported with 98%
899 bootstrap value in ML analysis (Fig. 1). In addition to *Neogymnomyces*, the generic types
900 *Auxarthronopsis bandhavgarhensis* (CBS 134524, from soil inside hollow tree, India), *Canomyces*
901 *reticulatus* (MCC 1486, from soil under a tree, India), *Currahmyces indicus* (MCC 1548, from hen-
902 populated soil, India), *Renispora flavissima* (CBS 708.79 from soil in barn housing *Myotis velifer*,
903 U.S.A.) were placed in the clade. Based on the generic types of the genera, Clade 7 can be divided into
904 two main groups as Group *Neogymnomyces* and Group *Auxarthronopsis*. *Canomyces reticulatus*,
905 *Auxarthronopsis stercicola* (CGMCC3.19639, from animal feces in karst Cave, China) and
906 *Auxarthronopsis pulvereae* (CGMCC3.19312, from plant debris in karst Cave, China) clustered in the
907 same group based on LSU and ML analyses (Fig. 1; Suppl. Figs 1, 2); however, *Canomyces* was in a
908 different group in the ITS tree (Fig. 8; Suppl. Figs 3, 4). Similarity of *Auxarthronopsis pulvereae* and
909 *Canomyces reticulatus* was found 84% for ITS and 98% for LSU. Similarly, ITS identity for
910 *Auxarthronopsis stercicola* and *Canomyces reticulatus* was found 85% while the LSU identity was
911 98%. Morphological differences between these species were recorded in previous studies (Zhang et al.
912 2021; Sharma and Shouche 2020). The ITS similarity of *Auxarthronopsis stercicola* and *A. pulvereae*

was found 97%, while the LSU similarity between these two species and the type species *A. bandhavgarhensis* was found to be 85% and 86%, respectively. These results support that *A. stercicola* and *A. pulvereus* belong to the same genus, but they should be excluded from *Auxarthronopsis*. Additionally, *Amauroascus purpureus* (type species UAMH 8294, from cultivated soil, Japan), *Amauroascus volatilis-patellus* (type species CBS 249.72, from clay soil, U.S.A.) and *Nannizziopsis mirabilis* (type species UAMH 7712, from forest soil, U.S.A.) in Clade 7 also need nomenclatural revision since they are remote from their generic types *Amauroascus niger* (CBS 114.61, from soil, U.S.A.) and *Nannizziopsis vriesii* (CBS 407.71, from lizard skin and lung, The Netherlands).

Another keratinophilic fungus, *Chlamydosauromyces punctatus* (type UAMH 9990, from skin of lizard, U.S.A.) is also placed in Clade 7 along with *Neogymnomyces* species, based on ITS phylogeny (Fig. 8; Suppl. Figs 3, 4). With the original description of *C. punctatus*, *Neogymnomyces* species were not included in the analyses since the molecular data was not available at that time (Sigler et al. 2002b). In the present study, ITS similarity between *C. punctatus* and *N. demonbreunii* was found to be 94%. Both genera are keratinophilic and have gymnothecial ascomata; however, their ascospore and culture morphologies are different (Sigler et al. 2002b; Doveri et al. 2012). The following recombination is proposed for *C. punctatus*:

Neogymnomyces punctatus (Sigler, Hambleton & Paré) Kandemir & de Hoog, **comb. nov.** – MycoBank XXXX. Basionym: *Chlamydosauromyces punctatus* Sigler, Hambleton & Paré - Stud. Mycol. 47: 127, 2002; type strain: UAMH 9990 from shed skin of lizard (*Chlamydosaurus kingii*), U.S.A., isolated by J. Paré, 2001.

Clade 8 *Incertae sedis*

Two original materials of the xerophilic species *Diploospora rosea* (epitype strain, DAOM 250100, from dust, Micronesia) and *Amauroascus aureus* (CBS 593.71, from decaying wood in cavity of stump, Japan) formed a clade in ML sequence analysis (Fig. 1). ITS Group I analysis revealed different results from ML and LSU data, such that *A. aureus* was found in a basal position to Clade 7

Neogymnomycetaceae and *D. rosea* was found close to Gymnoascaceae (Suppl. Fig. 3). Type strain CBS 593.71 (ATCC 18654 = NRRL 12,184 = Orr O-2512 = IMI 151274 from decayed wood ex tree stump cavity, Japan) of *A. aureus* was first described as neotype for *Arachniotus aureus* (Kuehn et al. 1964b) based on the descriptions provided by Eidam (1886) for *Gymnoascus aureus*. Currently, it is known as the type of *Amauroascus aureus* (von Arx 1971). In all phylogenetic analyses, this strain was found remote from the type species of these genera (Fig. 1; Suppl. Figs 1–4), therefore considered *incertae sedis*.

The genus *Diploospora* was described with the type species *Diploospora rosea* by Groove (1916). Nearly 100 years after its first discovery, another strain (DAOM 250100) was reported from dust in a residence in Micronesia (Tanney et al. 2015). It was described with dull pink colonies, and oblong, apiculate conidia borne in long chains showing mixed acropetal and basipetal extension. Conidiogenesis was also described as a mixture of blastic and thallic (Tanney et al. 2015). Considering the source of the reported strains, *D. rosea* seems to be xerophilic and adapted to the indoor environment. In addition, mite feces seen on the holotype were consistent with the dung affinity of Gymnoascaceae members (Tanney et al. 2015) (Fig. 9). Further molecular analyses are required to define this species' position in the Onygenales.

Clade 9 Gymnoascaceae Baranetzky

Type genus: *Gymnoascus* Baranetzky - Bot. Ztg. 30: 158, 1872; type species: *Gymnoascus reessii* Baran., type strain: CBS 392.64, from soil, U.S.A., G.F. Orr. Herb. No: CBS H-13156.

Ascocarps in this family are mostly of yellowish, greenish, reddish or brownish shades, with a gymnoperidium composed of a loose network of hyaline or pigmented hyphae. Asci are globose to ovoid; ascospores are hyaline, yellowish or greenish, spherical, ovoidal or oblate, smooth- and thick-walled, sometimes with equatorial grooves and ridges and/or polar thickenings (Currah 1985; Doveri et al. 2012).

On the basis of the number of described species, the Gymnoascaceae is one of the largest families of the Onygenales (Solé et al. 2002b). Members of the family are eutrophic and can be found in soil rich in organic matter, various types of dung, and decaying vegetation (Fig. 4). Species (e.g., *Gymnoascus reessii*) have also been isolated from the lungs of wood rat and prairie dog (Emmons 1954) without any lesions in the lungs, and they have been found to survive mouse passage without causing disease. This survival ability is similar to that of the dimorphic fungus *Emmonsia crescens* (now known as *Emergomyces crescens*) which is commonly carried asymptotically by terrestrial rodents (Jiang et al. 2020). Survival mechanisms in the lung for such environmental pathogens are mostly related with *in vitro* and *in vivo* conidial changes (Jiang et al. 2018, 2020) and for Gymnoascaceae members these mechanisms are not known to exist. Skin and nail scrapings, and animal hair are the main sources of dermatophytes because of their high keratin content (Currah 1985; de Hoog et al. 2017). Members of Gymnoascaceae are frequently found colonizing similar keratinized material shed from humans and other mammals (Currah 1985). Baiting techniques with horse and/or human hair or pieces of hooves have successfully been used for the selective isolation of keratinolytic Gymnoascaceae and the examination of their gymnothecial structures (Sharma and Singh 2013; von Arx 1986).

Osmotolerance might be another trait that enhances the wide distribution of Gymnoascaceae. *Sporendonema casei* and *Sphaerosporium equinum* have repeatedly been isolated from cheese, which seems to be their preferred habitat (Ropars et al. 2012; Hermet et al. 2014). According to available records, almost all strains have only been isolated from the rinds of hard cheeses. This habitat lacks moisture, and the relatively high free fatty acid content makes this part highly acidic compared to the interior of the cheese. In addition, the rind has higher levels of crude protein and salt (calcium and phosphorus) (Davies 1938). The ripening process takes place at low temperatures (4–18°C), and given the high acid and salt concentrations, these species can be considered xerophilic and halophilic. However, Scaramuzza et al. (2015) showed that *S. casei* can also be isolated from the air of cheese processing rooms.

Other members of the family Gymnoascaceae show other types of halotolerance, e.g., *Gymnoascus halophilus*, from lake sediments, can tolerate NaCl concentrations of up to 22.5% (Zhou et al. 2016). Species found under conditions of extreme dryness, such as *Gymnoascus desertorum*, may possess similar survival factors. Desert soil colonization can also be enhanced by oligotrophism. Possibly due to the wide range of habitat choices of the members of Gymnoascaceae, physiological trends are apparent in this family, suggesting alternative lifestyles, such as eutrophism on animal dung. Temperature relationships seem equally variable: *Gymnoascus stercorarius*, found in compost, can grow at temperatures up to 50°C, while *Arachniotus ruber*, from coyote dung, requires a low temperature of 5°C for its isolation (Zhou et al. 2016; Currah 1985).

After the description of the family with *Gymnoascus* in 1872, 20 genera were included (Table 1). Species were reclassified several times by different researchers, mostly using peridium and ascospore morphology as taxonomic criteria (e.g., von Arx 1986; Currah 1985; Apinis 1964). *Gymnascella* was introduced by Peck (1884) for the single species *Gymnascella aurantiaca* from old bones in a damp place. The fungus lacked an ascigerous fruitbody, and asci formed in clusters between undifferentiated hyphae. *Arachniotus* Schroeter (1893) was described as having three species that were originally classified in *Gymnoascus*: *G. candidus* Eidam, *G. aureus* Eidam and *G. ruber* van Tieghem. *Arachniotus candidus* (Eidam) Schroeter was considered the generic type species. The genus had snow-white or yellowish gymnothecia and thin-walled peridial elements covering the asci in a net-like form, similar to a fragile membrane (Orr et al. 1977a). *Pseudoarachniotus* Kuehn (1957) was described to separate some *Arachniotus* species that lacked discrete ascocarps or peridial elements, formation of croziers and lack of conidia on phialides. Type species was indicated as *Pseudoarachniotus roseus*. However, in describing this genus, *Gymnascella* was not taken into account. Later, *Pseudoarachniotus* was used to accommodate species that could not be classified in either *Arachniotus* or *Gymnascella* (Orr et al. 1977a). *Petalosporus* Ghosh et al. (1963), with the type species *Petalosporus nodulosus*, was described as having discrete ascocarps, characteristic enlargements at the nodes of smooth hyphae, which comprise a rudimentary peridium and petaloid arrangement of ascospores in asci. *Narasimhella* Thirum. & Mathur (1966) (type species, *N.*

poonensis) was described for species with well-developed stipitate fruitbodies without peridium; the stipe is composed of upward growing hyphal bundles, while the irregularly globular, fertile head portion contains groups of asci. Crozier formation was similar to that of *Pseudoarachnietus*. The genus *Plunkettomyces* Orr (1977a), represented by the type species *Plunkettomyces littoralis*, had peridial elements that were smooth or coarsely tuberculate, radiating outward from the centrum or the base of the asci. Ascospores were lenticular, with a yellow-orange to orange-brown longitudinal band. *Plunkettomyces littoralis* was thought to represent an intermediate between *Gymnascella* and *Pseudoarachnietus*. *Disarticulatus* Orr (1977a), with the type species *Disarticulatus devroeyi* had yellow-orange to orange gymnothecia which tended to disarticulate into components with variously shaped, thick-walled cells. Ascospores were described as spherical or ellipsoidal, with a slight lateral bulge. *Disarticulatus* was found to be similar to *Petalosporus*, except for the absence of the petaloid arrangement of ascospores in the asci. *Gymnoascoideus* was introduced (Orr et al. 1977b) to describe species lacking gymnothecia but having typical elements with branching at right angles, unsharpened at the apices and covered by asexual spores in and around the ascal clusters. *Gymnoascoideus* shows discrete gymnothecia lacking appendages and similar to *Petalosporus*, its ascospores show a petaloid pattern in the asci, but in contrast they lack lateral bulges. *Gymnoascoideus petalosporus* was assigned as the type species. *Kraurogymnocarpa* Udagawa & Uchiyama (1999a), represented by *Kraurogymnocarpa lenticulospora* was described with yellowish-green ascomata with a disarticulating reticuloperidium, bivalvate ascospores, and weak cellulolytic activity. The discrete ascomata have short spines and straight or slightly curved appendages. *Mallochia* Arx & Samson (1986) was introduced to classify *Pseudoarachnietus echinulatus* in a separate genus. In *Mallochia echinulata*, similar to *Narasimhella*, obovate asci develop from croziers. However, ascospores in the latter species are bivalvate, with an equatorial furrow surrounded by two rims and covered with blunt spines (von Arx and Samson 1986). The generic names introduced in Gymnoascaceae before December 2019, are shown in Fig. 10 with their basionyms/synonyms.

From this summary of genera attributed to Gymnoascaceae on morphological grounds, it appears that a limited set of characters is used in different combinations to define the genera. Many of

these fungi have impressive morphologies, which taxonomists acknowledge. However, re-examination of deposited strains or type materials revealed that the morphology may vary within species. For example, de Vroey (1966) examined several strains of *Pseudoarachnietus roseus* and noted that the presence or absence of discrete ascocarpic elements was variable and he consequently regarded *P. roseus* as a synonym of *Arachnietus dankaliensis*. Similarly, in describing *Arachnietus flavoluteus*, Kuehn and Orr (1959) observed some ascal clusters that were devoid of peridial elements as in *Pseudoarachnietus*. Phylogenetic studies also indicated that species with slight morphological differences may share the same molecular characteristics (Solé et al. 2002b), and *vice versa*. A Bayesian inference tree of the ITS locus of Gymnoascaceae (Fig. 9) showed that members of several of the genera mentioned above are not clearly separated into monophyletic groups; no generic substructure can be recognized that matches the current concepts. In contrast, *Sporendonema* and *Sphaerosporium*, which have not been associated with Gymnoascaceae, clustered within this amalgamate (Figs 1, 9).

Phylogenetic results in the current study revealed five groups in the family; Group I *Gymnascella*, Group II *Arachnietus*, Group III *Gymnoascus*, Group IV *Gymnoascoideus* and Group V *Narasimhella*. Group names were determined by choosing the well-supported branches with high bootstrap values. Type species for each genus in the group were detected. In case of more than one type species for different genera in the same group, the oldest type species is maintained to name the group.

Group 9-I *Gymnascella* Peck

Type species: *Gymnascella aurantiaca* Peck - Ann. Rep. N.Y. St. Mus. Nat. Hist. 35: 143, 1882.

Neotype designated here: UAMH 3138, from lizard dung, U.S.A., R.K. Benjamin, 1969. Alternative strain number: RSA 1483.

= *Arachnietus verruculosus* Orr & Kuehn - Mycologia 64(1): 62, 1972. Type strain: CBS 655.71 = ATCC 18897 = IMI 155648 = NRRL 3716 = QM 9290 = DPG 138 from clay soil, U.S.A.

1070 Orr and Kuehn (1972) described *A. verruculosus* based on presence of discrete ascocarps, smooth,
1071 thick-walled, ovoid to oblate ascospores and characteristic, coarsely verrucose, loose peridial elements
1072 around the asci. A type strain of this species was indicated (DPG 138). Currah (1985) synonymized *A.*
1073 *verruculosus* with *Gymnascella aurantiaca* Peck and results of the present study confirmed this, with
1074 99% ITS similarity between the type species (Suppl. Table 2).

1075 Habitats of the species in this group were mostly tend to be dung and soil, especially highly
1076 nutritional clay soil (Fig. 4; Suppl. Table 1). The group contains halotolerant and thermotolerant
1077 species such as *G. thermotolerans* and *G. stercorarius*. Similarly, *Petalosporus anodosus* has been
1078 reported to grow more rapidly at 37°C than at 30°C (Kuehn et al. 1964a). *Plunkettomyces littoralis*,
1079 which is known to occur only in marine habitats, clustered in the same group. These findings might be
1080 a clue for a common halophilic ancestor of Group 9-I *Gymnascella* and Group 9-II *Arachniotus*, which
1081 contains species predominantly isolated from environments with high salt content.

1082 The genus *Pseudoarachniotus* was introduced to include species without discrete ascomata
1083 and with a loose peridium, ascocarp initials and croziers, evanescent asci and ascospores in variable
1084 shapes (globose, ovoid, elliptical or lenticular) and colors (hyaline, red, or shades of yellow) (Kuehn
1085 1957). Although Kuehn did not consider *Gymnascella* with his description of *Pseudoarachniotus*,
1086 Currah (1985) placed several species previously described in *Arachniotus* and *Pseudoarachniotus* with
1087 oblate ascospores in *Gymnascella*. Phylogenetic analyses showed that these species can be united
1088 under the name *Gymnascella*, based on $\geq 90\%$ ITS similarity with the neotype of *G. aurantiaca*
1089 (Suppl. Table 2).

1090 *Gymnascella dankaliensis* (Castell.) Currah - Mycotaxon 24: 77, 1985; type strain: CBS 117.38 =
1091 UAMH 3552, from camel skin, Africa $\equiv$ *Arachniotus dankaliensis* (Castell.) v. Beyma - Antonie van
1092 Leeuwenhoek 8: 105, 1942 $\equiv$ *Gymnoascus dankaliensis* (Castell.) v. Arx - Persoonia 13(2): 177, 1986
1093 $\equiv$ *Trichophyton dankaliense* Castell. - J. Trop. Med. Hyg. 40: 315, 1937.
1094 = *Pseudoarachniotus terrestris* Thirum. & Mathur - Mycopath. Mycol. Appl. 40(2): 102, 1970 fide
1095 von Arx loc. cit.; type strain: CBS 339.65 from soil, India.

1096 = *Pseudoarachnietus flavoluteus* (Kuehn & Orr) Orr, Ghosh & Roy - Mycologia 69(1): 154, 1977 ≡
 1097 *Arachnietus flavoluteus* Kuehn & Orr - Mycologia 51(6): 864, 1961; type strain: CBS 627.71 from
 1098 soil, U.S.A.

1099 = *Pseudoarachnietus thirumalacharii* Mathur - Mycopath. Mycol. Appl. 40(2): 101, 1970 fide v. Arx
 1100 loc. cit.; type strain: CBS 294.66 from soil, India.

1101 = *Pseudoarachnietus roseus* Kuehn - Mycologia 49(5): 695, 1957; type strain: CBS 323.58, from
 1102 ulcerated chicken gizzard, U.S.A.

1103

1104 *Gymnascella nodulosa* (Ghosh, Orr & Kuehn) Currah - Mycotaxon 24: 88, 1985 ≡ *Petalosporus*
 1105 *nodulosus* Ghosh, Orr & Kuehn - Mycopath. Mycol. Appl. 21: 37, 1963 ≡ *Gymnoascus nodulosus*
 1106 (Ghosh, Orr & Kuehn) v. Arx - Persoonia 13(2): 179, 1986; type strain: CBS 577.63 = ATCC 15318 =
 1107 IFO 31789 = IMI 168760 = NRRL 2882 = QM 8527, from dung of Guinea pig, India.

1108 Gosh et al. (1963) described the genus *Petalosporus* primarily based on the floral-shaped arrangement
 1109 of ascospores. However, this can also be seen in other members of Gymnoascaceae, e.g., *Gymnoascus*
 1110 *boliviensis* and *G. petalosporus*. In the present study, the type of *Petalosporus nodulosus* was
 1111 phylogenetically similar to that of *P. afilamentosus*. These two species have thick-walled ascospores;
 1112 *P. nodulosus* forms a discrete and often fragmentary ascocarp and its ascospores lack lateral bulges.

1113

1114 *Gymnascella afilamentosa* (Orr & Kuehn) Currah - Mycotaxon 24: 69, 1985 ≡ *Petalosporus*
 1115 *afilamentosus* Orr & Kuehn - Mycologia 64(1): 62, 1972; type strain: CBS 658.71 = ATCC 18901 =
 1116 IFO 31787 = NRRL 3717 = DPG 115 = O-2601 = UAMH 3427, from clay soil, U.S.A.

1117 Orr and Kuehn (1972) described the type species of *Petalosporus afilamentosus* (DPG 115) as lacking
 1118 discrete ascocarps and having smooth, thick-walled and oblate ascospores with a faint lateral bulge.

1119 Our study revealed that *P. afilamentosus* clusters with *G. nodulosus* both of which are closely related
 1120 to *G. dankaliensis* and can be found in nutrient-rich environments.

1121

1122 *Gymnascella udagawae* (Arx) Currah - Syst. Ascom. 7(1): 5, 1988 $\equiv$ *Gymnoascus udagawae* v. Arx -
1123 Persoonia 13(2): 181, 1986; type strain CBS 950.69 = ATCC 24072 = IFO 8921 = NHL 2364 =
1124 NRRL 5963 = UAMH 5726, from soil, Japan.

1125 *Gymnoascus udagawae* is found phylogenetically in Group 9-I *Gymnascella*, with *Plunkettomyces*
1126 *littoralis* (98% ITS to MH860738) (Fig. 8). Reportedly (von Arx 1986), colonies of two species are
1127 bright lemon-yellow. However, *G. udagawae* colonies expand more rapidly (daily rate 3–4 mm at
1128 25°C on hay infusion agar), ascospores lack equatorial ridges, and the species has abundant conidia
1129 (von Arx 1986, 1971).

1130

1131 *Gymnascella littoralis* (Orr) Currah - Mycotaxon 24: 87, 1985 $\equiv$ *Plunkettomyces littoralis* Orr -
1132 Mycotaxon 6(1): 34, 1977 $\equiv$ *Arachniotus littoralis* (Orr) v. Arx - Persoonia 9(3): 397, 1977 $\equiv$
1133 *Gymnoascus littoralis* (Orr) v. Arx - Persoonia 13(2): 179, 1986; type strain CBS 454.73 = NRRL A-
1134 16025 = Orr 3053 = UAMH 3885, from conch shell collected on the beach, Canada.

1135 In the present study, CBS 454.73 was found in Group 9-I (*Gymnascella*), along with *G. citrinus* and *G.*
1136 *udagawae*. In the GenBank database, Sano et al. (2010) submitted several ITS sequences (AB566297,
1137 AB566285 and AB566287) for several *Arachniotus littoralis* strains (IFM 58442, IFM 58265 and IFM
1138 58266) which were obtained from skin scrapings of rats. However, these strains did not cluster with
1139 the type strain and identification of these strains requires more data. In the ITS tree, *P. littoralis* was
1140 found close to *G. udagawae* (98% ITS identity to MH859492) and *G. citrinus* (98% ITS identity to
1141 AJ315836). Morphologically, *P. littoralis* can be differentiated from *G. udagawae* by its ascospores
1142 having longitudinal rims, and from *G. citrinus* by having an asexual state, which is not known in *G.*
1143 *citrinus*. In addition, colonies of *G. citrinus* have distinct bright lemon-yellow color and ascospores are
1144 oblate with thickened poles (Currah 1985; Orr 1977). Considering this habitat choice, *P. littoralis* can
1145 be recognized as a halophilic species.

1146

1147 *Gymnascella citrina* (Masse & Salmon) Orr et al. - Mycologia 69: 134, 1977 $\equiv$ *Pseudoarachnietus*
 1148 *citrinus* (Masse & Salmon) Kuehn - Mycologia 49: 699, 1957 $\equiv$ *Arachnietus citrinus* Masse &
 1149 Salmon - Ann. Bot., Lond. 16: 62, 1902 $\equiv$ *Gymnoascus citrinus* (Masse & Salmon) v. Arx -
 1150 Persoonia 13: 177, 1986; type strain: 0-195 = CBS 638.72 = NRRL 5873, from soil, U.S.A.
 1151 Von Arx (1977) designated CBS 638.72 as the neotype of *Gymnascella citrina* because according to
 1152 his observations, this strain possesses the characteristics described by Masse and Salmon (1902) for
 1153 *A. citrinus*. In the present study, the ITS sequence obtained from GenBank for CBS 863.72 (*G.*
 1154 *citrinus*, from rat dung, India) was used. It clustered in the *Gymnascella* group and was found close to
 1155 the type of *G. udagawae* (99% ITS identity to MH859492); therefore, CBS 863.72 is considered a
 1156 synonym of *G. udagawae*. Previous studies revealed differences between these two species, in that the
 1157 ascospores of *G. udagawae* lacked equatorial thickenings and the colony growth rates of *G. udagawae*
 1158 and *G. citrinus* differed (von Arx 1986). Moreover, another strain, NRRL 5970, was also identified as
 1159 *G. citrina*; according to multilocus phylogeny analysis this strain formed a basal branch to Group II-
 1160 *Arachnietus*. More data are needed to determine the phylogeny of *G. citrina*.
 1161
 1162 ***Gymnascella thermotolerans*** (Zhou & Cai) Kandemir & de Hoog, **comb. nov.** – MycoBank XXXX.
 1163 Basionym: *Gymnoascus thermotolerans* Zhou & Cai, Mycologia 108(1): 188, 2016. Holotype: HMAS
 1164 246111. Ex-holotype culture CGMCC 3.17580 = LC 3877 from corn-field soil, China.
 1165 In its halo- and thermotolerance, *Gymnoascus thermotolerans* is identical to *G. stercorarius*, from
 1166 which it differs by 4% ITS. The nearest neighbor was *P. anodosus* (97% ITS identity to MH859182).
 1167 Morphologically, *G. thermotolerans* has yellowish ascomata, whereas *G. stercorarius* is only known
 1168 from its conidial state. The ascospores of *G. thermotolerans* show distinct equatorial and polar
 1169 thickenings, which are absent from *P. anodosus*. In addition, the arrangement of ascospores inside the
 1170 asci differs between the species: in reticular formation in *G. thermotolerans* and in petaloid form in *P.*
 1171 *anodosus* (Kuehn et al. 1964a).

1172 *Gymnascella anodosa* (Kuehn, Orr & Ghosh) Kandemir & de Hoog, **comb. nov.** – MycoBank
 1173 XXXX. Basionym: *Petalosporus anodosus* Kuehn, Orr & Ghosh - Mycopath. Mycol. Appl. 23: 29,
 1174 1964; type strain: CBS 518.68 = ATCC 18490 = IFO 31788 = IMI 168759 = NRRL A-10221 = QM
 1175 8526, from dung of rabbit, U.S.A.

 1176 Type specimen of *P. anodosus*, NRRL A-10221 was indicated by Kuehn et al. (1964). The species
 1177 was described as usually having a discrete ascocarp, absence of a distinct peridium, and a
 1178 characteristic, petaloid arrangement of ascospores in the asci. In the present study, the type strain was
 1179 found related to *G. thermotolerans* (94% ITS identity to KP278212) and *G. stercorarius* (90% ITS
 1180 identity to KP278214). These two species are known to be thermophilic, although the original
 1181 description of *P. anodosus* lacks this information. The isolates grow more rapidly at 37°C than at 30°C
 1182 (Zhou et al. 2016; Kuehn et al. 1964a). Currah (1985) accepted *P. anodosus* as synonym of *P.*
 1183 *nodulosus*, however, two species show morphological differences (Kuehn et al. 1964a), and this is
 1184 supported by 6% ITS difference.

 1185 *Gymnascella stercorarius* (Zhou & Cai) Kandemir & de Hoog, **comb. nov.** – MycoBank XXXX.
 1186 Basionym: *Gymnoascus stercorarius* Zhou & Cai, Mycologia 108(1): 188, 2016. Holotype: HMAS
 1187 246109. Ex-holotype culture: CGMCC 3.17574 = LC4076 from artificial compost (made from sheep
 1188 droppings and plant residues), China.

 1189 *Gymnoascus stercorarius* has been reported as a halo- and thermotolerant species (maximum near
 1190 50°C, optimum 35°C; growth up to 22.5% NaCl; Zhou et al. 2016). The species is sister to *G.*
 1191 *thermotolerans* (96% ITS identity to KP278212) and *G. anodosa* (94% ITS identity to MH859182) in
 1192 Group 9-I (*Gymnascella*).
 1193
 1194 *Gymnascella devroeyi* (Orr) Currah - Mycotaxon 24: 79, 1985 ≡ *Disarticulatus devroeyi* Orr -
 1195 Mycotaxon 6(1): 37, 1977 ≡ *Arachniotus devroeyi* (Orr) v. Arx - Persoonia 9(3): 398, 1977 ≡
 1196 *Gymnoascus devroeyi* (Orr) v. Arx - Persoonia 13(2): 178, 1986; type strain ATCC 34425 = O-3485 =
 1197 NRRL 5543 = RV 19682, from soil, Belgium.

1198 Orr (1977a) described the *D. devroeyi* with type strain ATCC 34425 and also examined secondary
1199 strain CBS 546.72 = RV 19653 = Orr 4390 in the same sample set. Both strains were proven to be
1200 identical (von Arx 1977). In the current study, only LSU sequences were available for CBS 546.72;
1201 based on this material, the species is placed in Group 9-I *Gymnascella*. Therefore, genus
1202 *Disarticulatus* was abandoned.

1203

1204 **Group 9-II *Arachnietus* Schröt. 1893**

1205 Type species: *Arachnietus ruber* (v. Tiegh.) Schröt. - Krypt. Fl. Schlesien (Breslau) 3.2(1–2): 210,
1206 1893 ≡ *Gymnoascus ruber* v. Tiegh. - Bull. Soc. Bot. Fr. 24: 159, 1877 ≡ *Pseudoarachnietus ruber* (v.
1207 Tiegh.) Orr, Ghosh & Roy - Mycologia 69(1): 153, 1977; type strain CBS 352.90 = Cox A 157 =
1208 MUCL 39748 = IMI 92796 = ATCC 15315 = NRRL 5951 = QM 9289, from soil, U.K. (Kuehn and
1209 Orr 1964).

1210 *Gymnoascus ruber* was described by van Tieghem (1877) as the type species of the genus. However,
1211 since the type material was lost, Schroeter described *Arachnietus ruber* (1893), and Kuehn and Orr
1212 (1964) indicated CBS 352.90 as a neotype for this species. This strain clustered in Group 9-II, with *A.*
1213 *desertorum*, *Gymnoascus confluens*, *Pseudoarachnietus aurantiacus*, *Sphaerosporium equinum* and
1214 *Sporendonema casei*. *Arachnietus ruber* is frequently isolated from alkaline or neutral soils, and from
1215 dog and sheep dung. Alkaline soils have a high pH (>8.0) and contain salts (Qin et al. 2012). This is
1216 consistent with the habitat choices of other members of the group. Even though the optimal growth
1217 temperature was not noted for *A. ruber*, it was unable to grow at 37°C (Kuehn and Orr 1964).

1218 *Sporendonema* is an ancient genus first described 45 years before the establishment of the
1219 family *Gymnoascaceae*, by Desmazières (1827) to accommodate the orange-red cheese fungus, *S.*
1220 *casei*. It was first classified in *Torula* (Berkeley and Broome 1850). Hammer and Gillman (1944) and
1221 Sigler and Carmichael (1976) conducted extensive studies on the morphology and physiology of this
1222 slow-growing fungus *in vitro*. In contrast to other members of the family, it produces broad,
1223 subhyaline to pale pink, hyphae that disarticulate into enteroarthric conidia, propagules being

produced within the outer walls of thick-walled hyphae (Sigler and Carmichael 1976; Hammer and Gilman 1944). This type of conidiogenesis is also typical for the soil-associated and systemic pathogen *Coccidioides* (Pan et al. 1994), which is also known to tolerate high salt concentrations and to grow in sandy alkaline soils that are rich in organic matter and salts (del Rocío Reyes-Montes et al. 2016). Optimal growth occurs between 15°C and 20°C, with good sporulation at 8°C and no growth at 30°C. Hammer and Gillman (1944) reported enhanced growth on cheese agar containing cheese and additional salts. Ropars et al. (2012) used a proprietary medium with a confidential composition provided by starter producers for *S. casei*, which enhanced growth and sporulation. The authors also compared *TUB*, *TEF1-α*, LSU and ITS sequences. They obtained the best matches for ITS and LSU loci with *Arachniotus ruber* (97% ITS homology and 99.4% LSU homology) using BLAST. According to the ITS+LSU phylogeny *A. ruber* grouped with *S. casei* strains, whereas in *TUB/TEF1-α* concatenated analyses, *A. ruber* took a separate, basal position (Ropars et al. 2012). Another isolate of *S. casei* (HDN16-802) was reported by Ge et al. (2019) from a sediment sample from Zhangzi Island, China, which was selected because of its orange color and remarkable metabolic profile. To our knowledge, this is the first report of *S. casei* from a substrate other than cheese. In the present study, strain strains HDN16-802 and CBS 543.75 showed a difference of four bases in ITS sequences (511 bp) and all available *S. casei* strains were found in the same group containing the type of *A. ruber* (Fig. 9). Based on the ITS sequences, similarity between *A. ruber* (MH862216) and *S. casei* cheese isolates (CBS 543.75, CBS 207.27, strain RS3, MUCL 38539, and MUCL 40630) was found to be 99% and 98% for the sediment isolate of *S. casei*. Typification and nomenclatural revision for the *Sporendonema casei* strains will be discussed after further analyses together with *Sphaerosporium equinum* strains.

Several of the isolates from cheese were reported as *Sphaerosporium* (Ropars et al. 2012) and were located in Group 9-II. The genus *Sphaerosporium* includes *S. argentinense* (Spegazzini 1911), *S. equinum* (Crane and Schoknecht 1986) and *S. lignatile* (type of the genus; Schweinitz 1832). The status of the first species is reported to be uncertain, since this type is not interpretable (Partridge and Morgan-Jones 2002). There is no known type material for *S. equinum* and the first description of the

species was based on a specimen H.G. 1510 (PC) from old and humid horse hoofs (Crane and Schoknecht 1986). The type material of *Sphaerosporium lignatile* (#3036, PH on dead wood, U.S.A.) was examined morphologically by Partridge and Morgan-Jones (2002) and reported to have larger conidia and more loosely structured sporodochia than those in *S. equinum*, while both species show similar thallic conidiogenesis. Our understanding of the molecular characteristics of *S. equinum* and *S. lignatile* is limited owing to inadequate data, taken from two studies; the first one reported on MUCL *S. equinum* strains isolated from cheese (Ropars et al. 2012), while the second reported on isolates of *S. lignatile* from decayed hardwood from the personal collection of Alden C. Dirks (Song et al. 2019). Wanderley Costa et al. (2012) also reported *S. equinum* isolates from the leaves of mangrove plants in Brazil; however, the researchers did not provide any information about their identification method. It is possible that the strains were misidentified. On the other hand, an isolate from a skin swab of a living bat (*Myotis lucifugus*) was deposited in the UAMH collection (UAMH 11516) and this strain was reported to be 99% identical to *S. equinum* MUCL 49171 from Pyrenean cheese from Belgium. Another strain, MUCL 54024, was isolated from an insect pupa in Belgium by C. Decock (personal communication). It was found as a separate branch in the same cluster containing cheese isolates and it showed 99% ITS and 99.5% LSU identity to MUCL 49171 in the present study (Fig. 9). Similar to previously described habitats for Group 9-II, both bat wings and insect pupae have an osmophilic nature, which supports the growth of *S. equinum*. Nomenclatural revision of this species will be discussed after further analyses.

Arachnietus aurantiacus (Kamyschko) Arx - Persoonia 6(3): 373, 1971 $\equiv$ *Pseudoarachnietus aurantiacus* Kamyschko - Nov. Sist. Niz. Rast. 1967(4): 224, 1967 $\equiv$ *Gymnascella kamyschkoi* Orr, Ghosh & Roy - Mycologia 69(1): 136, 1977 (name change); type strain: CBS 603.67 = ATCC 22394 = NRRL A-18287 = UAMH 3529 = VKM F-1140, from soil, U.S.S.R.

The type strain CBS 603.67 of *P. aurantiacus* has gymnothecia but lacks a peridium (Kamyschko 1967; Orr et al. 1977a). It differs from other *Pseudoarachnietus* species by its ascospore morphology and from *Arachnietus* species by its orange or yellow-orange gymnothecium (Orr et al. 1977a). The

1278 species phylogenetically is found in Group 9-II clustering with osmophilic *S. equinum* (98% ITS
 1279 identity to JQ434576).
 1280
 1281 *Arachniotus confluens* (Sartory & Bainier) Apinis - Mycol. Pap. 96: 37, 1964 $\equiv$ *Gymnoascus confluens*
 1282 Sartory & Bainier - Bull. Soc. Mycol. Fr. 29: 261, 1913 $\equiv$ *Gymnascella confluens* (Sartory & Bainier)
 1283 Currah - Mycotaxon 24: 75, 1985; type strain: CBS 352.66 = BDUN 375 = ATCC 22220 = IMI
 1284 100873 = NRRL 5979, from dung, U.K.
 1285 = *Arachniotus desertorum* Moustafa - Trans. Br. Mycol. Soc. 61(2): 392, 1973 $\equiv$ *Pseudoarachniotus*
 1286 *desertorum* (Moustafa) Orr, Ghosh & Roy - Mycologia 69(1): 158, 1977 $\equiv$ *Gymnoascus desertorum*
 1287 (Moustafa) v. Arx - Persoonia 13(2): 178, 1986; type strain: CBS 634.72 = ATCC 26464 = IMI
 1288 163480, from halomorphic soil, Kuwait.
 1289 Currah (1985) combined *Arachniotus desertorum* and *Gymnascella confluens* because the differences
 1290 between the two species (darker colonies and slightly larger ascospores for *A. desertorum*) did not
 1291 merit maintaining them as separate species. The ITS analysis provided by Solé et al. (2000a) and the
 1292 present study support this approach. Both species are placed in Group 9-II and have been isolated from
 1293 carnivore dung and halomorphic soil samples (Currah 1985). The name *Arachniotus confluens* was
 1294 used for both species in the present study because the isolates clustered with the type species of
 1295 *Arachniotus* and *A. confluens* has priority over *A. desertorum*. Members of *Arachniotus* are considered
 1296 halotolerant because they are highly adapted to environments with high salt content, such as cheese,
 1297 marine water sediments and saline soil.
 1298
 1299 **Group 9-III *Gymnoascus* Baran.**
 1300 Type species: *Gymnoascus reessii* Baran. - Bot. Ztg. 30: 158, 1872. **Neotype designated here:** Herb.
 1301 No: CBS H-13156, dried culture from soil, U.S.A., isolated by G.F. Orr, 1963. Living strain derived
 1302 from type CBS 392.64.

1303 = *Gymnoascus corniculatus* Orr & Plunkett - Mycopath. Mycol. Appl. 21: 1, 1963; type strain: CBS
 1304 410.72 = NRRL A-10099 = O-263 = UAMH 3159, from soil, U.S.A.

1305 Variability has been noted in ascocarp morphology and pigmentation among *G. reessii* isolates. The
 1306 presence of peridial hyphae may be extensive or rather limited, and they may be smooth or roughened;
 1307 further, the peridial apices may be simple or elaborate (Orr et al. 1963b). The main criterion for
 1308 separating *Gymnoascus corniculatus* from *G. reessii* was the number of appendages with trifurcate or
 1309 chandelieroid apical branching (almost 50% in *G. corniculatus*, versus infrequent in *G. reessii*), in
 1310 addition to ascocarp size. In the current ITS sequence data, CBS 410.72 was found in the same cluster
 1311 as *G. reessii* at 99% identity. Given the morphological variability of *G. reessii*, these data led to the
 1312 conclusion that *G. corniculatus* can be regarded as a younger synonym.

1313

1314 *Gymnoascus longitrichus* Orr & Kuehn - Mycopath. Mycol. Appl. 21(1): 9, 1963; type strain: CBS
 1315 366.64 = ATCC 18433 = IFO 8167 = IHEM 4416 = NRRL A-10096 = RV 20203, from soil, U.S.A.

1316 *Gymnoascus longitrichus* was treated as a synonym of *G. reessii* by Currah (1985). In the present
 1317 study, *G. longitrichus* is found separate from *G. reessii*, being more closely related to *G. dugwayensis*
 1318 (98% ITS identity to LC146737). Morphologically, *G. longitrichus* differs from that species by having
 1319 much longer appendages (160–500 µm vs. 36–164 µm; Orr and Kuehn 1972). Both species might
 1320 share the same ecology since *G. dugwayensis* was reported from sandy soil and *G. longitrichus* was
 1321 isolated from composite soil close to a hot spring area.

1322

1323 *Gymnoascus dugwayensis* Orr & Kuehn - Mycologia 64(1): 65, 1972; type strain: ATCC = 18899 =
 1324 O-3138 = DPG-132 = IFO 31716 = NRRL 3714, from sandy soil, U.S.A.

1325 Unlike the other *Gymnoascus* species, which have typical “boat-hooks” on their short appendages, *G.*
 1326 *dugwayensis* has hooks that are confined to the longer appendages. Appendages in *G. dugwayensis* are
 1327 shorter than those of its nearest neighbor, *G. longitrichus*.

1328

1329 *Gymnoascus uncinatus* Eidam - Cohn's Beitr. Biol. Pfl. 3: 292, 1880 $\equiv$ *Myxotrichum uncinatum*
1330 (Eidam) Schröt., Krypt. - Fl. Schlesien (Breslau) 3.2(1–2): 212, 1893 $\equiv$ *Uncinocarpus uncinatus*
1331 (Eidam) Currah - Mycotaxon 24: 186, 1985; type strain: CBS 408.72 = NRRL 3610 = O-3215 = RSA
1332 56 = UAMH 3913, from dung, U.S.A., R.K. Benjamin, 1949.

1333 Currah (1985) proposed RSA 56 as a neotype of *U. uncinatum*. Morphological characters of the strain
1334 were discussed again by Udagawa and Uchiyama (2000) and the species was included in *Gymnoascus*
1335 based on presence of lattice-like peridium, coiled ascomatal initials, smooth-walled ascospores and
1336 non-thermotolerant behavior. Phylogenetically, it is confirmed to be a member of Group 9-III,
1337 clustering with *G. exasperatus* (95% ITS identity to KU746682) in the present study.

1338

1339 *Gymnoascus exasperatus* Liu & Cai - Persoonia 39: 14, 2017; holotype: HMAS 246925; ex-type
1340 culture: CGMCC 3.17923 = LC5640, from bat guano, China.

1341 This species is only known from its asexual morph. Sequence data showed that it is related to *G.*
1342 *uncinatus* (95% ITS identity to KT155648).

1343

1344 *Gymnoascus flavus* Zhang & Cai - Fung. Div. 106: 29, 2021; holotype: HMAS 248010; ex-type
1345 culture: CGMCC3.19574 = LC12500, from karst cave soil, China.

1346 Zhang et al. (2021) reported that the species was unable to grow on oat meal agar, while growth was
1347 observed on synthetic nutrient agar at 23–25°C, underlining its oligotrophic character. Similar to ITS
1348 and LSU loci data provided by Zhang et al. (2021), *G. flavus* formed a basal cluster to *G.*
1349 *dugwayensis*, *G. exasperatus*, *G. longitrichus*, *G. reessii*, and *G. uncinatus* in the present study (Fig.
1350 9). Unlike *G. reessii* and *G. uncinatus*, there is no sexual morph known for *G. flavus*. The species can
1351 be distinguished from *G. exasperatus* by abundant intercalary in addition to terminal and lateral
1352 conidia.

1353

1354 *Gymnoascus intermedius* Orr - Mycotaxon 5(2): 470, 1977; type strain: ATCC 28555 = O-313 =
 1355 NRRL 6272, from soil, U.S.A.

1356 *Gymnoascus intermedius* has been isolated from soil and from the lung of a pocket mouse. The
 1357 original material is not known to be preserved. In the present study, two secondary isolates were
 1358 examined, i.e., IFM 47418 (= UAMH 3833 =NRRL A16935 = O-3139 from soil, Italy) and UAMH
 1359 11472 (from skin swab of a living bat, Canada). The first strain was found in Clade 4 (family
 1360 Auxarthraceae), while the latter clustered in the Gymnoascaceae, Group 9-III, along with *G.*
 1361 *longitrichus* and *G. dugwayensis*, with 99% ITS similarity to both species. In the original description
 1362 of *G. intermedius*, Orr (1977b) noted that the ascocarp lacks appendages as well as the "boat-hook"
 1363 type branches which can be observed in the former two species. Also, the ascospore morphology
 1364 differs, noted as oval to elliptical for *G. intermedius*, oblate for *G. dugwayensis* and oval to oblate for
 1365 *G. longitrichus* (Orr et al. 1963b; Orr and Kuehn 1972; Orr 1977b). Further analyses are required to
 1366 determine the status of *G. intermedius*.

1367 Members of Group 9-III are associated with various types of mammal dung and soil.

1368 *Gymnoascus longitrichus* was isolated from soil close to an alkaline hot spring (Orr et al. 1963b). Hot
 1369 spring soils have high temperatures, extreme pH values, sparse vegetation, and limited organic carbon
 1370 (Redman et al. 1999; Kumar et al. 2004). The habitat of *Gymnoascus dugwayensis* was found in
 1371 sandy, acidic soil with poor nutrient content. Both species are phylogenetically closely related to *G.*
 1372 *reessii* (Figs 1, 9). *Gymnoascus reessii* can be found in habitats with high nutritional content, such as
 1373 dung of various types of mammals and soil. All species of *Gymnoascus* have long gymnothecial
 1374 appendages. *Gymnoascus flavus* and *G. exasperatus* were found in karst caves, which constitute an
 1375 oligotrophic environment (Jiang et al. 2017). However, *G. exasperatus* was found on bat guano in one
 1376 of these caves, providing local patches of substrate rich in carbon, nitrogen, sulfur, phosphorus and
 1377 chitin (Liu et al. 2013).

1378

1379 **Group 9-IV *Gymnoascoideus* Orr, Roy & Ghosh**

- 1380 Type species: *Gymnoascoideus petalosporus* Orr, Roy & Ghosh - Mycotaxon 5(2): 460, 1977 =
- 1381 *Gymnoascus petalosporus* (Orr, Roy & Ghosh) v. Arx - Persoonia 9(3): 397, 1977; type strain: UAMH
- 1382 1665 = ATCC 34351 = NRRL 6001 = O-3325, from nodular cyst of human eye.
- 1383 = *Gymnoascus boliviensis* Guarro, Ulfig & De Vroey - Mycotaxon 45: 317, 1992; type strain: IMI
- 1384 351986 = FMR 3793, from soil of chicken yard, Bolivia, 1972.
- 1385 Orr et al. (1977) described *Gymnoascoideus petalosporus* with thick- and smooth-walled ascospores in
- 1386 a petaloid arrangement in the asci. Correctly identified strains suggest a preference for keratinous
- 1387 substrates such as human skin (CBS 630.72), horse skin (UAMH 3592), horn (UAMH 3525), and
- 1388 feathers (O-1299), in addition to soil (O-2013). Von Arx (1977) examined some of these strains and
- 1389 noted that they were variable in culture morphology, peridial hyphal formation and size of ascospores.
- 1390 He considered *Gymnoascoideus* (in the literature often as “*Gymnoascoides*”) intermediate between
- 1391 *Arachniotus* and *Gymnoascus*. Phylogenetically, the nearest neighbor of *G. petalosporus* is *G.*
- 1392 *boliviensis* (99% ITS identity to AJ315828), which differs by its brown ascomata and ascospores
- 1393 without equatorial thickening (Guarro et al. 1992b). *Gymnoascus boliviensis* has been reported to form
- 1394 clusters of asci and lack discrete ascocarps on sterilized soil supplemented with hair. The presence of
- 1395 interwoven peridial hyphae, ascospores in a petaloid pattern and limited growth at 37°C have also
- 1396 been reported (Guarro et al. 1992b).
- 1397
- 1398 *Gymnoascus verrucosus* Sharma & Singh - IMA Fungus 4(2): 178, 2013; holotype: AMH 9454; ex-
- 1399 type culture: NFCCI 2672, from soil, India.
- 1400 The species is described with verruculose ascospores with small tubercles over the entire surface. The
- 1401 type strain was found as a separate branch and with its neighbors, *G. petalosporus* and *G. boliviensis*
- 1402 at considerable distances (89% ITS identity to HM991270 and AJ315828, respectively). *Gymnoascus*
- 1403 *boliviensis* can easily be distinguished from *G. verrucosus* by its ascospores which are smooth and

1404 discoid with an equatorial rim and arranged in petaloid form in asci. In addition, *G. boliviensis* does
1405 not have peridial appendages, which are present in *G. verrucosus* (Guarro et al. 1992b).

1406

1407 **Group 9-V *Narasimhella*** Thirumalachar & Mathur

1408 Type species: *Narasimhella poonensis* Thirum. & Mathur - Sydowia 19(1-6): 185, 1966; type strain:

1409 CBS 393.71 = ATCC 16197 = HACC 171 = IHEM 3406 = IMI 113696, from soil, India.

1410 = *Pseudoarachnietus marginisporus* Kuehn & Orr - Mycopath. Mycol. Appl. 19: 257, 1963 ≡

1411 *Arachnietus marginisporus* (Kuehn & Orr) Udagawa - Trans. Mycol. Soc. Japan 10(3): 103, 1970 ≡

1412 *Gymnascella marginispora* (Kuehn & Orr) Currah - Mycotaxon 24: 87, 1985 ≡ *Narasimhella*

1413 *marginispora* (Kuehn & Orr) v. Arx - Persoonia 13(2): 179, 1986 ≡ *Gymnoascus marginisporus*

1414 (Kuehn & Orr) Solé, Cano & Guarro - Stud. Mycol. 47: 145, 2002; type strain: CBS 115.54 = NBRC

1415 9194 = ATCC 15314 = UAMH 3533 = NRRL 2850 = RSA 1553, from buried cable, U.S.A.

1416 The generic type species *Narasimhella poonensis* was described as having well-developed, stipitate

1417 fruitbodies. The sterile stipe is composed of upward-growing hyphae and an irregularly globular,

1418 fertile head portion with groups of asci. It lacks a peridium and shows crozier formation similar to that

1419 of *Pseudoarachnietus* species. The optimum growth temperature is 28°C (Thirumalachar and Mathur

1420 1966). NRRL 2850 was listed as the type of *P. marginisporus* by Kuehn and Orr (1963). Several

1421 taxonomic rearrangements were followed. *Narasimhella* has a peculiar ecology. All isolates of this

1422 species have been obtained from buried substrates, such as cables and fabrics buried in dung-enriched

1423 soil. Nutrient-rich soil is a common habitat for many Gymnoascaceae members, but none of them have

1424 been found to grow on hard underground substrates. ITS similarity between *Narasimhella poonensis*

1425 (MH857260) and *N. marginispora* (MH860180) was found to be 99% and the species were considered

1426 to be synonyms, confirming Thirumalachar and Mathur (1966), with *N. marginispora* as the oldest

1427 name. the fungus is described with its habitat choice, thin- and smooth-walled ascospores with minute

1428 rims, and ochraceous to very pale-yellow colonies (Kuehn and Orr, 1963).

1429

1430 *Narasimhella echinulata* (Dutta & Ghosh) v. Arx - Gen. Fungi Sporul. Cult., Edn 2 (Vaduz): 94, 1974
 1431 $\equiv$ *Pseudoarachnietus echinulatus* Dutta & Ghosh - Mycologia 55(6): 775, 1963 $\equiv$ *Amauroascus*
 1432 *echinulatus* (Dutta & Ghosh) v. Arx - Persoonia 6(3): 375, 1971 $\equiv$ *Mallochella echinulata* (Dutta &
 1433 Ghosh) v. Arx & Samson - Persoonia 13(2): 185, 1986; type strain: CBS 278.64 = ATCC 15317 =
 1434 UAMH 3561 = NRRL A-12062 = IFO 9192, from rice-field soil, India, G.F. Orr.

1435 The species was first included in *Pseudoarachnietus* because of the absence of discrete ascomata. It
 1436 was found to be morphologically different from other *Pseudoarachnietus* species, primarily by
 1437 globose and echinulate ascospores. Von Arx and Samson (1986) introduced the genus *Mallochella* to
 1438 classify *Pseudoarachnietus echinulatus*. Udagawa and Uchiyama (2002) examined the type specimen
 1439 and accepted the genus in the Amauroascaceae. In the present study, *N. echinulata* (IFO 9192) was
 1440 found close to *N. punctata* (98% ITS identity to AJ315825), *N. marginispora* (97% ITS identity to
 1441 MH857260) and *N. hyalinospora* (98% ITS identity to NR130659). Although morphologically the
 1442 nearest neighbor was noted to be *P. reticulatus* (Dutta et al. 1963), the two species were found
 1443 phylogenetically remote from each other (88% ITS identity to NR153508; 94% LSU identity to
 1444 NG056930). Morphological differences with *N. echinulata* include the absence of peripheral rims or
 1445 extensions and red-capped hyphae, changes in ascospore colors from purple-brown to red-brown with
 1446 age, and relatively large echinulate ascospores. The ability to grow at 37°C confirmed this separation.

1447

1448 *Narasimhella punctata* (Dutta & Ghosh) Kandemir & de Hoog, **comb. nov.** – MycoBank XXXX.
 1449 Basionym: *Pseudoarachnietus punctatus* Dutta & Ghosh - Mycologia 56(2):153, 1964 $\equiv$ *Arachnietus*
 1450 *punctatus* (Dutta & Ghosh) v. Arx - Persoonia 6(3): 373, 1971 $\equiv$ *Gymnascella punctata* (Dutta &
 1451 Ghosh) Currah - Mycotaxon 24: 93, 1985 $\equiv$ *Gymnoascus punctatus* (Dutta & Ghosh) v. Arx -
 1452 Persoonia 13(2): 180, 1986; type strain: CBS 279.64 = ATCC 22851 = NRRL A-12061 from rice-field
 1453 soil, India by B.G. Dutta. Herb. No: CBS H-6711.

1454 Strain NRRL A-12061 was described as having punctate ascospores with a broad rim. Discrete
 1455 ascocarps were absent and asexual spores could not be observed. The strain was located in Group 9-V

1456 and was found to be similar to *N. echinulata* (98% ITS similarity to AJ271562), differing by punctate
1457 ascospores with a rim, yellow in mass, while those of *N. echinulata* were echinulate without a rim and
1458 purple-brown in mass. Both species were isolated from paddy soil. Besides high humidity, the major
1459 characteristic of paddy soil is a higher amount of available silica content compared to highlands
1460 (Takahashi 1968). Although silicon is not a nutrient, it promotes the growth of fungi under
1461 oligotrophic conditions (Wainwright et al. 1997).

1462

1463 *Narasimhella hyalinospora* (Kuehn, Orr & Ghosh) v. Arx - Persoonia 6: 374, 1971 ≡
1464 *Pseudoarachnietus hyalinosporus* Kuehn, Orr & Ghosh - Mycopath. Mycol. Appl. 14: 217, 1961 ≡
1465 *Arachnietus hyalinosporus* (Kuehn, Orr & Ghosh) Apinis - Mycol. Pap. 96: 41, 1964 ≡ *Rollandina*
1466 *hyalinospora* (Kuehn, Orr & Ghosh) Roy, Orr & Ghosh - Taxonomy of Fungi (Proc. Int. Symp.
1467 Madras, 1973) 1: 221, 1978 ≡ *Gymnascella hyalinospora* (Kuehn, Orr & Ghosh) Currah - Mycotaxon
1468 24: 84, 1985 ≡ *Gymnoascus hyalinosporus* (Kuehn, Orr & Ghosh) Solé, Cano & Guarro - Stud.
1469 Mycol. 47: 145, 2002; type strain: CBS 548.72 = NRRL 2881 = BCCM/IHEM 3416 = IMI 099725 =
1470 RSA 1529 = UAMH 3155, from dung of Guinea pig, India, G.R. Ghosh, 1959.

1471 Kuehn et al. (1961) described CBS 548.72 as type for *Pseudoarachnietus hyalinospora*. In the present
1472 study, it clustered with *N. punctata*, *N. echinulata* and *N. marginispora*. These species are all
1473 morphologically similar by absence of discrete ascocarps. *Narasimhella punctata* can easily be
1474 distinguished by its punctate ascospores; *N. echinulata* has large, echinulate ascospores ($4.0\text{--}5.5 \times 5\text{--}6$
1475 μm vs. $2.2\text{--}2.5 \times 2.5\text{--}3.3 \mu\text{m}$ for *N. hyalinospora*). Ascospores of *N. marginispora* deviate by having
1476 a minute rim. Habitat choice of the members of this group is mostly nutrient-rich environments such
1477 as animal dungs and rhizosphere soil.

1478

1479 *Narasimhella armeniacus* (Solé, Cano & Guarro) Kandemir & de Hoog, **comb. nov.** – MycoBank
1480 XXXX. Basionym: *Gymnoascus armeniacus* Solé, Cano & Guarro - Stud. Mycol. 47: 145, 2002; type

1481 strain: CBS 125.78 = IMI 386570, from dung of kangaroo, India, J.A. von Arx. Herb. No: CBS H-
1482 14981.

1483 *Gymnoascus armeniacus* was found in Group 9-V close to *P. hyalinosporus* (95% ITS similarity in
1484 500 bp). Both *P. hyalinosporus* and *G. armeniacus* prefer nutritionally rich habitats and they were
1485 reported to be morphologically similar (Solé et al. 2002b). However, the latter lacks discrete ascomata
1486 (Currah 1985; Kuehn et al. 1961). Growth for *G. armeniacus* was reported at 37°C but not at 45°C
1487 (Solé et al. 2002b).

1488

1489 *Pseudoarachniotus reticulatus* Kuehn & Goos - Mycologia 52(1): 40, 1960 ≡ *Amauroascus reticulatus*
1490 (Kuehn & Goos) v. Arx - Persoonia 6(3): 375, 1971 ≡ *Amaurascopsis reticulata* (Kuehn & Goos)
1491 Guarro & Gené - Mycotaxon 45: 174, 1992 ≡ *Mallochia reticulata* (Kuehn & Goos) Solé, Cano &
1492 Guarro - Mycol. Res. 106(4): 395, 2002; type strain: CBS 392.61 = ATCC 14045 = IMI 084358, from
1493 rhizosphere soil of *Musa sapientum*, U.S.A., R.D. Goos, 1959.

1494 Kuehn and Goos (1960) characterized *Pseudoarachniotus reticulatus* by the absence of ascocarps,
1495 globose and reticulate ascospores, usually red-capped hyphae among tufts of asci, and peripheral
1496 extensions on the ascospores. In the present study, the type strain placed in a cluster containing a strain
1497 identified as *M. reticulata* (IFO 9196) by Solé et al. (2002a). A more detailed molecular and
1498 morphological examination is needed to establish the relationship between these two strains. The
1499 habitat choice of the rhizosphere indicates that *P. reticulatus* is not oligotrophic, as compared to bulk
1500 soil, which has higher nutrient availability (McNear, 2013).

1501

1502 *Pseudoarthropsis cirrhata* (Oorschot & de Hoog) Stehigel, Rodr.-Andr. & Cano - IMA Fungus 27(1):
1503 47, 2021 ≡ *Arthropsis cirrhata* Oorschot & de Hoog - Mycotaxon 20: 130, 1984; type strain: CBS
1504 628.83, from brick wall, The Netherlands.

1505 The genus *Arthrospis* is typified with *Arthrospis truncata* (UAMH 4430, from dead leaves, Peru;
1506 Sigler et al. 1982a) and the type species is classified in Sordariomycetes (Giraldo et al. 2014).
1507 However, two species *A. hispanica* and *A. cirrhata* are accommodated within the Onygenales (Fig. 1).
1508 Similar to *A. hispanica*, *A. cirrhata* shows basipetal septation to form enteroarthric conidia. However,
1509 the arthroconidia of *A. cirrhata* are light yellowish orange and the fungus shows restricted growth at
1510 25°C, with a maximum growth temperature of 30°C (van Oorschot and de Hoog 1984). During our
1511 study, only an LSU sequence was available and phylogeny showed *A. cirrhata* in Group 9-V, remote
1512 from *A. hispanica* (*incertae sedis*), the other member described in *Arthrospis* (Suppl Figs 1, 2).
1513 Rodríguez-Andrade et al. (2021) also analyzed ITS and LSU sequences of *A. cirrhata* and they
1514 proposed a new genus *Pseudoarthropsis*, for *A. cirrhata*.

1515

1516 *Gymnoascus halophilus* Zhou & Cai - Mycologia 108(1): 185, 2016. Holotype: HMAS 246110; ex-
1517 holotype culture: CGMCC 3.17579 = LC4751, from salt lake sediment, China.

1518 Ascomata are discrete or confluent, and peridial hyphae are surrounded by clumps of asci and lack
1519 appendages. Optimal growth occurs at 25°C and growth can still be observed near 40°C. This species
1520 is unable to grow on media without additional salt and tolerates NaCl up to 22.5% (Zhou et al. 2016).
1521 Therefore, it is an obligate halophilic fungus. However, phylogenetically, it is not found in Group 9-II
1522 which includes species predominantly isolated from saline environments. Based on the ITS phylogeny
1523 (Fig. 9), *G. halophilus* formed a single cluster in the family, whereas in the maximum likelihood (ML)
1524 tree, this cluster was found at the base of Group 9-V, *Narasimhella* (Fig. 9). Further studies are
1525 required to establish the correct nomenclature for *G. halophilus* (CGMCC 317579) as well as *G.*
1526 *verrucosus* (NFCCI 2672).

1527 *Kraurogymnocarpa trochleospora* (Kuehn & Orr) Udagawa & Uchiyama - Mycoscience 42(3): 281,
1528 2001 ≡ *Pseudoarachniotus trochleosporus* Kuehn & Orr - Mycologia 64(1): 58, 1972 ≡ *Arachniotus*
1529 *trochleosporus* (Kuehn & Orr) Udagawa - Nippon Kingakukai Kaiho 38(3): 154, 1997; type strain:

1530 CBS 591.71 = ATCC 18900 = NRRL A-16936 = DPG 71 = UAMH 3416 = UAMH 10101, from soil,
 1531 U.S.A.

1532 *Pseudoarachnietus trochleosporus* was described as lacking discrete ascocarps, mostly with globose
 1533 ascospores with an external rim, roughened walls, lenticular to pulley-shaped in side view and grooved
 1534 on the lateral axis, with crests on each side of the groove. The name *K. lenticulospora* was based on
 1535 morphological comparison with *K. lenticulospora* (Udagawa and Uchiyama 2001). In the present
 1536 study, the species was found to be a sister branch to *Diploospora rosea* in ITS analyses (Fig. 9), while
 1537 ML analyses revealed *D. rosea* as *incertae sedis* (Fig. 1). The latter species is both phylogenetically
 1538 (82% ITS identity to NR111882) and morphologically (by enteroarthric conidial formation) quite
 1539 different from *K. trochleospora*. Moreover, in contrast to the xerophilic nature of *D. rosea*, *K.*
 1540 *trochleospora* prefers sandy-clay and clay soils which have higher water-holding capacities than that
 1541 of most other soil types (Orr and Kuehn, 1972; O'Geen, 2013).

1542

1543 **Clade 10 Spiromastigaceae** Hirooka, Tanney & Seifert - Mycologia 108(1): 135, 2016
 1544 ≡ Spiromastixaceae Guarro, Cano & Stchigel - Mycoses 57(7): 425, 2014 ≡ Spiromastigoidaceae
 1545 Guarro, Cano & Stchigel - Mycopathologia: 976, 2017.

1546 Type genus: *Spiromastigoides* Doweld - Index Fungorum 30: 1, 2013 ≡ *Spiromastix* Kuehn & Orr -
 1547 Mycologia 54(2): 160, 1962; type species: *Spiromastigoides warcupii* (Kuehn & Orr) Doweld ≡
 1548 *Spiromastix warcupii* Kuehn & Orr - Mycologia 54(2): 160, 1962; type strain: CBS 576.63 = ATCC
 1549 14964 = IFO 31795 = MUCL 9856 = NRRL A-10679 = QM 9683, from wheat field soil, Australia,
 1550 J.H. Warcup, 1959, as *Myxotrichum* sp.

1551 *Spiromastix* was originally described as a member of the family Gymnoascaceae, with the type species
 1552 *Spiromastix warcupii* (Kuehn and Orr 1962). It was found to be unique because of its curved but never
 1553 completely coiled peridial appendages. However, since the name *Spiromastix* had already been applied
 1554 to an alga (Perfil'ev 1929), it was changed to *Spiromastigoides* by Doweld (2013). Rizzo et al. (2014)
 1555 proposed the order *Spiromastixales*, based on LSU D1-D2 sequence analysis. The species have

discrete or confluent, brown ascomata covered with orange-brown, curved or twisted appendages; eight-spored, subglobose, ovoid to ellipsoidal asci; and smooth-walled, yellowish to pale brown ascospores. However, Hirooka et al. (2016) reduced this to the family level as Spiromastigaceae in the Onygenales, using ITS and concatenated 18S + 28S data. This conclusion was supported by Stchigel et al. (2017), who changed the family name to Spiromastigoidaceae, because of its link with *Spiromastigoides*. In the current study, the family comprises the genera *Sigleria*, *Spiromastigoides* and *Pseudospiromastix*, as reflected in our LSU and ML analyses (Fig. 1; Suppl. Figs 1, 2), although with ITS data, *Sigleria* grouped separately, close to Clade 14 (Suppl. Figs 3, 4). The original family name, Spiromastigaceae, is nomenclaturally correct and is maintained here.

All members of *Spiromastigoides* are known to be cellulolytic and non-keratinolytic, except *Spiromastigoides pyramidalis* which has been reported to be weakly keratinolytic (Currah 1994; Hirooka et al. 2016). Human and animal infections have been suggested for *S. albida* and *S. asexualis* because of culture from biopsy specimens, and they are considered potential opportunistic pathogens (Stchigel et al. 2017; Rizzo et al. 2014). While all members of the genus have hemolytic and urease activity, only *S. albida* and *S. asexualis* also have lipolytic activity (Stchigel et al. 2017; Rizzo et al. 2014). Phylogenetically, these two species are placed far apart (Figs 1, 11), suggesting that lipolysis emerged more than once during the separation of the species, or that it might be an atavism.

For two species, *S. saturnispora* (Uchiyama et al. 1995b, type strain: CBM BF54422, from meadowy soil, Indonesia), and *S. sphaerospora* (Udagawa and Uchiyama 1999b; type strain: SUM 3128, from sports field, Japan,) material was not available for study (Hirooka et al. 2016). The asexual morph of *Spiromastigoides* was reported in the literature either as malbranchea- or chrysosporium-like (Hirooka et al. 2016). During our analyses, the type strain of *Malbranchea gypsea*, CBS 134.77 was found amidst *Spiromastigoides* species. This strain was reported to be cellulolytic, not keratinolytic and it was recovered from lesions on the spleens and livers of mice after experimental passages (Orr 1972; Sigler and Carmichael 1976). The following recombination is proposed for *M. gypsea*:

Spiromastigoides gypsea (Sigler & Carmichael) Kandemir & de Hoog, **comb. nov.** – MycoBank XXXX. Basionym: *Malbranchea gypsea* Sigler & Carmichael - Mycotaxon 4(2): 455, 1976; type

1583 strain: CBS 134.77 = ATCC 35432 = UAMH 1975, Herb. IMI 211203 from soil, U.S.A., G.F. Orr,
1584 1964.

1585 A strain identified as *Chrysosporium pseudomerdarium*, CBS 279.77 was found in Clade 10, but it
1586 clustered remote from the type strain of this species (CBS 631.79 = IMI 282432), which clustered
1587 outside the order Onygenales. Similarities between ITS and LSU loci of *S. warcupii* (CBS 576.63) and
1588 *C. pseudomerdarium* CBS 279.77 were found to be 94% and 97%, respectively. Therefore, CBS
1589 279.77 is provisionally identified as *Spiromastigoides* sp. Rodríguez-Andrade et al. (2021) provided a
1590 key for the identification of the *Spiromastigioides* species.

1591 ***Sigleria*** Hirooka, Tanney & Seifert - Mycologia 108(1): 140, 2016; type species: *Sigleria carmichaelii*
1592 Hirooka, Tanney & Seifert; type strain: CBS 138264 = DAOM 250076, from house dust, Micronesia.

1593 The genus *Sigleria* is represented by two species, *Sigleria amendiana* (Hirooka et al. 2016; type strain:
1594 CBS 138357 = DAOM 588476) and *Sigleria carmichaelii*. Both type species were isolated from house
1595 dust. Although they are morphologically similar to *Spiromastigoides* species, *Sigleria* conidiophores
1596 tend to show opposite branching, whereas *Spiromastigoides* species have a predominantly unilateral
1597 branching pattern (Hirooka et al. 2016). The most distinguishing characteristic of *Sigleria* is its limited
1598 ability to utilize nitrate as a nitrogen source. Furthermore, growth rates on malt extract agar (MEA) are
1599 slow, and ascomata have not been observed (Hirooka et al. 2016). Morphological differences between
1600 the two genera were supported by phylogenetic results (Figs 1, 11). Interestingly, *S. carmichaelii* was
1601 often found to co-occur with *Wallemia* species on MEA with high sugar content (Hirooka et al. 2016).
1602 The genus *Wallemia* is known to be xerophilic and halophilic (Zalar et al. 2005; Zajc and Gunde-
1603 Cimerman 2018). Low water activity is a major environmental condition in dust.

1604

1605 ***Pseudospiromastix*** Guarro, Stchigel & Cano - Mycoses 57(7): 425, 2014; type species:
1606 *Pseudospiromastix tentaculata* (Guarro, Gené & De Vroey) Guarro, Stchigel & Cano $\equiv$ *Spiromastix*
1607 *tentaculata* Guarro, Gené & De Vroey - Mycotaxon 46: 308, 1993; type strain: CBS 184.92 = FMR
1608 3842 = IMI 351264 = MUCL 40569 = UAMH 7098, from soil, Somalia, J. Guarro, 1968.

1609 The genus *Pseudospiromastix* thus far contains only *P. tentaculata*, which differs from other members
1610 of the family by its ascomata bearing undulate appendages with swollen ends (Guarro et al. 1993). As
1611 in *Spiromastigoides* species, *P. tentaculata* can use nitrate its sole nitrogen source (Hirooka et al.
1612 2016).

1613

1614 **Clade 11 *Incertae sedis***

1615 In the present study, Clade 11 was treated separately because incompatible results were obtained for
1616 members of the clade. The monotypic genus *Polytolypa* (Scott et al. 1993) is represented by its type
1617 species *Polytolypa hystricis* (type strain: UAMH 7299, from porcupine dung, Canada). It is non-
1618 keratinolytic, unable to grow at 37°C and possesses gymnothecia with helical peridial appendages,
1619 globose, irregularly disposed asci and apricot yellow, smooth to minutely roughened ascospores; and a
1620 chrysosporium-like anamorph (Scott et al. 1993). Morphological characteristics have been reported
1621 similar to *Helicocarpus griseus* (Untereiner et al. 2002). Based on results of LSU locus analysis and
1622 whole genome analysis, *P. hystricis* was reported as a basal clade of Ajellomycetaceae (Untereiner et
1623 al. 2002; Muñoz et al. 2018), whereas it was found close to Spiromastigaceae by ITS locus analysis
1624 (Hirooka et al. 2016). In the current multilocus study, the type strain was found to be a basal clade
1625 with Spiromastigaceae, together with *Chrysosporium chiropterum* (type strain: MUCL 45495, from
1626 bat fur, France) (Beguin et al. 2005) and *Chrysosporium lobatum* (type strain: CBS 666.78, from
1627 mouse hair, Russia) (Scharapov 1978) (Fig. 11). ITS identity with *P. hystricis* and *C. chiropterum* was
1628 found to be 91%. *Chrysosporium lobatum* (CBS 666.78) showed 90% ITS similarity with *P. hystricis*.
1629 Nevertheless, more detailed genome analyses including members from closely related families, i.e.,
1630 Spiromastigaceae and Ascospaeraceae, combined with physiological and morphological data, are
1631 required to conclusively determine the taxonomic position of *Polytolypa*.

1632

1633 **Clade 12 Ajellomycetaceae** Untereiner, Scott & Sigler

1634 Type genus: *Ajellomyces* McDonough & Lewis; type species: *Ajellomyces dermatitidis* McDonough &
1635 Lewis - Mycologia 60: 77, 1968; type strain: CBS 674.68 = ATCC 18188 = UAMH 3539, from
1636 human patient, U.S.A., E.S. McDonough, 1968.

1637 The family Ajellomycetaceae is based on the genus *Ajellomyces*, which was described for several
1638 sexual states of members of this family. Many Ajellomycetaceae members are causative agents of
1639 systemic diseases in mammals. The type species of *Ajellomyces* is *Ajellomyces dermatitidis*, the sexual
1640 state of *Blastomyces dermatitidis*, the main agent of human and canine blastomycosis. Other
1641 *Ajellomyces* species have been found by *in vitro* mating in *Histoplasma*, *Emergomyces* (formerly
1642 *Emmonsia*) and *Helicocarpus*. Today, separate sexual names have been abandoned and the genus
1643 *Ajellomyces* has become superfluous.

1644 Clade 12 contains the thermally dimorphic fungi including *Blastomyces* (Gilchrist and Stokes
1645 1898; type strain: *B. dermatitidis* CBS 674.68), *Emergomyces* (Dukik et al. 2017; type strain: *E.*
1646 *pasteurianus*, CBS 101426), *Emmonsiiellopsis* (Marin-Felix et al. 2015; type strain: *E. terrestris*, CBS
1647 273.77), *Helicocarpus* (Marin-Felix et al. 2015; type strain: *H. griseus*, CBS 128.88), *Histoplasma*
1648 (Darling 1906; type strain: *H. capsulatum*, CBS 136.72), *Lacazia* (Taborda et al. 1999; type specimen:
1649 *L. loboi*, BPI 792295) and *Paracoccidioides* (type strain: *P. brasiliensis*, Pb18 = B17). Another genus,
1650 *Emmonsia* (Ciferri and Montemartini 1959; type strain: *E. parva* CBS 139881 = UAMH 130) was also
1651 described in the Ajellomycetaceae but later the species of this genus were re-classified in *Blastomyces*
1652 and *Emergomyces*, based on the results of multiphasic approaches including multi-locus sequencing,
1653 morphological and physiological data (Jiang et al. 2018, 2020).

1654 *Lacazia loboi* was described with the basionym *Paracoccidioides loboi*, which was invalidly
1655 published (Taborda et al. 1999a). The phylogenetic position of *L. loboi* was found to be ancestral to
1656 *Paracoccidioides* species (Fig. 12). Although phylogenetically close, the process of yeast cell
1657 formation in tissue is different in the two genera, i.e., unilateral *versus* multilateral. In addition,
1658 *Lacazia* contains melanin in its cell wall (Taborda et al. 1999b) and causes only (sub)cutaneous
1659 infections, whereas *Paracoccidioides* does not contain melanin and is an agent of disseminated
1660 infections (Taborda et al. 1999a). All available records of *L. loboi* were obtained from tissue samples,

1661 since the fungus has not been cultured *in vitro*. Although the histological features of lobomycosis in
 1662 humans and dolphins are similar, the fungus was reported to differ in morphology between the two
 1663 hosts (Haubold et al. 2000). In the present study, *Lacazia* clustered with *Paracoccidioides* (with >
 1664 88% ITS identity; Fig. 12), but the phylogenetic distance between the genera remained significant
 1665 (Fig. 1). In accordance with the available data (Cowan 1993; Simose-Lopes et al. 1993; Haubold et al.
 1666 1998; 2000; Taborda et al. 1999a; Schaefer et al. 2016; Esperón et al. 2012), the etiological agents of
 1667 lobomycosis in humans and dolphins are likely to be different species. Vilela and Mendoza (2018)
 1668 proposed the name *Paracoccidioides brasiliensis* var. *ceti* to describe the uncultivated fungus causing
 1669 cutaneous disease in dolphins, and used the name *L. loboi* to describe the etiological agents of the
 1670 same disease in humans. Several ITS sequences from dolphins (AF035674, AF035675) and plants
 1671 (GU361967, FJ037740) were recorded in GenBank as *L. loboi*, but might be considered contaminants
 1672 or misidentifications. The phylogenetic structure of Clade 12 was inconsistent between the ITS and
 1673 LSU analyses. In LSU, the family Eremasaceae was found in Clade 12, whereas it formed a separate
 1674 clade in ITS and multilocus analyses (Figs 1, 12; Suppl. Figs 1, 2).

1675

1676 **Clade 13 Ascosphaeraceae** Olive & Spiltoir

1677 = Synascomycetaceae Varitchak - Le Botaniste 25: 365, 1933 (invalid, ICBN Art. 36; see Cooke and
 1678 Hawksworth, 1970).

1679 = Pericystaceae Bessey - Morph. Tax. Fungi, p. 352, 1950 (invalid, ICBN Art. 36; see Cooke and
 1680 Hawksworth, 1970).

1681 Type genus: *Ascosphaera* Olive & Spiltoir - Mycologia 47(2): 242, 1955; type species: *Ascosphaera*
 1682 *apis* (Maasen ex Claussen) Olive & Spiltoir - Mycologia 47(2): 242, 1955 ≡ *Pericystis apis* Maasen ex
 1683 Claussen - Mitt. Biol. BundesAnst. Land- u. Forstw. 16: 51–58, 1916.

1684 = *Pericystis apis* var. *major* Pröschl & Zobl - Arch. Mikrobiol. 18(2): 200, 1953 ≡ *Ascosphaera apis*
 1685 var. *major* Pröschl & Zobl ex Olive & Spiltoir - Mycologia 47(2): 243, 1955.

1686 = *Pericystis apis* var. *minor* Pröschl & Zobl - Arch. Mikrobiol. 18(2): 200, 1953.

1687 **Neotype designated here:** Herb. No: CBS H-9145, dried culture isolated from *Apis mellifera*, Baarn,
1688 The Netherlands, J.B. Pannebakker, 1969. Ex-type culture: CBS 534.69 = IHEM 3748.

1689 The family Synascomycetaceae was proposed by Varitchak (1933) to describe fungi that have a sexual
1690 reproduction organ called the synascus, i.e., a single large vesicle with an acellular membranous
1691 peridium containing masses of “endospores” (spore balls). Since the fungi have reduced gametangia,
1692 *Pericystis* was concluded to be related to Plectascales and primitive Ascomycetes (Bessey 1950;
1693 Spiltoir and Olive 1955; Berbee and Taylor 1992; Geiser et al. 2006).

1694 The name *Pericystis* was changed to *Ascospaera* by Spiltoir and Olive (1955) because it was
1695 already in use for red alga (*Pericystis* Agardh 1847). Although the authors reclassified the genus and
1696 designated *Ascospaera apis* as the type species, no type material was indicated. *Ascospaera* was
1697 later reclassified in the family Ascospaeraceae in the order Ascospaerales (Gäumann 1964; invalid,
1698 ICBN Art. 37) and validated by Benny and Kimbrough (1980). Subsequently, *Ascospaera*, *Bettsia*
1699 (Skou 1972) and *Arrhenosphaera* (Stejskal 1974) were included in the family. *Arrhenosphaera*,
1700 represented by the type species *Arrhenosphaera craneae*, was isolated from pollen and larvae in a
1701 comb of *Apis mellifera* in Venezuela (Stejskal 1974). However, no type was indicated and the studied
1702 material was not known to be preserved; therefore, this name is considered doubtful. Although *Bettsia*
1703 also produces spore cysts and shares the same niche as saprophytic *Ascospaera* species (Skou 1972;
1704 Wynns 2015), it is found in Leotiomycetes, phylogenetically far from *Ascospaera* (Pitt et al. 2013)
1705 Currently, Ascospaeraceae is classified in the Onygenales as a monophyletic family with the single
1706 genus *Ascospaera* (Fig. 1) and it is described with spore cysts with a double-layered wall and spore
1707 balls formed by groups of asci covered by a single membrane (Wynns et al. 2013).

1708 Ascospaeraceae comprises a group of fungi with a very specific ecology. Members of the
1709 family have thus far only been isolated from pollen, bee larvae/cadavers or nest cells (Suppl. Table 1;
1710 Fig. 4). They can also grow in habitats related to other pollenivorous insects and have a high sugar
1711 content (Wynns et al. 2013). Only *Ascospaera atra*, a solitary bee-related saprobe, has been isolated

1712 from grass silage, apparently outside the bee habitat (Skou 1986). Some species are bee pathogens.
1713 *Ascosphaera apis* and *A. aggregata* are of special interest because of their etiologies of chalkbrood
1714 disease in economically important bee species (Aronstein and Murray 2010; Pitts-Singer and Cane
1715 2011). Available ecological data in this study showed that most *Ascosphaera* species are associated
1716 with solitary bees in the Megachilidae family ($n=24/28$; Fig. 13) rather than with economically
1717 important social bees. Megachilidae have a worldwide distribution, which is matched by the widely
1718 distributed family Ascosphaeraceae (Marinho et al. 2018; Wynns et al. 2013).

1719 The presence of simple, sac-like fruitbodies is a common feature among the bee-related fungi,
1720 shared by *Ascosphaera* (Onygenales; Spiltoir and Olive 1955), *Bettsia* (Leotiales; Wynns 2015) and
1721 *Eremascus* (Onygenales; Gueidan et al. 2008; Wijayawardene et al. 2017; Wynns 2015). This
1722 characteristic seems to have emerged more than once in the course of evolution and may have an
1723 ecological adaptation to this specific habitat and dispersion of propagules (Wynns 2015). In contrast to
1724 *Ascosphaera* and *Bettsia*, *Eremascus* is described with completely naked asci (Wynns 2015).
1725 Rudimentary development or near-absence of gymnothecia has also been observed in other
1726 onygenalean genera, such as *Narasimhella* and *Pseudoarachnietus* (von Arx, 1986; Orr et al. 1977a,
1727 de Hoog et al. 2020). In the present study, *Chrysosporium alvearium* Liu & Cai (Zhao et al. 2018)
1728 (type: LC11684), originating from hive-stored pollen, was also found to be a member of the
1729 Onygenales (Fig 1; Suppl. Figs 1–4); and has been reclassified above in *Keratinophyton* (Fig. 6).

1730

1731 **Clade 14 Eremascaceae Engler & Gilg**

1732 Type genus: *Eremascus* Eidam; type species: *Eremascus albus* Eidam - Beitr. Biol. Pfl. 3: 385; 1883.
1733 **Neotype designated here:** CBS 975.69, isolated by H.J. Phaff, from an unknown source, U.S.A.,
1734 deposited by W.D. Gray.

1735 The family Eremascaceae (Engl. & Gilg 1924) was introduced with the type species *Eremascus albus*
1736 (Eidam 1883) and *Eremascus fertilis*. The family was found in the Onygenales, close to
1737 Ascosphaeraceae, by several researchers (Gueidan et al. 2008; Johnston et al. 2015; Wijayawardene et

al. 2017), while it was recorded as a member of the Coryneliales (Seaver and Chardón 1926) in the Index Fungorum database. *Eremascus albus* is a very rare species (Eidam 1893; Harrold 1950; Paugh and Gray 1969), sharing with Wallemia and Sigleria an obligate osmophilic nature in habitats with low water activity due to high sucrose content. The second species, *E. fertilis* Stoppel (1907), also thrived in an osmotic habitat (apple and red currant jelly); but was morphologically different (Kreger-van Rij et al. 1974). Molecular studies have shown that *E. fertilis* can be classified in Leotiomycetes, remote from *E. albus*, and was reclassified as *Skoua fertilis* (Wynns 2015). *Eremascus terrestris* Asthana & Mahmud (1944), from a betel vine (*Piper betle*) in a garden in India, has also been included in *Eremascus*, but no type was indicated and original material is not known to be preserved; therefore, this name is considered doubtful. Since type material is not known to exist for *E. albus*, the following **neotype is indicated here**: CBS 975.69, isolated by H.J. Phaff, U.S.A.

In our phylogenetic studies, the cluster Eremascaceae comprises *E. albus* and *Dactylodendron pinicola*. Typification of the latter genus was established with *Arthrographis kalrae* in Eremomycetaceae, which is a genus of Dothideomycetes (Giraldo et al. 2014; Hernández-Restrepo et al. 2020). *Arthrographis alba* (non-*Eremascus albus*) is also found in the Onygenales (Clade 3, *incertae sedis*) and is synonymized with *Leucothecium emdenii*. The reduced characteristics of ascoma morphology, with naked asci and a preference for high-osmotic habitats, are similar to those of Ascosphaeraceae.

Relative Divergence Time Estimation

The results of RelTime analysis showed that the diversification of species in the Onygenales occurred 103 Mya and in two main directions: one with Ajellomycetaceae, Ascosphaeraceae, Eremascaceae and Spiromastigaceae and the other one with Arthrodermataceae, Auxarthraceae, Gymnoascaceae, Neogymnomycetaceae and Onygenaceae. The earliest species of the order were found to be related to Gymnoascaceae (79–70 Mya) while the most recent species were found close to Arthrodermataceae (43–15 Mya). The results are summarized in Fig 14.

1764

1765 **Discussion**

1766 Different interpretations of morphological characteristics and a lack of additional physiological and/or
1767 biochemical data about Onygenales isolates have led to divergent approaches for the classification of
1768 taxa in this fungal order. While the implementation of molecular taxonomic approaches provides faster
1769 identification, higher precision increases the number of recognized taxa. This is particularly obvious in
1770 the classical dimorphic agents of systemic disease, which had been treated as monotypic genera for
1771 many decades, but today comprise clusters of closely related species (Sepúlveda et al. 2017;
1772 Mavengere et al. 2020; Jiang et al. 2020). However, the application of the One Fungus-One Name
1773 (1F1N) concept and multiphasic approaches comprising molecular, morphological, clinical and
1774 physiological characteristics of species should lead to abandoning many names to simplify
1775 nomenclature. To this end, the stabilization of reference points by indicating the type materials of the
1776 species is essential. In the present study, multilocus phylogeny of the Onygenales was presented with
1777 the indication of type materials where possible, and conclusions were compared with ecological,
1778 physiological and morphological parameters.

1779 The order Onygenales is particularly known for its ecological association with mammals,
1780 either via dung or keratin, or via pathogenicity, which can be superficial or systemic. The majority of
1781 the species included have environmental sexual phases with elaborate gymnothecia, and invariably
1782 thallic conidiogenesis. Generic delimitations based solely on morphology have been problematic, as
1783 was demonstrated in the family Gymnoascaceae, where numerous species have been recombined over
1784 time in nearly the same list of generic names (Fig. 10).

1785 Some species in the order Onygenales share characteristics with members of adjacent orders;
1786 therefore, the determination of the borderline of the order is needed. However, this can be challenging
1787 because the effects of the chosen methods, number of samples, number of genes and outgroup choice
1788 may be crucial (Li et al. 2021). For instance, the phylogenetic position of the genus *Arachnomycetes*
1789 was debated; it was classified in the Onygenales (Abbott et al. 1996; Malloch and Cain 1970) before a

separate order, Arachnomycetales, was established (Gibas et al. 2002a). Similarly, the genus *Ascospaera* was classified in the Ascospaerales together with *Eremascus* (Geiser and LoBuglio 2001), but later, both genera were included in the Onygenales (Geiser et al. 2006). In the present study, using *Aspergillus fumigatus* as an outgroup (Eurotiales), the position of the Arachnomycetales was confirmed as an individual order. Morphological differences in the ascomata structures of *Ascospaera* and *Eremascaceae* were supported by phylogenetic results and they were kept in separate families within the order Onygenales.

Taxonomic methods have changed from morphological to molecular level and this process is likely to continue to become more detailed. Thus, changes in nomenclature remain inevitable. Taxon sampling and inclusion of type species are particularly essential to minimize changes and stabilize nomenclature for longer periods. In addition, providing molecular data for the isolates and making them publicly available is also important to prevent taxonomic disagreements. For example, *Chlamydosauromyces* was introduced as a new genus (Sigler et al. 2002b) because molecular data of its closest relative, *Neogymnomyces*, were not available at that time, even though it had been described earlier. Whole-genome data of the strain CBS 281.48 of *Onygena corvina* are available in databases (Huang et al. 2015); however, as confirmed in the present study, this strain represented an *Arthroderma* species (Garces et al. 2019). This misidentification led to another one: *Pectinotrichum chinense* was described using the misidentified *Onygena corvina* CBS 281.48 as the reference, while the generic type, *P. llanense* (Zhang et al. 2017b) clustered elsewhere.

Calculation of the supported/unsupported ratio, together with high support values for all clades, was shown to be effective to find the “best tree”, i.e., the one with the most resolved backbone for the members of the Chaetothyriales (Quan et al. 2020) and therefore, this approach was followed in the current study. However, the groups variously formed supported clades and hence, the ratio of supported/unsupported clades increased, while the backbone of the trees became less resolved, as in the ITS phylogeny (Table 3, Fig. 3).

The present study also aimed to investigate whether the ecological parameters can assist in defining groups within the Onygenales at the family level, and whether the interpretation of these

parameters can provide a model to estimate the course of evolution in this order. Evolution from geophilic lifestyles to anthropophilic association with *Homo sapiens* is an intuitively logical order of events. However, evolution may be ongoing at any branch of the evolutionary tree and thus, none of the clades has priority for an ultimate position; ancestral reconstruction is therefore applicable within branches, using ecological traits of environmental life style. Significant ecological traits that determine evolution in the Onygenales are osmophily, thermophily, cellulolysis, eutrophism, oligotrophism, keratinolysis, and dimorphism (Fig. 2). In particular, osmophily, keratinolysis and dimorphism are highly exceptional in the fungal Kingdom, and therefore, reemergence in the course of evolution is less likely. These characters are pronounced in the osmophilic, keratinolytic and dimorphic families, namely, the Ascosphaeraceae, Arthrodermataceae and Ajellomycetaceae, respectively (Fig. 2). While dimorphism is present in all members of the Ajellomycetaceae, albeit sometimes with reluctance (Jiang et al. 2018), it is shared by *Coccidioides* at a remote position in Onygenaceae. By combining the results of the phylogenetic analyses in the present study and genome analyses performed by Muñoz et al. (2018), it may be hypothesized that pathogenic Ajellomycetaceae evolved from a non-thermophilic and non-dimorphic ancestor, which encountered a mammalian host (e.g., armadillo) and developed several mechanisms (i.e., producing yeast-like forms *in vivo*) to adapt to the new host.

Pathogenic Ajellomycetaceae, along with Onygenaceae members such as *Coccidioides*, *Amauroascus*, *Uncinocarpus* and *Byssoonygena*, have elevated levels of proteases and carbohydrate-active enzymes, whereas *Helicocarpus griseus*, a non-pathogenic geophilic member of Ajellomycetaceae, still has more carbohydrate-active enzymes related to plant cell degradation in its genome (Muñoz et al. 2018). The relationship between non-pathogenic *Helicocarpus* and pathogenic, systemic Ajellomycetaceae may be comparable to that of *Uncinocarpus*, which is known to be the closest genus to *Coccidioides*, but is non-pathogenic and non-dimorphic. These data suggest that dimorphism may have occurred independently in Ajellomycetaceae and Onygenaceae or that the other dimorphic species between these two groups no longer exist. Nevertheless, why this characteristic is restricted to only *Coccidioides* in Onygenaceae and what the molecular background of the relationship between *Uncinocarpus* and *Coccidioides* remains unknown.

The majority of the Onygenaceae and Gymnoascaceae species are found in association with dung and in different types of soil, while only a few species have been reported from plant debris. On comparing the dung types from which members of both these families were isolated, Gymnoascaceae members were mainly found in herbivore dung, while Onygenaceae members were often isolated from carnivore dung (Suppl. Table 1). Carnivore dung is more nutrient-rich than herbivore dung (Frank et al. 2017), providing a suitable habitat for keratinophilic species because it may also contain hair of prey. Environments such as dung and agricultural soil provide wide opportunities to fungi with respect to nutrition, but this requires proper metabolic mechanisms for competition since these habitats are colonized by a plethora of microbes. On the other hand, some onygenalean fungi prefer poor environments where few competing microbes reside but where they need efficient nutrient scavenging. Remarkably, these two opposite habitat choices can be seen among members of the family Gymnoascaceae, suggesting that this group may contain the starting points of several evolutionary lines.

Niche adaptation requires metabolic and reproductive efficiency; therefore, morphological and physiological characteristics may be informative for habitat choice and evolutionary processes. In the present study, gymnothecium with reticuloperidium was found to be the most common ascoma type. Compared to the closed structure of a cleistothecium, loosely composed gymnothecia can be disrupted easily enhancing spore dispersal, while the ascomal appendages may be helpful for attachment to animal surfaces (Currah 1985), such as the impressive comb-like appendages of *Ctenomyces* that attach to feathers. In onygenalean fungi, two main ways of feeding are encountered: keratinolytic and cellulolytic. Families in ancestral positions, or those that drifted in other directions, such as Ajellomycetaceae and Spiromastigaceae, were found to lack keratinase, which is one of the main characteristics of the relatively derived family Arthrodermataceae. Cellulolytic activity in the Onygenales seems to have been lost in most clades, as noted earlier in genomic comparisons (Muñoz et al. 2018).

While most animal-associated species are confined to environmental sources, others are established pathogens for humans and/or other mammals, sometimes with a restricted host range.

1871 *Coccidioides*, *Blastomyces*, *Emergomyces*, *Histoplasma* and *Paracoccidioides* are all dimorphic
1872 environmental pathogens with a double life cycle (de Hoog et al. 2018). The Onygenaceae, especially
1873 Group VI, contain species that consistently cause skin infections in reptiles, and they only extremely
1874 rarely on other hosts. Reptile association is found in several, phylogenetically separated genera,
1875 including *Aphanoascus*, *Emydomyces*, *Nannizziopsis*, *Paranannizziopsis*, and *Ophidiomyces*.
1876 Although the Arthrodermataceae is known as the main family in the Onygenales with keratinolytic
1877 ability and the ability to cause skin infections in mammals, there is only a single report (Rees 1967a)
1878 on isolates obtained from the skin of a skink (*Egernia* sp.) and a monitor lizard (*Varanus* sp.) infected
1879 by *Arthroderma cuniculi* and *Paraphyton cookei*, respectively. Similarly, despite the regular
1880 occurrence of members of Gymnoascaceae on feather remains, only a single dermatophyte,
1881 *Lophophyton gallinae*, occurs on fowl (de Hoog et al. 2020). Keratin- and lipid-associated differences
1882 between mammalian, reptilian and avian skin may cause the selection of keratinophilic fungi. For
1883 instance, the presence of α -keratin has been shown in all vertebrates, whereas β -keratin is exclusively
1884 found in reptiles and birds (Greenwold et al. 2014). In reptiles, β -keratin provides strength and
1885 hardness (Rutland et al. 2019). The introduction of a reptile host during evolution may have caused the
1886 divergence of keratinolytic Onygenaceae and later Arthrodermataceae, from a common ancestor. In
1887 humans, long-chain fatty acids in sebum have been thought to have a fungistatic effect (Khosravi et al.
1888 2016; Hay et al. 2017), a role in preventing water loss from skin, as well as pro- and anti-inflammatory
1889 functions (Macrantonaki et al. 2011). Since the effect of sebum increases with age, sebum activity is
1890 considered an important factor in occurrence of tinea capitis caused by *T. violaceum* (Su et al. 2019).
1891 Similarly, avian epidermis lipids provide antimicrobial functions in addition to their roles in
1892 evaporative cooling and permeability (Menon and Menon 2000).

1893 Several groups in the Onygenales, such as *Arachniotus* in Gymnoascaceae, and members of
1894 Spiromastigaceae, Ascospaeraceae and Eremascaceae show an osmophilic tendency. Among these
1895 groups, the Ascospaeraceae are remarkable because of the unique habitat choice. Although the
1896 morphology and taxonomy of the members of this family have been well studied, little is known about
1897 their enzymatic abilities. Studies with *Ascospaera apis* showed that this species does not possess

1898 many of lytic enzymes, including chitinases, which can be found in other insect pathogens (Gochnauer
1899 and Margetts 1979; Heath 1982). Given that members can also be isolated from cocoons, which are
1900 made of silk, composed of fibroin and sericin, different types of proteolytic properties might play a
1901 role in these bee-specialist fungi. Similar to dung-associated fungi, *Ascosphaera* spores depend on
1902 their passage through an animal gut. However, the spores of *Ascosphaera* species germinate in the
1903 midgut of larvae, and subsequently, fungal hyphae break through the outer cuticula of larvae
1904 (Holloway et al. 2012; Wynns et al. 2013; Heath 1982). The biochemical mechanisms of anaerobic
1905 spore germination and the aerobic hyphal growth cycle of pathogenic *Ascosphaera* species are
1906 currently not well understood. As in the Neogymnomycetaceae clade, multilocus analyses revealed a
1907 high degree of specialization in the Ascosphaeraceae clade, suggesting that evolution might have
1908 occurred within a relatively short timeframe in these groups.

1909 A similar conclusion can be reached for the whole order based on the divergence time
1910 estimations and the Onygenales can be considered as a relatively recently (103 Mya) evolved order.
1911 Non-keratinolytic basal families appeared earlier than the keratinophilic members of the order,
1912 suggesting that the cellulolytic and osmophilic abilities might be ancestral characters. In contrast,
1913 dimorphism, as in *Coccidioides* species and members of Ajellomycetaceae, can be a result of
1914 independent adaptation.

1915 In the present study, some of the phylogenetic trees showed different topologies, particularly
1916 in Gymnoascaceae and Onygenaceae. However, these differences were affected by the number of
1917 distantly related samples used in the analyses, which necessitated shortening of the sequence length,
1918 with concomitant loss of information. Another pitfall was the presence of incomparable sequences
1919 obtained from public databases. Although the universal barcode for fungi is the ITS sequences
1920 (Stielow et al. 2015), it is often necessary to use alternative universal primers for genes with multiple
1921 recommended primer locations such as *TEF1*, *TEF3*, *RP60S*, and *RPB2* to appropriately differentiate
1922 species from each other (Stielow et. al. 2015; Thines et al. 2018). This approach might also lend more
1923 reproducibility to further studies.

Considering that the many species with special ecology, such as in *Nannizziopsis*, *Auxarthronopsis*, *Sigleria*, and *Spiromastigoides*, have been discovered only during the last decade, our results likely suffer from taxon sampling effects. In addition, molecular, morphological and physiological data are insufficient for the majority of species, hampering the establishment of degrees of intraspecific variation. Ongoing collection from divergent types of environments, increasing the sample size and observed variation, and using a polyphasic methodology may lead to changes in the chosen boundaries. However, consistent re-estimation of these boundaries can provide a better understanding of the phylogeny and evolutionary process of this fascinating order.

Even though the Onygenales are a recent order, they have been on the earth longer than human existence and at some point, some members encountered animals and humans. Similar to some other fungi, onygenalean members either gained new abilities or used their ready-made abilities to adapt and survive on these new hosts (Casadevall et al. 2003; Naranjo-Ortiz and Gabaldón 2019). Almost all families in the order have members that can be found on skin and nails, which can cause asymptomatic or symptomatic infections; or members which are able to grow at 37°C and cause systemic infections (Fig. 4). This is particularly important because environmental and host alterations can lead to the emergence of new fungal pathogens, which can be either currently unknown species or species that are currently known as non-pathogens. Just like *Cryptococcus* was not associated with a human disease 127 years ago and *Candida auris* was not known before the 2000s, it is very likely that we will face new fungal pathogens as a result of increased captivity of wild animals, changes in the environmental temperature and continued human activity involving soil and animals. Although temperature adaptation is not the only criterion for fungal virulence, soil fungi, especially those that can grow at 37°C, might have an increased potential to be encountered because they also have an opportunity to undergo selection by their ongoing interactions with other soil microorganisms. Therefore, the order Onygenales continues to deserve close attention.

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1958

1959 **Conflict of interest**

1960 The authors declare that there is no conflict of interest.

1961

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3129

3130 Legends

- 3131 **Fig. 1** Combined results of the ecology, key physiological features and phylogeny of the Onygenales.
 3132 Phylogenetic tree (ML) obtained by combined analysis of eight loci using 342 sequences based on the
 3133 GTR+I+G4+F model in IQ-TREE-ML. Branches with $\geq 80\%$ SH-aLRT/bootstrap support are shown
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 3135 nomenclatural revision are written in square brackets. *Aspergillus fumigatus* was used as an outgroup
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 3139 are shown as empty red circles. Type of ascomata and ascomatal appendages are used as

3140 morphological parameters. **a** peridial hyphae with coiled appendages of the genus *Arthroderma*
 3141 (Currah 1985); **b** ascomata of *Ctenomyces* surrounded by pectinate appendages (Currah 1985); **c**
 3142 ascomata of *Shanorella* covered with incompositoperidium and spiral appendages (Currah 1985); **d**
 3143 reticuloperidium of *Auxarthronopsis* with spine-like, straight to curved appendages (Currah 1985); **e**
 3144 reticuloperidium of *Uncinocarpus* with uncinata appendages (Currah 1985); **f** fruiting body of
 3145 *Onygena* species (Currah 1985); **g** cleistothecial ascomata of *Aphanoascus* and *Keratinophyton*
 3146 without appendages (Currah 1985); **h** reticuloperidium of *Auxarthron* with spine-like, straight to
 3147 curved appendages (Currah 1985), the difference between the appendage morphology of *Auxarthron*
 3148 and *Auxarthronopsis* being that *Auxarthron* never produces multi-septate appendages (Sharma et al.
 3149 2013); **i** boat hook-shaped appendages of the genus *Gymnoascus* (Currah 1985); **j** mature stalked
 3150 fruiting body of *Narasimhella* (Thirumalachar and Mathur 1966); **k** ascomata of *Blastomyces* with
 3151 spiral appendages (Currah 1985); **l** ascomata of *Spiromastigoides* with curved appendages (Rizzo et al.
 3152 2014); **m** coiled appendages of *Polytolypa* (Scott et al. 1993); **n** spore cyst of *Ascospaera* (David
 3153 Minter, Whitby); **o** completely naked asci of *Eremascus* (de Bary 1884).

3154 **Fig. 3** Phylogenetic analyses of Onygenales species based on **a** *RP60S*; **b** *RPB1*; **c** *TUB*; **d** *TEF3*; **e**
 3155 *RPB2*; **f** *TEF1-α*; **g** multilocus sequences; **h** multilocus sequences without *incertae sedis*; **i** LSU Group
 3156 I; **j** LSU Group II; **k** ITS Group II; and **l** ITS Group I obtained using the maximum likelihood
 3157 criterion. *Aspergillus fumigatus* was used as the outgroup. Note that *Leucothecium emdenii* and
 3158 *Arthrographis alba* represent the same species; therefore, they were not considered as a separate clade.
 3159 Tree characteristics are listed in Table 2

3160 **Fig. 4 a** General and **b** family-based ecology distribution of the Onygenales based on Suppl. Table 1,
 3161 normalized to 100%

3162 **Fig. 5** Phylogenetic tree of Arthrodermataceae based on ITS sequences, obtained with the
 3163 GTR+G4+I+F model in IQ-TREE-ML. Branches with SH-aLRT/bootstrap values of $\geq 85\%$ and type
 3164 species of the genera are shown in bold. The species that need nomenclatural revision are enclosed in
 3165 square brackets. *Shanorella spirotricha*, *Chrysosporium vallenarense* and *Arthrographis alba* were
 3166 used as the outgroup species

3167 **Fig. 6** Phylogenetic tree of Onygenaceae based on ITS sequences, obtained with the GTR+G4+I+F
3168 model in IQ-TREE-ML. Branches with SH-aLRT/bootstrap values of $\geq 80\%$ and type species of the
3169 genera are shown in bold. Neotypes and new combinations are indicated in red. The species that need
3170 nomenclatural revision are enclosed in square brackets. *Arthroderma redellii* and *Arthroderma*
3171 *quadrifidum* were used as the outgroup species

3172 **Fig. 7** Phylogenetic tree of Auxarthraceae based on ITS sequences, obtained with the TIM3e+G4+I+F
3173 model in IQ-TREE-ML. Branches with SH-aLRT/bootstrap values of $\geq 80\%$ and type species of the
3174 genera are shown in bold. *Arthroderma curreyi* was used as the outgroup

3175 **Fig. 8** Phylogenetic tree of Neogymnomycetaceae based on ITS sequences, obtained with the
3176 TNe+G4+F model in IQ-TREE-ML. Branches with SH-aLRT/bootstrap values of $\geq 80\%$ and type
3177 species of the genera are shown in bold. A new combination is indicated in red. The species that need
3178 nomenclatural revision are enclosed in square brackets. *Nannizziopsis arthrosporioides* and
3179 *Nannizziopsis vriesii* were used as outgroup species

3180 **Fig. 9** Phylogenetic tree of Gymnoascaceae based on ITS sequences, obtained by Bayesian analysis.
3181 Branches with values of $\geq 80\%$ for Bayesian probability and type species of the genera are shown in
3182 bold. Neotypes and new combinations are indicated in red. The species that need nomenclatural
3183 revision are enclosed in square brackets. *Uncinocarpus reesii*, *Testudomyces verrucosus* and
3184 *Neogymnomyces demonbreunii* were used as the outgroup species

3185 **Fig. 10** Summary of the genera described in the Gymnoascaceae. Basionyms/Synonyms used in the
3186 literature are shown in the gray boxes. *Sphaerosporium* is described with the type species *S. lignatile*
3187 Schwein. (1832) which is not classified in the Gymnoascaceae, therefore, only *S. equinum* is shown in
3188 the figure

3189 **Fig. 11** Phylogenetic tree of Spiromastigaceae based on ITS sequences, obtained by maximum
3190 likelihood analysis using the Kimura-2 parameter model gamma distribution in MEGA v6. Branches
3191 with bootstrap values of $\geq 80\%$ and type species of the genera are shown in bold. Neotypes and new

3192 combinations are indicated in red. *Arthroderma ciferrii* and *Arthroderma eboreum* are used as
3193 outgroup species

3194 **Fig. 12** Phylogenetic tree of Ajellomycetaceae based on ITS sequences, obtained with the
3195 TNe+G4+I+F model in IQ-TREE-ML. Branches with SH-aLRT/bootstrap values of $\geq 80\%$ and type
3196 species of the genera are shown in bold. *Arthroderma flavescens* and *Arthroderma vespertilii* are used
3197 as outgroup species

3198 **Fig. 13** Combination of the data for the host preference, pathogenicity and phylogeny of
3199 Ascosphaeraceae members. Phylogenetic tree based on ITS sequences, obtained by maximum
3200 likelihood analysis using Kimura-2 parameter model gamma distribution in MEGA v6. Branches with
3201 bootstrap values of $\geq 80\%$ and type species of the genera are shown in bold. The designated neotype is
3202 indicated in red. *Bettsia alvei* was used as the outgroup

3203 **Fig. 14** Estimated times of molecular divergence in the Onygenales by RelTime analysis with
3204 multilocus phylogeny of 356 taxa. The tree has been scaled to time on the basis of the calibration point
3205 of Pezizomycotina given by Samarakoon et al. 2019. Estimated times are given in red and values in
3206 black on the branches represent SH-aLRT, bootstrap, gene concordance factor (gCF) and site
3207 concordance factor (CF) (%). Two main extinction events, the Permian–Triassic (251 Mya) and
3208 Cretaceous–Tertiary (K-T, 66 Mya) are shown in red circles on the timeline. According to these
3209 results, current members of the Onygenales appeared at the end of the Cretaceous period in the
3210 Mesozoic era. Therefore, the Onygenales can be concluded as a recently evolved order. The first
3211 members of the order, Spiromastigaceae and Gymnoascaceae, are found at the end of the Cretaceous
3212 period when flowering plants became abundant (Silvestro et al. 2021) and bees (Genise et al. 2020)
3213 and snakes (Caldwell et al. 2015) evolved. Nevertheless, the results showed that both bee- and reptile-
3214 associated members of the order appeared after the K-T extinction 62 Mya and 54 Mya, respectively.

3215 **Table 1** Overview of the families and genera described in the order Onygenales with the data of the
3216 type species

3217 **Table 2** Characteristics of the phylogenetic trees used in the study

3218 **Table 3** Comparison of the phylogenetic trees to determine their quality

3219 **Suppl. Fig. 1** Phylogenetic tree of the species based on Group I LSU sequences ($n = 409$), obtained
 3220 with the TIM3e+G4+I+F model in IQ-TREE-ML. *Aspergillus fumigatus* was used as the outgroup and
 3221 Arachnomycetaceae was found outside the order

3222 **Suppl. Fig. 2** Phylogenetic tree of the species based on Group II LSU sequences of type species ($n =$
 3223 269), obtained with the TIM3e+G4+I+F model in IQ-TREE-ML. *Aspergillus fumigatus* was used as
 3224 the outgroup and Arachnomycetaceae was found outside the order

3225 **Suppl. Fig. 3** Phylogenetic tree of the species based on Group I ITS sequences ($n = 488$), obtained
 3226 with the GTR+G4+I+F model in IQ-TREE-ML. *Aspergillus fumigatus* was used as outgroup and
 3227 Arachnomycetaceae was found outside the order

3228 **Suppl. Fig. 4** Phylogenetic tree of the species based on Group II ITS sequences ($n = 324$), obtained
 3229 with the GTR+G4+I+F model in IQ-TREE-ML. *Aspergillus fumigatus* was used as the outgroup and
 3230 Arachnomycetaceae was found outside the order

3231 **Suppl. Table 1** GenBank data of the sequences, together with source and origin of each species

3232 **Suppl. Table 2** ITS sequence similarity (%) among the species described in Gymnoascaceae

Figures

Figure 1

Combined results of the ecology, key physiological features and phylogeny of the Onygenales. Phylogenetic tree (ML) obtained by combined analysis of eight loci using 342 sequences based on the GTR+I+G4+F model in IQ-TREE-ML. Branches with $\geq 80\%$ SH-aLRT/bootstrap support are shown in bold.

The names and neotypes proposed in the present study are shown in red. The species that need nomenclatural revision are written in square brackets. *Aspergillus fumigatus* was used as an outgroup

Fig. 2

Figure 2

Summary of the morphology, physiology, ecology and phylogeny of the Onygenales. A circular maximum-likelihood tree was constructed with IQ-TREE-ML (Nguyen et al. 2015) using ClipKIT -trimmed alignments (Steenwyk et al. 2020) of eight loci (Suppl. Table 1). Non-thermophilic species are shown as empty red

circles. Type of ascomata and ascomatal appendages are used as morphological parameters. a peridial hyphae with coiled appendages of the genus *Arthroderma* (Currah 1985); b ascomata of *Ctenomyces* surrounded by pectinate appendages (Currah 1985); c ascomata of *Shanorella* covered with incompositoperidium and spiral appendages (Currah 1985); d reticuloperidium of *Auxarthronopsis* with spine-like, straight to curved appendages (Currah 1985); e reticuloperidium of *Uncinocarpus* with uncinata appendages (Currah 1985); f fruiting body of *Onygena* species (Currah 1985); g cleistothecial ascomata of *Aphanoascus* and *Keratinophyton* without appendages (Currah 1985); h reticuloperidium of *Auxarthron* with spine-like, straight to curved appendages (Currah 1985), the difference between the appendage morphology of *Auxarthron* and *Auxarthronopsis* being that *Auxarthron* never produces multi-septate appendages (Sharma et al. 2013); i boat hook-shaped appendages of the genus *Gymnoascus* (Currah 1985); j mature stalked fruiting body of *Narasimhella* (Thirumalachar and Mathur 1966); k ascomata of *Blastomyces* with spiral appendages (Currah 1985); l ascomata of *Spiromastigoides* with curved appendages (Rizzo et al. 2014); m coiled appendages of *Polytolypa* (Scott et al. 1993); n spore cyst of *Ascosphaera* (David Minter, Whitby); o completely naked asci of *Eremascus* (de Bary 1884).

Fig. 3

Figure 3

Phylogenetic analyses of Onygenales species based on a RP60S; b RPB1; c TUB; d TEF3; e RPB2; f TEF1-α; g multilocus sequences; h multilocus sequences without incertae sedis; i LSU Group I; j LSU Group II; k ITS Group II; and l ITS Group I obtained using the maximum likelihood criterion. *Aspergillus fumigatus* was used as the outgroup. Note that *Leucothecium emdenii* and *Arthrographis alba* represent the same species; therefore, they were not considered as a separate clade. Tree characteristics are listed in Table 2

Fig.4

Figure 4

a General and b family-based ecology distribution of the Onygenales based on Suppl. Table 1, normalized to 100%

Figure 5

Phylogenetic tree of Arthrodermataceae based on ITS sequences, obtained with the GTR+G4+I+F model in IQ-TREE-ML. Branches with SH-aLRT/bootstraps values of $\geq 85\%$ and type species of the genera are shown in bold. The species that need nomenclatural revision are enclosed in square brackets. Shanorella spirotricha, Chrysosporium vollenarense and Arthrographis alba were used as the outgroup species

Figure 6

Phylogenetic tree of Onygenaceae based on ITS sequences, obtained with the GTR+G4+I+F model in IQ-TREE-ML. Branches with SH-aLRT/bootstrp values of $\geq 80\%$ and type species of the genera are shown in bold. Neotypes and new combinations are indicated in red. The species that need nomenclatural revision are enclosed in square brackets. *Arthroderma redellii* and *Arthroderma quadrifidum* were used as the outgroup species

Fig.7

Figure 7

Phylogenetic tree of Auxarthraceae based on ITS sequences, obtained with the TIM3e+G4+I+F model in IQ-TREE-ML. Branches with SH-aLRT/bootstrap values of $\geq 80\%$ and type species of the genera are shown in bold. *Arthroderma curreyi* was used as the outgroup

Phylogenetic tree showing relationships among various Ascomycota species. The tree is rooted at the bottom left. Bootstrap values are indicated at the nodes. The species names are listed on the right, with some in bold and others in italics. The tree is color-coded by genus: Neogymnomyces (light blue), Renispora (light green), Chrysosporium (orange), Auxarthronopsis (light blue), Nannizziopsis (orange), Auxarthronopsis (light green), Amauroascus (orange), Canomyces (light green), Currahmyces (light blue), and Nannizziopsis (grey).

- Neogymnomyces demonbreunii* (*Gymnoascus demonbreunii*) CBS 122.67
- Neogymnomyces demonbreunii* CBS 427.70 T**
- Neogymnomyces punctatus* (*Chlamydosauromyces punctatus*) UAMH 9990 T
- Neogymnomyces virgineus* DCDL7716 T
- Renispora flavissima* CBS 708.79 MT**
- Renispora flavissima* CEH 404
- [*Chrysosporium speluncarum*] CCF 3760 T
- [*Auxarthronopsis stercicola*] CGMCC3.19639 T
- [*Auxarthronopsis stercicola*] LC12611
- [*Auxarthronopsis pulverea*] CGMCC3.19312 T
- [*Auxarthronopsis pulverea*] LC12522
- [*Nannizziopsis mirabilis*] UAMH 7712
- Auxarthronopsis globiascus* CGMCC3.19305 T
- Auxarthronopsis globiascus* LC12667
- Auxarthronopsis guizhouensis* LC5705 T
- Auxarthronopsis guizhouensis* LC6219
- Auxarthronopsis pedicellaris* CGMCC3.1918 T
- Auxarthronopsis pedicellaris* LC12576
- Auxarthronopsis bandhavgarhensis* CBS 134524 T**
- [*Amauroascus purpureus*] UAMH 8294 T
- [*Amauroascus volatilis-patellis*] CBS 249.72 T
- [*Amauroascus volatilis-patellis*] (*Amauroascus albicans*) IMI 155645
- Canomyces reticulatus* MCC 1486 T**
- Currahmyces indicus* MCC 1548 T**
- Nannizziopsis arthrosporioides* CBS 133988 T
- Nannizziopsis vriesii* CBS 407.71 T

Scale bar: 0.06

Phylogenetic tree of Neogymnomycetaceae based on ITS sequences, obtained with the TNe+G4+F model in IQ-TREE-ML. Branches with SH-aLRT/bootstrp values of $\geq 80\%$ and type species of the genera are shown in bold. A new combination is indicated in red. The species that need nomenclatural revision are enclosed in square brackets. *Nannizziopsis arthrosporioides* and *Nannizziopsis vriesii* were used as outgroup species

Figure 9

Phylogenetic tree of Gymnoascaceae based on ITS sequences, obtained by Bayesian analysis. Branches with values of $\geq 80\%$ for Bayesian probability and type species of the genera are shown in bold. Neotypes and new combinations are indicated in red. The species that need nomenclatural revision are enclosed in square brackets. *Uncinocarpus reesii*, *Testudomyces verrucosus* and *Neogymnomycetes demonbreunii* were used as the outgroup species

Fig.10

Figure 10

Summary of the genera described in the Gymnoascaceae. Basionyms/Synonyms used in the literature are shown in the gray boxes. *Sphaerosporium* is described with the type species *S. lignatile* Schwein. (1832) which is not classified in the Gymnoascaceae, therefore, only *S. equinum* is shown in the figure

Fig.11

Figure 11

Phylogenetic tree of Spiromastigaceae based on ITS sequences, obtained by maximum likelihood analysis using the Kimura-2 parameter model gamma distribution in MEGA v6. Branches with bootstrap values of $\geq 80\%$ and type species of the genera are shown in bold. Neotypes and new combinations are indicated in red. *Arthroderma ciferrii* and *Arthroderma eboreum* are used as outgroup species

Figure 12

Phylogenetic tree of Ajellomycetaceae based on ITS sequences, obtained with the TNe+G4+I+F model in IQ-TREE-ML. Branches with SH-aLRT/bootstrap values of $\geq 80\%$ and type species of the genera are shown in bold. *Arthroderma flavesceus* and *Arthroderma vespertilii* are used as outgroup species

Fig.13

Figure 13

Combination of the data for the host preference, pathogenicity and phylogeny of *Ascospaeraceae* members. Phylogenetic tree based on ITS sequences, obtained by maximum likelihood analysis using Kimura-2 parameter model gamma distribution in MEGA v6. Branches with bootstrap values of $\geq 80\%$ and type species of the genera are shown in bold. The designated neotype is indicated in red. *Bettsia alvei* was used as the outgroup

Estimated times of molecular divergence in the Onygenales by RelTime analysis with multilocus phylogeny of 356 taxa. The tree has been scaled to time on the basis of the calibration point of Pezizomycotina given by Samarakoon et al. 2019. Estimated times are given in red and values in black on the branches represent SH-aLRT, bootstrap, gene concordance factor (gCF) and site concordance factor (CF) (%). Two main extinction events, the Permian–Triassic (251 Mya) and Cretaceous–Tertiary (K-

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Supplementary Files

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