The Current State of *Trichoderma* Taxonomy and Species Identification

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1 Introduction

Molds from the genus *Trichoderma* (*Hypocreales*, *Ascomycota*) are among of the most common fungi; they are easy to isolate and handle in a pure culture (Migheli et al. 2009; Zachow et al. 2009; Chen et al. 2021). Consequently, the taxonomy of

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Trichoderma started with the beginning of the modern fungal taxonomy in the eighteenth century (Persoon 1794). Similar to other fungi, it was in the descriptive stage for two centuries and before entering a period of turbulence caused by molecular methods (Bissett 1984; Bissett 1991a, b, c; Kuhls et al. 1997; Kindermann et al. 1998; Kullnig et al. 2000). Ideally, taxonomy should reflect the nature of the organism and help its investigation. The biology of *Trichoderma* offers a convenient example to illustrate this relationship. Many *Trichoderma* strains have properties of environmental opportunism meaning that they are capable of fast colonization of a great variety of natural and artificial substrates, are highly competitive in microbial communities, are resistant to xenobiotics including chemical fungicides, and are potent producers of various metabolites such as enzymes, secondary metabolites, or surface-active proteins (Druzhinina et al. 2011; Sun et al. 2019; Gao et al. 2020; Druzhinina and Kubicek 2017; Pang et al. 2020). Some *Trichoderma* species can survive in soil and colonize rhizosphere possessing almost no harm to plants but stimulating their growth and development (Druzhinina et al. 2011; Harman et al. 2004; Marra et al. 2019; Rivera-Méndez et al. 2020). Being mycoparasitic, a growing number of *Trichoderma* species are proposed as biofungicides for plant protection in agriculture (Ding et al. 2020; Wu et al. 2018). However, the same property also makes *Trichoderma* species causative agents of the green mold disease on mushroom farms (Komoń-Zelazowska et al. 2007; Kredics et al. 2010) (see Kredics et al. in this book). Finally, some *Trichoderma* strains also have clinical significance as causative agents of nosocomial mycoses in immunocompromised humans (Chouaki et al. 2002; Myoken et al. 2002; Kredics et al. 2003). These versatile, largely beneficial, but also harmful properties of *Trichoderma* make the taxonomy of this genus a high priority task because the correct identification of a species can predict its properties and thus facilitate applications. The taxonomy of *Trichoderma* has been intensively studied over the last two decades resulting in a hundred-fold increase in the species number from a few "species aggregates" of Rifai (1969) to several hundred molecularly defined species enumerated in several recent reviews (Druzhinina et al. 2006; Atanasova et al. 2013; Bissett et al. 2015; Cai and Druzhinina 2021). Thus, today *Trichoderma* comprises the genus of very common fungi with most species that have been characterized using modern molecular techniques.

The large number of species in *Trichoderma* appears to be reasonable: Whole genomic investigations of this genus and other hypocrealean fungi have estimated the origin of the genus at the edge of Cretaceous-Paleogene mass extinction event 66–67 million years ago (Kubicek et al. 2019). The most recent phylogenomic tree (Kubicek et al. 2019) indicates that the formation of the major infrageneric clades such as Sections *Trichoderma* and *Longibrachiatum* recognized by John Bissett in the 1990s or the *Harzianum* Clade (Bissett 1984; Chaverri et al. 2003) was formed somewhat 20–25 million years ago, while some closely related species such as *T. reesei* and *T. parareesei* shared a common ancestor 4–8 million years ago. This vast evolutionary time and the relatively high evolutionary rates (compared to, e.g., vertebrates) offer the genus *Trichoderma* tremendous possibilities for the adaptation to the environmental conditions and speciation. However, similar to other fungi, many evolutionary different strains of *Trichoderma* still share remarkable morphological and ecophysiological similarities. It appears that many traits suitable and accessible for direct examination by taxonomists are homoplasious and appeared due to convergent evolution. Thus, the most difficult task of modern taxonomy of *Trichoderma* is to retrieve the traits that would allow one to distinguish a great number of species.

The general fungal taxonomy is regulated by the Code, i.e., CN International Code of Nomenclature for algae, fungi, and plants (Turland et al. 2018), that now contains an advanced section for fungi in Chapter F, San Juan Chapter F (May et al. 2019). Even though the Code strictly regulates nomenclatural acts, it assumes a heterogeneity of approaches to define species (Turland et al. 2018). This can be explained by the complexity of lineage-dependent evolutionary processes (Steenkamp et al. 2018; Inderbitzin et al. 2020) or numerous pragmatic criteria used by the taxonomists for the classification of particular fungal groups. Lücking et al. (2020) found that the best practice depends on the group in question and the required level of precision. Some fungi can be grouped based on phenotype characteristics; however, most fungi, especially asexual forms such as *Trichoderma*, require time-consuming and labor-intensive methods that include culturing, DNA barcoding, and phylogenetic analysis as well as discipline- or taxon-specific approaches such as physiological profiling (Lücking et al. 2020). Therefore, it is common for species concepts determined by the taxonomy providers to vary even within one genus. However, taxonomy users expect that the identification of species should be precise and accurate. For *Trichoderma*, this collision of possibly vague species delimitation and the need for the exact species identification was recently addressed in Cai and Druzhinina (2021). This topic requires a thoughtful discussion that will also be presented in this chapter and continued elsewhere.

The biology of *Trichoderma* offers a number of exclusive opportunities to the taxonomists. Fungi from this genus are ubiquitous and relatively simple to recognize and collect in natural and human-made habitats. They are easy to isolate directly from specimens and from a broad range of substrates based on the characteristic genus-specific features. Most strains have fast growth in vitro on all common laboratory media and do not require demanding cultivation conditions such as temperature, illumination, or humidity. Importantly, and as it will be described in most chapters of this book, many *Trichoderma* spp. have highly valuable properties for industry and agriculture. Respectively, *Trichoderma* has attracted the attention of classical mycologists and people focusing on applied microbiology and developmental applications. Therefore, all collections of microorganisms have numerous *Trichoderma* isolates. Public depositories of gene sequences contain thousands of *Trichoderma* DNA barcodes, and the number of the whole genome sequences has grown exponentially. However, the identification of *Trichoderma* is also considered to be extremely difficult. Fungal taxonomists including experts working with this genus for many years now frequently fail to determine the species (Cai and Druzhinina 2021).

In this chapter, we investigate the theoretical background of these collisions in *Trichoderma* research aiming for a concise review of the taxonomic state of the genus. We present a brief synopsis of *Trichoderma* taxonomy through January 2021, list all *Trichoderma* species names, and explain the latest identification protocol for *Trichoderma* species.

2 The Numerical State of *Trichoderma* Taxonomy and Species Identification

After the implementation of the "One fungus – One name" concept of fungal nomenclature (Taylor 2011)—and based on the voting organized by the International Commission on *Trichoderma* Taxonomy (ICTT) (formerly www.isth.info, now www.trichoderma.info) of the International Commission on the Taxonomy of Fungi (ICTF, www.fungaltaxonomy.org)—*Trichoderma* was selected as a single generic name that should be used for all stages such as holo-, ana-, and teleomorphs. Consequently, the taxonomy of the genus *Trichoderma* was updated to include the species names previously attributed to teleomorphs from such genera as *Hypocrea*, *Sarawakus*, and *Protocrea* (Jaklitsch 2009a; Jaklitsch et al. 2014). The formal transfer of a few species of *Hypocrea* to *Trichoderma* is still pending (Cai and Druzhinina 2021); nevertheless, these species are valid names of the genus (Table 1).

As of January 2021, the genus *Trichoderma* contains 468 species epithets, among which 379 names are currently in use, while 89 names (19%) are synonyms of different categories (abandoned names, orthographic variants, synonyms) (Cai and Druzhinina 2021) updated with materials from Gu et al. (2020). Forty names were introduced before the twentieth century. Of these, only five are currently in use including such important species as *T. viride* and *T. atroviride*. Sixty species were introduced in the twentieth century based on their morphology, (sometimes) ecophysiological properties, and biogeography (Rifai 1969; Bissett 1984, 1991a, b, 1992). The end of the century coincided with the introduction of molecular methods in *Trichoderma* taxonomy and the proposal of the genealogical concordance phylogenetic species recognition concept (GCPSR) as the most powerful approach to distinguish fungal taxa (Taylor et al. 2000; Lücking et al. 2020). These changes resulted in a rapid increase in the number of taxa adding the majority of modern *Trichoderma* species names (364, 78%) delineated in the first two decades of the twenty-first century. Consequently, only 14 (4%) currently valid *Trichoderma* species have not been characterized by molecular markers (Cai and Druzhinina 2021), while 365 species (96%) have been DNA barcoded. This makes the genus *Trichoderma* a suitable model for DNA barcoding and molecular evolutionary studies in fungi.

The largest database of *Trichoderma* names is available in MycoBank (http://www.mycobank.org/) followed by Index Fungorum (http://www.indexfungorum.org). Most species names are recorded in both taxonomic depositories, but MycoBank still has 14 and Index Fungorum has 8 unique records. Therefore, none of the official depositories of fungal taxonomy has the full list of *Trichoderma* species names (Fig. 1). To date, the most complete list of *Trichoderma* species can be found in Table 1 (sorted alphabetically for convenience). Alternatively, the newly

Table 1 The alphabetic list of all species names deposited for *Trichoderma* in Index Fungorum (http://www.indexfungorum.org/), MycoBank (https://www.mycobank.org/), NCBI Taxonomy Browser (https://www.ncbi.nlm.nih.gov/Taxonomy/Browser/wwwtax.cgi), and scientific literature as of February 2021

Species name	Author(s)	Year	Reference strain
Trichoderma acremonioides	Zhang & Zhuang	2018	HMAS 279611
Trichoderma adaptatum	Chen & Zhuang	2017	HMAS 248800
Trichoderma aeroaquaticum	Yamag., Tsurumi, Chuaseehar. & Nakagiri	2012	NBRC 108034
Trichoderma aerugineum	Jaklitsch	2009	CBS 120541
Trichoderma aeruginosum	Link	1816	not in use
Trichoderma aestuarinum	Gonçalves & Alves	2019	MUM H-19.05
Trichoderma aethiopicum	Mulaw, Kubicek & Samuels	2012	CBS 130628
Trichoderma afarasin	Chaverri & Rocha	2015	CBS 130755
Trichoderma afroharzianum	Chaverri, Rocha, Degenkolb & Druzhin.	2015	CBS 124620
Trichoderma aggregatum	Chen & Zhuang	2017	HMAS 248863
Trichoderma aggressivum	Samuels & Gams	2002	DAOM 222156
Trichoderma albocorneum	(Doi) Jaklitsch & Voglmayr	2014	G.J.S. 97-28
Trichoderma albofulvopsis	Qin & Zhuang	2016	HMAS 273760
Trichoderma albofulvum	(Berk. & Broome) Jaklitsch & Voglmayr	2014	CBS 114787
Trichoderma albolutescens	Jaklitsch	2011	CBS 119286
Trichoderma alboviride	Chen & Zhuang	2017	HMAS 247224
Trichoderma album	Preuss	1851	not in use
Trichoderma alcalifuscescens	(Overton) Jaklitsch & Voglmayr	2014	CBS 122303
Trichoderma alni	Jaklitsch	2008	CBS 120633
Trichoderma alpinum	Chen & Zhuang	2017	HMAS 248821
Trichoderma alutaceum	Jaklitsch	2011	CBS 120535
Trichoderma amazonicum	Chaverri & Gazis	2011	CBS 126898
Trichoderma americanum	(Canham) Jaklitsch & Voglmayr	2014	CBS 976.69
Hypocrea ampulliformis	Doi & Yamat.	1989	JCM 11982
Trichoderma andinense	(Samuels & Petrini) Samuels, Jaklitsch & Voglmayr	2014	CBS 345.97
Trichoderma angustum	Qin & Zhuang	2017	HMAS 273784

(continued)

Table 1 (continued)

Species name	Author(s)	Year	Reference strain
Trichoderma appalachiense	Samuels & Jaklitsch	2013	CBS 133558
Trichoderma applanatum	Zhu & Zhuang	2015	HMAS 245081
Trichoderma arachnoidea	Kuritzina & Sizova	1967	not in use
Trichoderma arachnoideum	Kuritzina & Sizova	1967	not in use
Trichoderma arenarium	Cai, Ding & Druzhin.	2020	CGMCC 19611
Trichoderma arundinaceum	Zafari, Gräfenhan & Samuels	2008	CBS 119575
Trichoderma asperelloides	Samuels	2010	CBS 125938
Trichoderma asperellum	Samuels, Lieckf. & Nirenberg	1999	CBS 433.97
Trichoderma asterineum	Qin & Zhuang	2016	HMAS 271353
Trichoderma atlanticum	Jaklitsch	2011	CBS 120632
Trichoderma atrobrunneum	Rocha, Chaverri & Jaklitsch	2015	CBS 548.92
Trichoderma atrogelatinosum	(Dingley) Jaklitsch & Voglmayr	2014	CBS 237.63
Trichoderma atroviride	Bissett	1984	not in use
Trichoderma atroviride	Karst.	1892	IMI 206040
Trichoderma attinorum	Montoya, Meirelles, Chaverri & Rodrigues	2016	CBS 139783
Trichoderma auranteffusum	Jaklitsch	2011	not in use
Trichoderma aurantioeffusum	Jaklitsch	2011	CBS 119284
Trichoderma aureoviride	Rifai	1969	CBS 120536
Trichoderma aureum	Pers.	1796	not in use
Trichoderma austriacum	Jaklitsch	2011	CBS 122494
Trichoderma austrokoningii	Samuels & Druzhin.	2006	CBS 119092
Trichoderma avellaneum	(Rogerson & Carey) Jaklitsch & Voglmayr	2014	CBS 121667
Trichoderma azevedoi	Valadares-Inglis & Inglis	2020	CEN 1422
Trichoderma balearicum	Jaklitsch & Voglmayr	2015	CBS 133222
Trichoderma bannaense	Chen & Zhuang	2017	CGMCC 3.18394
Trichoderma barbatum	Samuels	2012	CBS 125733
Trichoderma bavaricum	Jaklitsch	2011	WU 29196a
Trichoderma beijingense	Chen & Zhuang	2017	HMAS 248804
Trichoderma beinartii	du Plessis, Druzhin., Atan., Yarden & Jacobs	2018	PPRI 19281
Trichoderma bifurcatum	Chen & Zhuang	2017	HMAS 248795
Trichoderma bissettii	Sand.-Den. & Guarro	2014	CBS 137447
Trichoderma bomiense	Zhang & Zhuang	2019	W.Z. 2018a
Trichoderma brassicae	Schumach.	1803	not in use

(continued)

Table 1 (continued)

Species name	Author(s)	Year	Reference strain
Trichoderma breve	Chen & Zhuang	2017	CGMCC 3.18398
Trichoderma brevicompactum	Kraus, Kubicek & Gams	2004	CBS 109720
Trichoderma brevicrassum	Chen & Zhuang	2017	CGMCC 3.18407
*Trichoderma brevipes**	(Mont.) Samuels	2015	CBS 139044
Trichoderma britannicum	(Rifai & Webster) Jaklitsch & Voglmayr	2014	CBS 253.62
Trichoderma britdaniae	(Jaklitsch & Voglmayr) Jaklitsch & Voglmayr	2014	WU 31610
Trichoderma brunneoviride	Jaklitsch	2008	CBS 121130
Trichoderma byssinum	Chen & Zhuang	2017	CGMCC 3.18393
Trichoderma caeruleimontis	du Plessis & Jacobs	2018	PPRI 23903
Trichoderma caerulescens	(Jaklitsch & Voglmayr) Jaklitsch & Voglmayr	2014	CBS 130011
Trichoderma caesareum	Samuels	2012	CBS 124369
Trichoderma caesium	Pers.	1794	not in use
Trichoderma calamagrostidis	Jaklitsch	2011	WU 29198a
Trichoderma camerunense	Chaverri & Samuels	2015	CBS 138272
Trichoderma candidum	Chaverri & Samuels	2003	not in use
Trichoderma candidum	Alb. & Schwein.	1805	not in use
Trichoderma capillare	Samuels & Kubicek	2012	CBS 130629
Trichoderma caribbaeum	Samuels & Schroers	2006	CBS 119093
Trichoderma carneum	Schumach.	1803	not in use
Trichoderma catoptron	Chaverri & Samuels	2003	CBS 114232
Trichoderma ceciliae	Jaklitsch & Voglmayr	2015	CBS 130010
Trichoderma centrosinicum	Qin & Zhuang	2016	HMAS 252910
Trichoderma ceraceum	Chaverri & Samuels	2003	BPI 843654
Trichoderma ceramicum	Chaverri & Samuels	2003	CBS 114576
Trichoderma ceratophylli	Yu	2019	YMF 1.04621
Trichoderma cerebriforme	(Berk.) Samuels	2015	G.J.S. 85-245
Trichoderma cerinum	Bissett, Kubicek & Szakács	2003	DAOM 230012
Trichoderma changbaiense	Chen & Zhuang	2017	HMAS 247198
Trichoderma chetii	du Plessis, Druzhin., Atan., Yarden & Jacobs	2018	PPRI 19363
Trichoderma chlamydosporicum	Chen & Zhuang	2017	HMAS 248850
Trichoderma chlamydosporum	Chen & Zhuang	2017	not in use

(continued)

Table 1 (continued)

Species name	Author(s)	Year	Reference strain
Trichoderma chlorosporum	Chaverri & Samuels	2003	CBS 114231
Trichoderma christiani	Jaklitsch & Voglmayr	2015	CBS 132572
Trichoderma christianii	Jaklitsch & Voglmayr	2015	not in use
Trichoderma chromospermum	Chaverri & Samuels	2003	CBS 114577
Trichoderma cinnabarinum	Wallr.	1833	not in use
Trichoderma cinnamomeum	Chaverri & Samuels	2003	G.J.S. 97-237
Trichoderma citrinella	(Ellis) Zhuang & Zeng	2017	
Trichoderma citrinoviride	Bissett	1984	CBS 258.85
Trichoderma citrinum	(Pers.) Jaklitsch, Gams & Voglmayr	2014	CBS 894.85
Trichoderma collae	(Schwein.) Sacc.	1886	not in use
Trichoderma compactum	Yu & Zhang	2007	CBS 121218
Trichoderma composticola	Samuels & Jaklitsch	2013	CBS 133497
Trichoderma concentricum	Chen & Zhuang	2017	HMAS 248833
Trichoderma confertum	Chen & Zhuang	2017	HMAS 248896
Trichoderma confluens	Qin & Zhuang	2016	HMAS 244993
Hypocrea coprosmae	Dingley	1952	PDD 10453
Trichoderma cordobense	Speg.	1926	not in use
Trichoderma corfecianum	Sacc.	1911	not in use
Trichoderma corneum	(Pat.) Jaklitsch & Voglmayr	2014	CBS 100541
Trichoderma cornu-damae	(Pat.) Zhu & Zhuang	2014	G.J.S. 06-03
Trichoderma corrugatum	(Doi, Liu & Tamura) Liu, Zhu & Zhuang	2014	not in use
Trichoderma costaricense	(Chaverri & Samuels) Chaverri, Jaklitsch & Voglmayr	2014	P.C. 21
Trichoderma crassum	Bissett	1992	CBS 336.93
Trichoderma cremeoides	Jaklitsch & Voglmayr	2015	S112
Trichoderma cremeum	Chaverri & Samuels	2003	CBS 111146
Trichoderma croceum	Bissett	1992	not in use
Trichoderma crystalligenum	Qin & Zhuang	2017	not in use
Trichoderma crystalligenum	Jaklitsch	2006	CBS 118980
Trichoderma cuenisporum	Chaverri & Samuels	2003	not in use
Trichoderma cuneisporum	Chaverri & Samuels	2003	not in use
Trichoderma cyanodichotomus	Li & Chen	2018	not in use
Trichoderma dacrymycellum	Jaklitsch	2009	WU 29042a
Trichoderma danicum	(Jaklitsch) Jaklitsch & Voglmayr	2014	CBS 121273
Trichoderma decipiens	(Jaklitsch, Põldmaa & Samuels) Jaklitsch & Voglmayr	2014	G.J.S. 97-207

(continued)

Table 1 (continued)

Species name	Author(s)	Year	Reference strain
Trichoderma delicatulum	Jaklitsch	2011	CBS 120631
Trichoderma deliquescens	(Sopp) Jaklitsch	2011	CBS 121131
Trichoderma densum	Qin & Zhuang	2016	HMAS 273758
Trichoderma desrochii	Sartory & Bainier	1913	
Hypocrea dichromospora	Doi	1968	CBS 337.69
Trichoderma dimorphum	Chen & Zhuang	2017	HMAS 247199
Trichoderma dingleyae	Samuels & Dodd	2006	CBS 119056
Trichoderma dorotheae	Samuels & Dodd	2006	CBS 119089
Trichoderma dorothopsis	Tomah & Zhang	2020	HMAS 248251
Trichoderma dubium	Pers.	1801	not in use
Trichoderma dubium	Alb. & Schwein.	1805	not in use
Trichoderma effusum	Bissett, Kubicek & Szakács	2003	DAOM 230007
Trichoderma eijii	Kim & Maek.	2013	CBS 133190
Trichoderma endophyticum	(Jaklitsch, Põldmaa & Samuels) Jaklitsch & Voglmayr	2015	CBS 130729
Trichoderma epimyces	Jaklitsch	2008	CBS 120534
Trichoderma erinaceum	Bissett, Kubicek & Szakács	2003	DAOM 230018
Trichoderma estonicum	Chaverri & Samuels	2003	CBS 111147
Trichoderma eucorticioides	(Overton) Jaklitsch & Voglmayr	2014	G.J.S. 99-61
Trichoderma europaeum	Jaklitsch & Voglmayr	2015	CBS 121276
Trichoderma euskadiense	Jaklitsch & Voglmayr	2015	CBS 130013
Trichoderma evansii	Samuels	2009	CBS 123079
Trichoderma fasciculatum	Bissett	1992	not in use
Trichoderma fassatiae	Nováková, Kubátová, Valinová, Hubka & Kolařík	2015	PRM 933821
Trichoderma fertile	Bissett	1992	CBS 339.93
Trichoderma flagellatum	Mulaw, Kubicek & Samuels	2012	CBS 130626
Trichoderma flavescens	Zhu, Zhuang & Li	2017	HMJAU 34730
Trichoderma flaviconidium	(Chaverri, Druzhin. & Samuels) Jaklitsch & Voglmayr	2014	CBS 130688
Trichoderma flavipes	(Peck) Seifert, Jaklitsch & Voglmayr	2014	CBS 123070
Trichoderma flavofuscum	(Mill., Giddens & Foster) Bissett	1992	not in use
Trichoderma flavum	Sommerf.	1826	not in use
Trichoderma floccosum	Samuels	2011	CBS 124372
Trichoderma foliicola	(Jaklitsch & Voglmayr) Jaklitsch & Voglmayr	2014	CBS 130008

(continued)

Table 1 (continued)

Species name	Author(s)	Year	Reference strain
Trichoderma fomiticola	Jaklitsch	2009	CBS 121136
Trichoderma fomitopsis	(Liu & Doi) Liu, Zhu & Zhuang	2014	not in use
Trichoderma fragile	(Doi) Jaklitsch & Voglmayr	2014	
Trichoderma fujianense	Zhu, Zhuang & Li	2017	HMJAU 34830
Trichoderma fuliginoides	Pers.	1801	not in use
Trichoderma fuscum	Schumach.	1803	not in use
Trichoderma gamsii	Samuels & Druzhin.	2006	CBS 120075
Trichoderma ganodermatis	Chen & Zhuang	2017	HMAS 248856
Trichoderma gelatinosum	Chaverri & Samuels	2003	CBS 114246
Trichoderma ghanense	Doi, Abe & Sugiy.	1987	ATCC 208858
Trichoderma gillesii	Samuels	2012	CBS 130435
Trichoderma glaucum	Abbott	1927	not in use
Trichoderma gliocladium	Jaklitsch & Voglmayr	2015	CBS 130009
Trichoderma globoides	Qin & Zhuang	2017	HMAS 248747
Trichoderma globosum	Schwein.	1822	not in use
Trichoderma gracile	Samuels & Szakács	2012	CBS 130714
Trichoderma grande	Qin & Zhuang	2016	HMAS 248749
Trichoderma granulosum	Fuckel	1870	not in use
Trichoderma gregarium	Chen & Zhuang	2017	HMAS 248887
Trichoderma guizhouense	Li, McKenzie & Wang	2012	CBS 131803
Trichoderma guttatum	Alb. & Schwein.	1805	not in use
Trichoderma hainanense	Chen & Zhuang	2017	HMAS 248837
Trichoderma hamatum	(Bonord.) Bainier	1906	CBS 102160
Trichoderma harzianum	Rifai	1969	CBS 226.95
Trichoderma hausknechtii	Jaklitsch & Voglmayr	2015	CBS 133493
Trichoderma hebeiense	Chen & Zhuang	2017	HMAS 248743
Trichoderma helicolixii	Jaklitsch & Voglmayr	2015	CBS 133499
Trichoderma helicum	Bissett, Kubicek & Szakács	2003	DAOM 230022
Trichoderma henanense	Qin & Zhuang	2016	HMAS 252891
Trichoderma hengshanicum	Chen & Zhuang	2017	HMAS 248852
Trichoderma hexasporum	(Boedijn) Jaklitsch & Voglmayr	2014	
Trichoderma hirsutum	Chen & Zhuang	2017	HMAS 248834

(continued)

Table 1 (continued)

Species name	Author(s)	Year	Reference strain
Trichoderma hispanicum	(Jaklitsch & Voglmayr) Jaklitsch & Voglmayr	2014	CBS 130540
Trichoderma hongkongensis	(Zhu & Zhuang) Zeng & Zhuang	2017	HMAS 75530
Trichoderma hubeiense	Qin & Zhuang	2016	HMAS 252888
Trichoderma hunanense	Chen & Zhuang	2017	HMAS 248841
Trichoderma hunua	(Dingley) Jaklitsch & Voglmayr	2014	CBS 238.63
Trichoderma hypoxylon	Sun, Liu & Hyde	2016	CGMCC 3.17906
Trichoderma ingratum	Chen & Zhuang	2017	HMAS 248822
Trichoderma inhamatum	Veerkamp & Gams	1983	CBS 273.78
Trichoderma intricatum	Samuels & Dodd	2006	CBS 119059
Trichoderma istrianum	Jaklitsch & Voglmayr	2015	CBS 130539
Trichoderma italicum	Jaklitsch & Voglmayr	2015	CBS 132567
Trichoderma ivoriense	Samuels	2012	CBS 125734
Trichoderma izawae	(Doi) Jaklitsch & Voglmayr	2014	
Trichoderma junci	Jaklitsch	2011	WU 29229a
Trichoderma konilangbra	Samuels, Petrini & Kubicek	1998	CBS 100808
Trichoderma koningii	Oudem.	1902	G.J.S. 96-117
Trichoderma koningiopsis	Samuels, Carm. Suárez & Evans	2006	CBS 119075
Trichoderma koreanum	Oh, Park & Lim	2019	SFC 20131005-S066
Trichoderma kunigamense	Yabuki & Okuda	2014	TNS-F 38436
Trichoderma kunmingense	Yu & Li	2018	YMF 1.02659
Trichoderma lacteum	Bissett	1992	not in use
Trichoderma lacuwombatense	(Lu, Druzhin. & Samuels) Jaklitsch & Voglmayr	2014	CBS 122668
Trichoderma laeve	Pers.	1796	not in use
Trichoderma laeve	Schumach.	1803	not in use
Trichoderma laevisporum	Qin & Zhuang	2016	not in use
Trichoderma lanuginosum	Samuels	2012	CBS 125718
Trichoderma lateritio-roseum	Lib. ex Cooke	1880	not in use
Trichoderma latizonatum	(Peck) Samuels	2015	
Trichoderma leguminosarum	Jaklitsch & Voglmayr	2015	CBS 130014
Trichoderma lentiforme	(Rehm) Chaverri, Samuels & Rocha	2015	CBS 100542
Trichoderma lentinulae	Sun & Liu	2020	HMAS 248256
Trichoderma leucopus	Jaklitsch	2011	CBS 122499
Trichoderma liberatum	Chen & Zhuang	2017	HMAS 248831

(continued)

Table 1 (continued)

Species name	Author(s)	Year	Reference strain
Trichoderma lieckfeldtiae	Samuels	2009	CBS 123049
Trichoderma lignorum	(Tode) Harz	1872	not in use
Trichoderma limonium	Qin & Zhuang	2016	HMAS 248751
Trichoderma linzhiense	Chen & Zhuang	2017	HMAS 248846
Trichoderma lixii	(Pat.) Chaverri	2015	CBS 110080
Trichoderma longibrachiatum	Rifai	1969	CBS 816.68
Trichoderma longifialidicum	Montoya, Meirelles, Chaverri & Rodrigues	2016	CBS 139785
Trichoderma longipile	Bissett	1991	CBS 120953
Trichoderma longipilis	Bissett	1992	not in use
Trichoderma longipilum	Bissett	1992	not in use
Trichoderma longisporum	Chen & Zhuang	2017	HMAS 248843
Trichoderma luteffusum	Jaklitsch	2011	not in use
Trichoderma luteocrystallinum	Jaklitsch	2011	CBS 123828
Trichoderma luteoeffusum	Jaklitsch	2011	CBS 120537
Trichoderma lycogaloides	(Berk. & Broome) Jaklitsch, Lechat & Voglmayr	2014	CBS 123493
Trichoderma mangshanicum	Chen & Zhuang	2017	HMAS 248810
Trichoderma margaretense	Jaklitsch	2011	CBS 120540
Trichoderma martiale	Samuels	2008	CBS 123052
Trichoderma matsushimae	(Webster) Yamag., Tsurumi, Chuaseehar. & Nakagiri	2012	IMI 266915
Trichoderma mediterraneum	Jaklitsch & Voglmayr	2015	CBS 136469
Trichoderma medusae	Samuels	2012	CBS 125719
Trichoderma megalocitrinum	(Doi) Jaklitsch & Voglmayr	2014	B.E.O. 00-09
Trichoderma melanomagnum	Chaverri & Samuels	2003	G.J.S. 99-153
Trichoderma microcitrinum	(Doi) Jaklitsch & Voglmayr	2014	G.J.S. 91-61
Trichoderma mienum	Kim, Nakagiri & Maek.	2012	CBS 132690
Hypocrea mikurajimensis	Doi	2001	JCM 12018
Trichoderma minima	(Speg.) Gunth. Müll.	1965	not in use
Trichoderma minimum	(Speg.) Gunth. Müll.	1965	not in use
Trichoderma minutisporum	Bissett	1992	CBS 341.93
Trichoderma minutum	Bainier	1906	not in use
Trichoderma moravicum	Jaklitsch	2011	CBS 120539

(continued)

Table 1 (continued)

Species name	Author(s)	Year	Reference strain
Hypocrea muroiana	Hino & Katum.	1958	NBRC 31293
Trichoderma mycophilum	(Pers.) Schwein.	1822	not in use
Trichoderma narcissi	(Tochinai & Shimada) Tochinai & Shimada	1931	not in use
Trichoderma neocrassum	Samuels	2015	CBS 114230
Trichoderma neokoningii	Samuels & Soberanis	2006	CBS 120070
Trichoderma neorufoides	Jaklitsch	2011	CBS 119506
Trichoderma neorufum	(Samuels, Dodd & Lieckf.) Jaklitsch & Voglmayr	2014	CBS 111144
Trichoderma neosinense	Samuels & Jaklitsch	2013	CBS 134884
Trichoderma neotropicale	Chaverri & Rocha	2015	CBS 130633
Trichoderma nigrescens	Pers.	1794	not in use
Trichoderma nigrovirens	Goddard	1913	not in use
Trichoderma nigrovirens	Chaverri & Samuels	2001	not in use
Trichoderma nigrovirens	Chaverri & Samuels	2003	not in use
Trichoderma nothescens	Samuels & Jaklitsch	2013	CBS 134882
Trichoderma novae-zelandiae	(Samuels & Petrini) Jaklitsch & Voglmayr	2014	CBS 639.92
Trichoderma nunbergii	Svilv.	1932	not in use
Trichoderma nybergianum	(Ulvinen & Chamb.) Jaklitsch & Voglmayr	2014	CBS 122500
Trichoderma oblongisporum	Bissett	1992	CBS 343.93
Trichoderma ochroleucum	(Berk. & Ravenel) Jaklitsch & Voglmayr	2014	CBS 119502
Trichoderma odoratum	Qin & Zhuang	2016	HMAS 271354
Trichoderma oligosporum	Zhu & Zhuang	2015	HMAS 252870
Trichoderma olivascens	Jaklitsch, Samuels & Voglmayr	2013	CBS 132574
Trichoderma orientale	(Samuels & Petrini) Jaklitsch & Samuels	2014	CBS 130428
Trichoderma ovalisporum	Samuels & Schroers	2004	CBS 113299
Hypocrea pachybasioides	Doi	1972	not in use
Trichoderma pachypallidum	Jaklitsch	2011	CBS 122126
Trichoderma panacis	Liu, Zhang, Yu & Zhang	2020	CGMCC 3.18297
Trichoderma paraceramosum	Bissett	1992	not in use
Trichoderma parapiluliferum	(Lu, Druzhin. & Samuels) Jaklitsch & Voglmayr	2014	CBS 112771
Trichoderma parareesei	Atan., Jaklitsch, Komoń-Zel., Kubicek & Druzhin.	2010	CBS 125925
Trichoderma pararogersonii	Jaklitsch & Voglmayr	2015	CBS 133496

(continued)

Table 1 (continued)

Species name	Author(s)	Year	Reference strain
Trichoderma paratroviride	Jaklitsch & Voglmayr	2015	CBS 136489
Trichoderma paraviridescens	Jaklitsch, Samuels & Voglmayr	2013	CBS 119321
Trichoderma parceramosum	Bissett	1992	not in use
Trichoderma parepimyces	Jaklitsch	2009	CBS 122769
Trichoderma parestonicum	Jaklitsch	2009	CBS 120636
Trichoderma parmastoi	(Overton) Jaklitsch & Voglmayr	2014	TFC 97-143
Trichoderma patella	(Cooke & Peck) Jaklitsch & Voglmayr	2014	CBS 110081
Trichoderma patellotropicum	Samuels	2015	CBS 110084
Trichoderma paucisporum	Samuels, Carm. Suárez & Solis	2006	CBS 118645
Trichoderma peberdyi	Valadares-Inglis & Inglis	2020	CEN 1426
Trichoderma pedunculatum	Schumach.	1803	not in use
Trichoderma peltatum	(Berk.) Samuels, Jaklitsch & Voglmayr	2014	G.J.S. 08-207
Trichoderma penicillatum	Wallr.	1833	not in use
Trichoderma perviride	Qin & Zhuang	2017	HMAS 273786
Trichoderma petersenii	Samuels, Dodd & Schroers	2006	G.J.S. 91-99
Trichoderma pezizoides	(Berk. & Broome) Samuels, Jaklitsch & Voglmayr	2014	G.J.S. 01-257
Trichoderma pezizoideum	Wallr.	1833	not in use
Trichoderma phellinicola	Jaklitsch	2011	CBS 119283
Trichoderma phyllostachydis	Chaverri & Samuels	2003	CBS 114071
Trichoderma piluliferum	Webster & Rifai	1969	CBS 120927
Trichoderma pinicola	Oh, Park, & Lim	2019	KACC 48486
Trichoderma pinnatum	Samuels	2012	CBS 131292
Trichoderma placentula	Jaklitsch	2011	CBS 120924
Trichoderma pleuroti	Yu & Park	2006	CBS 124387
Trichoderma pleuroticola	Yu & Park	2006	CBS 124383
Trichoderma pleurotum	Yu & Park	2006	not in use
Trichoderma pollinicola	Liu & Cai	2018	CGMCC 3.18781
Trichoderma polyalthiae	Nuankaew & Boonlue	2018	TBRC 8737
Trichoderma polypori	Chen & Zhuang	2017	HMAS 248855
Trichoderma polysporum	(Link) Rifai	1969	CBS 820.68
Trichoderma poronioideum	(Möller) Samuels	2015	CBS 139046
Trichoderma priscilae	Jaklitsch & Voglmayr	2015	CBS 131487
Trichoderma protopulvinatum	(Doi) Jaklitsch & Voglmayr	2014	CBS 739.83

(continued)

Table 1 (continued)

Species name	Author(s)	Year	Reference strain
Trichoderma protrudens	Samuels & Chaverri	2008	CBS 121320
Trichoderma pruinosum	Chen & Zhuang	2017	HMAS 247217
Trichoderma pseudobritdaniae	Qin & Zhuang	2016	HMAS 271355
Trichoderma pseudocandidum	Minnis, Samuels & Chaverri	2009	BPI 843652
Trichoderma pseudodensum	Chen & Zhuang	2017	HMAS 248828
Trichoderma pseudogelatinosa	(Komatsu & Doi) Kim	2012	not in use
Trichoderma pseudogelatinosum	(Komatsu & Doi) Kim	2017	TUFC 60186
Trichoderma pseudokoningii	Rifai	1969	CBS 408.91
Trichoderma pseudolacteum	Kim & Maek.	2013	CBS 133191
Trichoderma pseudonigrovirens	Minnis, Samuels & Chaverri	2009	G.J.S. 99-64
Trichoderma pseudostraminea	(Doi) Kim	2012	not in use
Trichoderma pseudostramineum	(Doi) Kim	2012	TUFC 60104
Trichoderma psychrophilum	Jaklitsch	2011	CBS 119129
Trichoderma pubescens	Bissett	1992	CBS 345.93
Trichoderma pulvinatum	(Fuckel) Jaklitsch & Voglmayr	2014	CBS 121279
Trichoderma purpureum	Qin & Zhuang	2017	HMAS 273787
Trichoderma pyramidale	Jaklitsch & Chaverri	2015	CBS 135574
Trichoderma pyrenium	Pers.	1801	not in use
Trichoderma pyrenium	Schumach.	1803	not in use
Trichoderma racemosum	McAlpine	1902	not in use
Trichoderma reesei	Simmons	1977	CBS 383.78
Trichoderma restrictum	du Plessis & Jacobs	2018	PPRI 19367
Trichoderma rhododendri	(Jaklitsch) Jaklitsch & Voglmayr	2014	CBS 119288
Trichoderma rifaii	Rocha, Chaverri & Samuels	2015	CBS 130746
Trichoderma rodmanii	(Samuels & Chaverri) Jaklitsch & Voglmayr	2014	CBS 120895
Trichoderma rogersonii	Samuels	2006	G.J.S. 94-115
Trichoderma rosellum	Jaklitsch & Voglmayr	2014	
Trichoderma roseum	Pers.	1794	not in use
Trichoderma rossicum	Bissett, Kubicek & Szakács	2003	ATCC MYA-4839
Trichoderma rosulatum	Zhu & Zhuang	2015	HMAS 244906

(continued)

Table 1 (continued)

Species name	Author(s)	Year	Reference strain
Trichoderma rubi	Jaklitsch & Voglmayr	2015	CBS 127380
Trichoderma rubropallens	Schwein.	1832	
Trichoderma rufobrunneum	Zhu & Zhuang	2015	HMAS 252547
Trichoderma rugosum	Zhang & Zhuang	2018	not in use
Trichoderma rugulosum	Park, Oh & Lim	2019	SFC 20180301-001
Trichoderma sambuci	(Jaklitsch & Voglmayr) Jaklitsch & Voglmayr	2014	WU 29467
Trichoderma samuelsii	Jaklitsch & Voglmayr	2012	CBS 130537
Trichoderma saturnisporopsis	Samuels & Jaklitsch	2012	CBS 128829
Trichoderma saturnisporum	Hammill	1970	CBS 330.7
Trichoderma scalesiae	Samuels & Evans	2006	CBS 120069
Trichoderma semiorbis	(Berk.) Jaklitsch & Voglmayr	2014	CBS 130716
Trichoderma sempervirentis	Jaklitsch & Voglmayr	2013	CBS 133498
Trichoderma seppoi	Jaklitsch	2008	CBS 122498
Trichoderma shaoguanicum	Chen & Zhuang	2017	HMAS 248809
Trichoderma shennongjianum	Chen & Zhuang	2016	HMAS 245009
Trichoderma sichuanense	Chen & Zhuang	2017	HMAS 248737
Trichoderma silvae-virgineae	Jaklitsch	2011	CBS 120922
Trichoderma simmonsii	Chaverri, Rocha, Samuels, Degenkolb & Jaklitsch	2015	CBS 130431
Trichoderma simplex	Chen & Zhuang	2017	HMAS 248842
Trichoderma sinense	Bissett, Kubicek & Szakács	2003	DAOM 230004
Trichoderma sinensis	Bissett, Kubicek & Szakács	2003	not in use
Trichoderma sinoaustrale	Zhu & Zhuang	2014	HMAS 23403
Trichoderma sinokoningii	Qin & Zhuang	2016	HMAS 271397
Trichoderma sinoluteum	Zhu & Zhuang	2015	HMAS 252868
Trichoderma sinuosum	Chaverri & Samuels	2003	CBS 114247
Trichoderma solani	Samuels	2012	CBS 130506
Trichoderma solum	Chen & Zhuang	2017	HMAS 248848
Trichoderma songyi	Park, Seung Oh & Lim	2014	CBS 138099
Trichoderma sordidum	(Doi) Jaklitsch & Voglmayr	2014	

(continued)

Table 1 (continued)

Species name	Author(s)	Year	Reference strain
Trichoderma spadiceum	Schwein.	1822	not in use
Trichoderma sparsum	Qin & Zhuang	2016	HMAS 273759
Trichoderma speciosum	Yu & Du	2018	CGMCC 3.19079
Trichoderma sphaerosporum	Qin & Zhuang	2016	HMAS 273763
Trichoderma spinulosum	(Fuckel) Jaklitsch & Voglmayr	2014	CBS 311.5
Trichoderma spirale	Bissett	1992	CBS 346.93
Hypocrea splendens	Phillips & Plowr.	1885	CBS 336.69
Trichoderma sporulosum	(Link) Hughes	1958	not in use
Trichoderma stellatum	(Lu, Druzhin. & Samuels) Jaklitsch & Voglmayr	2014	not in use
Trichoderma stercorarium	(Barrasa, Martínez & Moreno) Jaklitsch & Voglmayr	2015	CBS 148.85
Trichoderma stilbohypoxyli	Samuels & Schroers	2006	CBS 992.97
Trichoderma stipitatum	Zhu & Zhuang	2015	HMAS 266613
Trichoderma stramineum	Chaverri & Samuels	2003	BPI 843667
Trichoderma strictipile	Bissett	1992	CBS 347.93
Trichoderma strictipilis	Bissett	1992	not in use
Trichoderma strigosellum	López-Quint., Gams, Boekhout & Druzhin.	2013	CBS 102817
Trichoderma strigosum	Bissett	1992	CBS 348.93
Trichoderma stromaticum	Samuels & Pardo-Schulth.	2000	CBS 101875
Trichoderma subalni	Zhang & Zhuang	2018	not in use
Trichoderma subalpinum	Jaklitsch	2011	CBS 119128
Hypocrea subcitrina	Kalchbr. & Cooke	1880	J.A.C. 14420
Trichoderma subeffusum	Jaklitsch	2011	W.M.J. 2009-17
Trichoderma subiculoides	Zeng & Zhuang	2019	not in use
Trichoderma subsulphureum	(Syd. & Syd.) Jaklitsch & Voglmayr	2014	not in use
Trichoderma subtrachycarpum	(Doi) Jaklitsch & Voglmayr	2014	
Trichoderma subviride	Qin & Zhuang	2016	HMAS 273761
Trichoderma succisum	(Rifai) Jaklitsch & Voglmayr	2014	
Trichoderma sulawesense	(Doi) Jaklitsch & Voglmayr	2014	GJS 85-228
Trichoderma sulphureum	(Schwein.) Jaklitsch & Voglmayr	2014	CBS 119929
Trichoderma surrotundum	Chaverri & Samuels	2003	BPI 843668
Trichoderma sympodianum	Kulik	1960	not in use
Trichoderma taiwanense	Samuels & Wu	2006	CBS 119058
Trichoderma tardum	Chen & Zhuang	2017	HMAS 248798

(continued)

Table 1 (continued)

Species name	Author(s)	Year	Reference strain
Trichoderma tawa	Chaverri & Samuels	2003	CBS 114233
Trichoderma taxi	Zhang, Lin & Kubicek	2007	CGMCC 1672
Trichoderma tenue	Qin & Zhuang	2017	HMAS 273785
Trichoderma texanum	Montoya, Meirelles, Chaverri & Rodrigues	2016	CBS 139784
Trichoderma thailandicum	Chaverri & Samuels	2003	CBS 114234
Trichoderma thelephoricola	Chaverri & Samuels	2003	CBS 114237
Trichoderma theobromicola	Samuels & Evans	2006	CBS 119120
Trichoderma thermophilum	Qin & Zhuang	2016	HMAS 252912
Trichoderma tiantangzhaiense	Zhu & Zhuang	2015	HMAS 252872
Trichoderma tibetense	Chen & Zhuang	2016	HMAS 245010
Trichoderma todica	Sokoloff & Toda	1967	not in use
Trichoderma tomentosum	Bissett	1992	CBS 349.93
Trichoderma trachycarpum	(Syd.) Jaklitsch & Voglmayr	2014	
Trichoderma tremelloides	Jaklitsch	2011	CBS 121140
Trichoderma trixiae	Samuels & Jaklitsch	2013	CBS 134702
Trichoderma tropicosinense	(Liu) Zhu & Zhuang	2015	HMAS 252546
Trichoderma tsugarense	Yabuki & Okuda	2014	NBRC 109641
Trichoderma tuberculatum	Pers.	1795	not in use
Trichoderma turrialbense	Samuels, Degenkolb, Nielsen & Gräfenhan	2008	CBS 112445
Trichoderma undatipile	Chen & Zhuang	2017	not in use
Trichoderma undatipilosum	Chen & Zhuang	2017	not in use
Trichoderma undulatum	du Plessis & Jacobs	2018	PPRI 19365
Trichoderma valdunense	Jaklitsch	2011	CBS 120923
Trichoderma varians	Sartory & Bainier	1912	not in use
Trichoderma varium	Ehrenb.	1818	not in use
Trichoderma velutinum	Bissett, Kubicek & Szakács	2003	DAOM 230013
Trichoderma vermifimicola	Sun & Liu	2020	HMAS 248255
Trichoderma vermipilum	Samuels	2012	CBS 127103
Trichoderma verticillatum	Chen & Zhuang	2017	HMAS 248740
Trichoderma victoriense	(Overton) Jaklitsch & Voglmayr	2014	CBS 140064
Trichoderma vinosum	Samuels	2006	CBS 119087
Trichoderma violaceum	Oudem.	1904	not in use

(continued)

Table 1 (continued)

Species name	Author(s)	Year	Reference strain
Trichoderma virens	(Mill., Giddens & Foster) Arx	1987	CBS 249.59
Trichoderma virescentiflavum	(Speg.) Jaklitsch & Voglmayr	2014	P.C. 278
Trichoderma virgatum	Cserjesi & Johnson	1972	not in use
Trichoderma viridarium	Jaklitsch, Samuels & Voglmayr	2013	CBS 132568
Trichoderma viride	Schumach.	1803	not in use
Trichoderma viride	Pers.	1794	not in use
*Trichoderma viride***	Pers.	1832	CBS 119325
Trichoderma viridescens	(Horne & Will.) Jaklitsch & Samuels	2006	CBS 433.34
Trichoderma viridialbum	Jaklitsch, Samuels & Voglmayr	2013	CBS 133495
Trichoderma viridicollare	Zhang & Zhuang	2019	W.Z. 2018b
Trichoderma viridiflavum	Zhu & Zhuang	2014	HMAS 252549
Trichoderma viridulum	Qin & Zhuang	2017	HMAS 273865
Trichoderma virilente	Jaklitsch & Voglmayr	2013	CBS 132569
Trichoderma voglmayrii	Jaklitsch	2006	CBS 117711
Trichoderma vulgatum	Chen & Zhuang	2017	HMAS 248796
Trichoderma vulpinum	Fuckel	1874	not in use
Trichoderma xanthum	Chen & Zhuang	2017	HMAS 247202
Trichoderma xixiacum	Sun & Liu	2020	HMAS 248253
Trichoderma yui	Zhu & Zhuang	2015	HMAS 266633
Trichoderma yunnanense	Yu & Zhang	2007	CBS 121219
Trichoderma zayuense	Chen & Zhuang	2017	HMAS 248835
Trichoderma zelobreve	Sun & Liu	2020	HMAS 248254
Trichoderma zeloharzianum	Yu & Du	2018	CGMCC 3.19082
Trichoderma zonatum	Zhu, Zhuang & Li	2017	CGMCC 3.18758

* *T. brevipes* was transferred from *Cordyceps* (Hypocreales) to *Trichoderma* (Bissett et al. 2015). No DNA barcoding information is available for this species.
** The name of *Trichoderma viride* is presented diferently in the three databases, namely the NCBI Taxonomy Browser contains *T. viride* Pers. 1832, while MycoBank and Index Fungorum refer to *T. viride* Pers. 1794.

re-established website of the ICTT (www.trichoderma.info) contains the other copy of the complete list of species and is designed to be regularly updated. The interactive, updated, and searchable version of the complete list of *Trichoderma* species is available as a supplementary tool in the species identification protocol

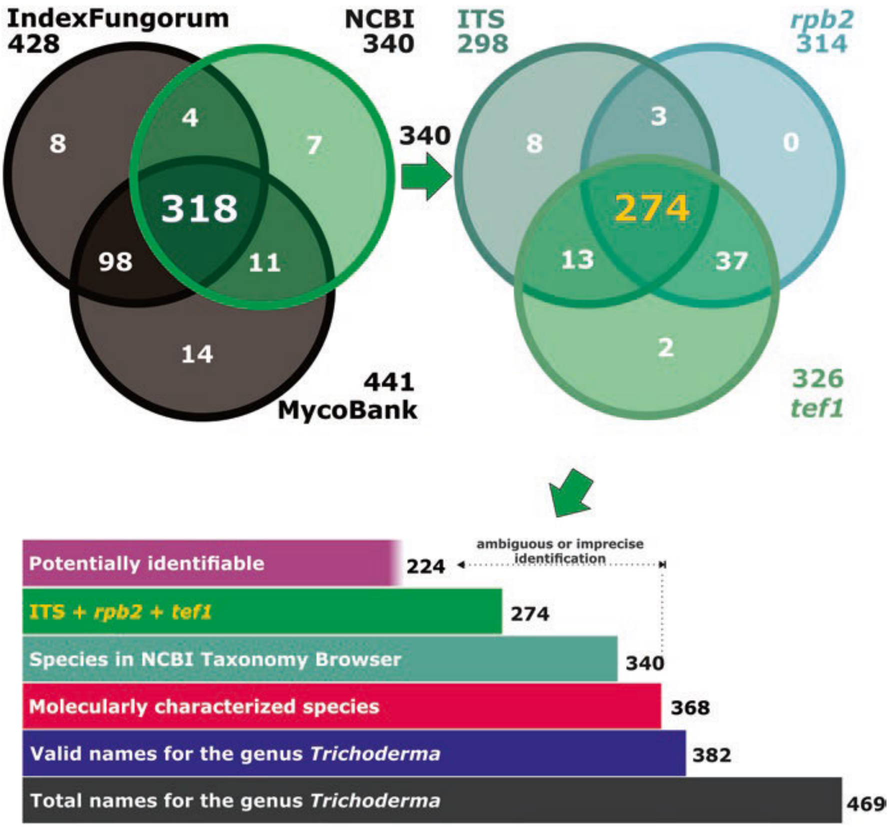

Fig. 1 The numerical representation of *Trichoderma* taxonomy. The left Venn diagram shows the number of *Trichoderma* species deposited in the major depositories of fungal taxonomy such as Index Fungorum (http://www.indexfungorum.org/), MycoBank (https://www.mycobank.org/), and NCBI Taxonomy Browser (https://www.ncbi.nlm.nih.gov/Taxonomy/Browser/wwwtax.cgi). The right Venn diagram shows the numbers of species that have one or several of the three DNA barcode sequences required for the molecular identification of *Trichoderma*. The bar plot illustrates the alarming situation related to identifiability of *Trichoderma* species. Numbers near the bars show the numbers of species (based on the estimates updated from Cai and Druzhinina 2021, www.trichokey.com and www.trichoderma.info)

(www.trichokey.com) (Cai and Druzhinina 2021). However, as the number of species grows rapidly (Cai and Druzhinina 2021), it has been suggested to screen the most recent taxonomic literature and compare it to the data on recent website updates.

The introduction of molecular methods in *Trichoderma* taxonomy not only resulted in the rapid growth of the species number but it also ended the morphological identification of *Trichoderma* (Kullnig-Gradinger et al. 2002; Druzhinina and Kubicek 2005; Druzhinina et al. 2005). Regardless of the experience and training of the taxonomist, the analysis of many morphological features cannot lead to unambiguous diagnosis of *Trichoderma* taxa even at the level of clades or sections. Thus, identification can only be achieved via analysis of DNA barcodes.

Even though 96% of *Trichoderma* species are characterized molecularly and the sequences are preserved in public databases, the Taxonomy Browser of NCBI (https://www.ncbi.nlm.nih.gov/taxonomy) contains only 340 species names (89% from all and 93% from molecularly characterized) meaning that sequence records for at least several dozen described species were not updated; however, these are still deposited as taxonomically undefined records (i.e., *Trichoderma* sp. strain ID). Consequently, these species will not appear in the results of the sequence similarity search using NCBI BLAST. The vouchered sequences can be retrieved based on sequence accession numbers provided in the publications.

Due to the high number of cryptic and closely related species, the accurate molecular identification of *Trichoderma* species requires analysis of at least three DNA barcodes (Cai and Druzhinina 2021) (see below). Considering the updated records for early 2021, the largest number of species have been DNA barcoded for *tef1* (86%) followed by *rpb2* (82%) and ITS (78%); only 270 (71%) have all 3 DNA barcodes (Fig. 1). Other commonly provided DNA barcodes (*chi18-5=ech42*, *cal1*, *act*, *acl1*, 18S rRNA=SSU, and 28S rRNA=LSU) are sequenced for less than one-half of the species; therefore, they currently have limited or no suitability for molecular identification regardless of their properties.

We notice that the number of species suitable for accurate species identification based on molecular markers is even lower than the estimate provided above (71%, Fig. 1). Our analysis showed that the identification of at least 50 recently described species is compromised by either incomplete reference sequences or sequences indistinguishable from the sister species (Cai and Druzhinina 2021). Thus, we counted only 224 (60%) of *Trichoderma* species that can be potentially identified based on available DNA barcodes (ITS, *tef1*, and *rpb2*). Still, this number appears to be an overestimate because the individual analysis of species frequently reveals further taxonomic collisions and leads to ambiguous results.

Thus, we conclude that while the taxonomy of *Trichoderma* attracted considerable attention over the last two decades, the taxonomic situation in the genus is alarming and requires urgent improvements (Fig. 1). The reasons for this unfortunate state of *Trichoderma* taxonomy and possible measures that can be taken for its improvement will be discussed below.

3 Three Stages of *Trichoderma* DNA Barcoding

The development of DNA barcoding of *Trichoderma* went through three pronounced stages: First, the species could be identified based on the combination of diagnostic oligonucleotide sequences in specific areas of ITS sequences of the rRNA gene cluster when the total diversity of the genus did not exceed 100 taxa (Druzhinina et al. 2005). This method was implemented in the web-based tool *TrichO*KEY and was supported by the public database of the reference sequences. At least for a decade, the *TrichO*KEY tool was appreciated by users of *Trichoderma* taxonomy because of its simplicity. For most species recognized at that time, a pasting of an ITS sequence in the web form provided an unambiguous and final identification result that did not require further analyses (reviewed at Druzhinina et al. (2006)). The identification could be performed by people having no experience in fungal taxonomy or molecular phylogeny. However, there were already several pairs of species that shared the same phylotypes of ITS and therefore were not distinguishable. Upon subsequent introduction of more and more new species, insufficient variability of ITS was demonstrated for many infrageneric groups especially for the clades within Section *Trichoderma* and Section *Longibrachiatum* as well as the *Harzianum* Clade. Therefore, ITS started to lose its reputation as the diagnostic marker for *Trichoderma* species (Druzhinina et al. 2012; Atanasova et al. 2010).

A new effort was focused on a search for the so-called "secondary" DNA barcode loci that would aid in unambiguous species identification. At that stage, the suitability of various loci was tested based either on the random use of recently cloned and characterized genes (e.g., *ech42* = *chi18-5*) or more commonly following the practices used for the large DNA barcoding initiatives such as the Fungal Tree of Life project (Lutzoni et al. 2004). Thus, *rpb2* (Liu et al. 1999), *cal1* (Carbone and Kohn 1999), *act* (Carbone and Kohn 1999), 18S rRNA=SSU (White et al. 1990), and 28S rRNA=LSU were sequenced for a broad range of species, but only *tef1* locus received broad support by the community (Cai and Druzhinina 2021). Therefore, the second phase of *Trichoderma* DNA barcoding was associated with the use of the large intron of *tef1* gene (Kopchinskiy et al. 2005) for sequence similarity search. The sequences of *tef1* were sufficiently polymorphic and allowed species identification with quite high precision versus the curated database of vouchered sequences using such tools as *Tricho*BLAST or (with more caution) NCBI BLAST. At that stage, we estimated that intraspecific variability of *tef1* large (4th) intron could be as high as 4–5% meaning there was a 95% similarity threshold for most of the species in BLAST.

Rahimi et al. (2021) recently offered a way to identify *T. reesei* strains by searching for the long (400 bp) sequence of *tef1* fragment that they postulated to be diagnostic for this species. However, no such hallmarks were reported for other *Trichoderma* spp. This "*tef1*" stage ended with the so-called species boom that occurred in *Trichoderma* in 2014–2015 when more than 100 new species were added mainly due to the taxonomic studies in Europe and China (reviewed in Cai and Druzhinina 2021). Dou et al. (2020) were the first group to realize that the single secondary barcode—the partial *tef1* sequence—was no longer sensitive enough for the identification of *Trichoderma* species. For this purpose, they programmed MIST (The Multiloci Identification System for *Trichoderma* (http://mmit.china-cctc.org/)) that relied on the gradual application of sequence similarity search for the three loci: ITS, *tef1*, and *rpb2*. This started the third stage of *Trichoderma* DNA barcoding. This program offered a reasonable replacement to *TrichO*KEY that was consequently shut down (Cai and Druzhinina 2021). The strength of MIST was the most complete database of the reference sequences for *Trichoderma* and included the tree DNA barcoding loci for many type strains; it also contained numerous unverified records and thus could not result in highly accurate or precise identification. Interestingly, the two secondary DNA barcodes (the partial sequences of *tef1* and *rpb2*) have unequal levels of polymorphism. Therefore, no single value of the similarity threshold could be used for either markers. To overcome this issue, we recently collected all DNA barcoding records for all contemporary valid *Trichoderma* species and proposed the species identification protocol (Cai and Druzhinina 2021). There, we reviewed the interspecific polymorphism of ITS, *tef1*, and *rpb2* sequences of closely related *Trichoderma* species to find the most reasonable sequence similarity values for each of the three DNA barcoding loci. This allowed us to formulate the sequence similarity standard:

$$\textit{Trichoderma}\ \left[\mathrm{ITS}_{76}\right] \sim \mathrm{sp}\exists!\ \left(rpb2_{99} \cong tef1_{97}\right).$$

Here, “Trichoderma” means the genus *Trichoderma*, “sp” means a species, “~” indicates an agreement between ITS and other loci, “≅” refers to the concordance between “*rpb2*” and “*tef1*,” and “∃!” indicates the uniqueness of the condition (only one species can be identified). Subscripts show that the similarity per locus is sufficient for identification based on the assumptions of the protocol. This standard was then implemented in the molecular identification protocol (Cai and Druzhinina 2021) that required a manual analysis of every set of sequences per individual strain. Still, due to the high number or poorly characterized reference taxa, this protocol would also result in some ambiguous identifications. Moreover, the application of the identification procedure requires training in sequence analysis and can be difficult for inexperienced people. However, no “easy” solution appears to be feasible at this phase of *Trichoderma* taxonomy.

The current (third) stage of DNA barcoding of *Trichoderma* is based on the three DNA loci that are considered to be the most reliable. Still the identification process remains complex. Even though Cai and Druzhinina (2021) argue that all three loci are required for the accurate and precise species identification, ITS can only be used to identify *Trichoderma* at the generic level. Most species recognition comes from the diagnostic fragments of *tef1* and *rpb2* gene sequences. The choice of these loci is not determined by their particular suitability for the purpose but rather by their availability in public databases for most species (Fig. 1).

The advantage of *tef1* is the high polymorphism of its large (4th) intron sequence that is 250–300 base pairs long. We determined that individual strains within most of the contemporary species share >97% similarity of this fragment meaning that the polymorphism can reach up to 3% or 20–25 single mutations. This “identification window” is small versus that during the second stage of DNA barcoding, but it still offers a reasonable resolution and may potentially lead to unambiguous identification of strains having *tef1* phylotypes highly similar to that of the type strain for a given species. However, the disadvantage of *tef1* is also linked to its high polymorphism because it prevents combining strains from different infrageneric clades on a single alignment (Jaklitsch 2009a, 2011). Consequently, many *Trichoderma* taxonomy providers keep sequencing *tef1* for newly described species but have largely abandoned the polymorphic fragment and shifted toward the 3′ end of the gene to the highly conserved fragment of the last (6th) exon (Jaklitsch 2009b, 2011). Consequently, the taxonomic value of this version of the *tef1* DNA barcode locus is neglectable. This shift coincided with the “species boom” and resulted in the description of the large number of species that cannot be distinguished based on existing DNA barcodes (Cai and Druzhinina 2021).

The properties of *rpb2* are the reverse versus *tef1*: The DNA barcoding fragment of this gene covers an area of relatively highly conserved exon sequence. Contrary to *tef1*, these sequences are easily aligned genus-wide and therefore are suitable for the construction of whole genus phylograms (Atanasova et al. 2013; Cai and Druzhinina 2021). Consequently, the polymorphism of *rpb2* is essentially lower than *tef1*, and such well-defined pairs of sister species such as *T. asperellum* and *T. asperelloides, T. reesei* and *T. parareesei*, and *T. harzianum* and *T. afroharzianum* differ by only 1% or a few single mutations of *rpb2* (usually less than eight). Unfortunately, we have detected numerous recently described species that share identical or highly similar (>99%) sequences of *rpb2* (Cai and Druzhinina 2021). The consideration of above-described limitations of *tef1* and *rpb2* DNA barcodes is the main but not the only source of identification complexity.

The other issue causing the identification ambiguity is related to the cases of unconcordant similarities of the three DNA barcoding loci. For example, Cai and Druzhinina (2021) pointed to the ambiguous taxonomic position of their model whole genome sequenced strain NJAU 4742 (Zhang et al. 2016, 2019; Pang et al. 2020; Cai et al. 2020; Gao et al. 2020; Druzhinina et al. 2018; Kubicek et al. 2019; Jiang et al. 2019; Zhao et al. 2021). This strain has the *tef1* DNA barcode identical to the type strain of *T. guizhouense*. Therefore, it was attributed to this species at the second stage of DNA barcoding of *Trichoderma*. However, the *rpb2* sequence of this strain is less than 95% similar to that of the type strain of *T. guizhouense* and has most affinity to *T. pyramidale* (97.8%, which is still below the identification threshold). Interestingly, we came across several other strains with the same haplotype of *tef1* and *rpb2* as NJAU 4742. These data suggest the existence of a putative new species (*T. shenii* nom. prov., Cai and Druzhinina 2021). This and numerous other cases of incongruent similarities point to the need for phylogenetic analyses of *tef1* and *rpb2* alignments along with the consideration of the similarities. In turn, these data explain why any attempts at automated identification of sequences such as *TrichO*KEY and MIST do not appear feasible.

4 Notes on the Identification of *Trichoderma* Species

The protocol for molecular identification of a single *Trichoderma* strain is detailed in Cai and Druzhinina (2021). That work also contains several dozen practical examples that provide an overview of various situations related to the implementation of this protocol. In this chapter, we do not repeat the description of the protocol but rather comment on it and highlight a few aspects that appear critical for its understanding and correct use (Fig. 2).

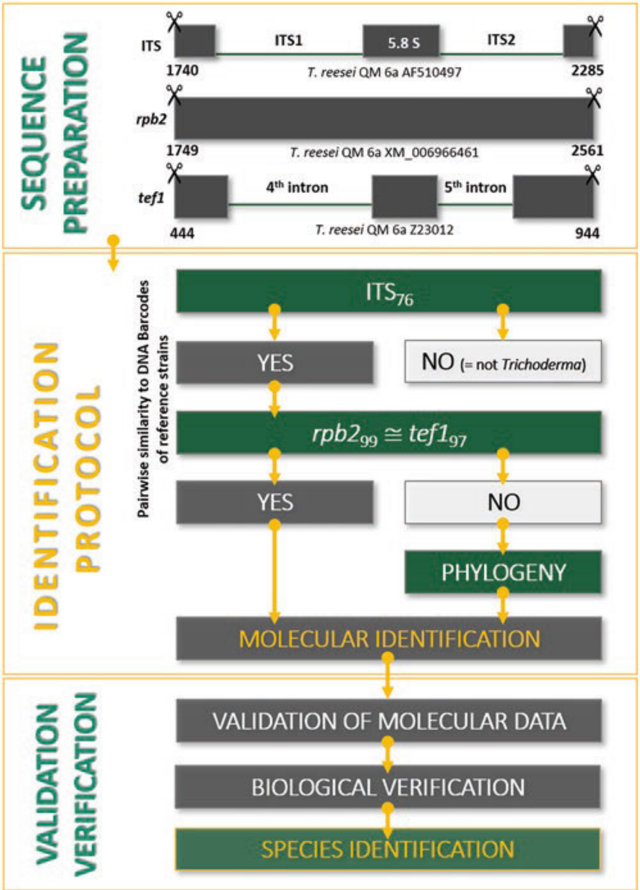

Fig. 2 The summary of the current molecular identification protocol for *Trichoderma* species (Cai and Druzhinina 2021)

First, it is important to bear in mind that neither the choice of DNA barcode markers nor the sequence similarity threshold values were selected based on their properties or particular suitability for the species recognition in *Trichoderma*. The decision to use these loci was merely pragmatic because these were the only three DNA barcoding markers that were available in public databases for the majority of species (Fig. 1). Accordingly, the similarity values were picked such that they could distinguish most of the contemporary species (Cai and Druzhinina 2021). We admit that the whole genome sequences for *Trichoderma* (Druzhinina et al. 2018; Kubicek et al. 2019) could be used for the detection of essentially more powerful DNA barcoding loci in a hypothetical situation of a taxonomic revision of the entire genus. However, it is important to understand that no such revision appears to be envisioned in the near future for nonscientific reasons. The comparison of closely related *Trichoderma* strains is impeded by the strain exchange barriers between countries.

For instance, at least 100 *Trichoderma* species have been recently described in China, and this number will likely keep growing (Cai and Druzhinina 2021). Due to the quarantine rules, sending strains across the borders between some specific countries for examination in other laboratories appears to be difficult. Thus, at this stage of DNA barcoding of *Trichoderma*, the selection of diagnostic loci and criteria for the identification were determined by the availability and other practical considerations.

Second, the protocol largely relies on the sequence similarity values, and its successful implementation requires precisely defined sequence fragments per each locus. Consequently, preparation of the protocol by trimming the sequences is an essential step that must not be omitted (Fig. 2). Every DNA barcoding locus can be PCR amplified using a variety of primer pairs (Jaklitsch et al. 2005; Carbone and Kohn 1999; Liu et al. 1999) resulting in fragments of different lengths. Therefore, the base pairs flanking the diagnostic regions must be removed either manually following the instructions in Cai and Druzhinina (2021) or using online support such as www.trichokey.com (Fig. 2).

Third, sequencing ITS is compulsory for the identification of *Trichoderma* species and the analysis of infrageneric diversity. Unfortunately, to date, the database of vouchered ITS sequences is smaller compared to *tef1* and *rpb2* (Fig. 1) because sequencing of ITS was abandoned by some providers of *Trichoderma* taxonomy after this locus lost its power in distinguishing many pairs or groups of closely related species. However, ITS still has an exceptional value in fungal taxonomy (Schoch et al. 2012). Even in *Trichoderma*, many species have unique phylotypes of ITS and can therefore contribute to the identification precision. More critically, ITS is highly diagnostic at the generic border of *Trichoderma* where the limited polymorphism of the protein-coding genes appears to be less informative (Cai and Druzhinina 2021). It is also necessary to determine ITS sequences for all new fungal taxa because it is the main locus used for fungal metagenomic studies and has a vast database of environmental records (reviewed in Lücking et al. (2020)).

Fourth, it is important to specify that the protocol allows one to identify some species through the analysis of sequence similarity values with no need to run phylogenies. For example, it might be common when a certain strain has the trimmed ITS and *rpb2* phylotypes identical to that of *T. asperelloides* CBS 125938 (type) and the trimmed *tef1* phylotype having one or two SNPs different from that of the above strain. In this case, the application of the *Trichoderma* $[\text{ITS}_{76}]\sim\text{sp}\exists!(\mathit{rpb2}_{99} \cong \mathit{tef1}_{97})$ standard is unambiguous and leads to the molecular identification of the query strain as *T. asperelloides*. Many other cases require phylogenetic analysis. This is in particular necessary when *tef1* and *rpb2* are not concordant or the reference DNA barcoding material is incomplete. The quality of phylogenetic analysis is also strongly influenced by the taxonomic completeness of the reference materials. The dataset suitable for phylogeny should have no gaps, i.e., it should include all species reported for this infrageneric group. The protocol of Cai and Druzhinina (2021) offers a list of *Trichoderma* species and reference strains sorted based on their phylogenetic relation (PhyloOrder in Table 2 there and on www.trichokey.com). This should assist people searching for a taxonomically complete set of sequences required for their analysis.

The fifth note on the implementation of the molecular identification protocol for *Trichoderma* species refers to the validation and verification steps (Fig. 2). These steps were not considered important at the first and second stages of *Trichoderma* DNA barcoding but now appear critical.

In Cai and Druzhinina (2021), validation refers to the quality control step in the reference materials for DNA barcoding. The most common issue leading to ambiguous identifications is the deposition of the reference *tef1* sequences that contain only a portion of the last large intron (Jaklitsch 2009a) that is diagnostic for *Trichoderma* DNA barcoding. One or another end of this sequence is the mission (more frequently the 5′ end of the intron sequence). The taxonomically relevant map and the structure of the *tef1* gene were provided in Rahimi et al. (2021). As mentioned above, many taxonomists sequence the 3′ end of the *tef1* gene spanning over the last large exon that can be aligned for across the genus, but it has limited or no suitability for DNA barcoding. This refers to numerous new species introduced from Europe and China in prior and over the recent "species boom" in 2009–2015. The missing diagnostic *tef1* DNA barcodes should be provided on the first instance because with the current high number of taxa, even a single incomplete reference sequence per species will result in ambiguous identification.

This situation is less frequently noticed for *rpb2* sequences. However, *rpb2* can sometimes contain sequences of poor quality that are also not suitable for references. For the cases when the DNA barcoding sequences for the reference strains are either incomplete or of poor quality, the protocol of Cai and Druzhinina (2021) suggests using the *T*. cf. [species name] construct. The users of taxonomy (researchers that perform the identification) are advised to seek or request the completion of reference materials from their respective taxonomy providers. Alternatively (and as it was practiced at early stages of *Trichoderma* DNA barcoding), the reference strains can be obtained from the respective strain collections and sequenced.

The validation step can also fail when several species share the same phylotype of one or several DNA barcodes. Unfortunately, this is also a common situation in *Trichoderma* taxonomy (Cai and Druzhinina 2021). For example, *T. afarasin* and *T. endophyticum* share a highly similar *tef1* phylotype (>99% similarity); *T. yunnanense* and *T. kunmingense* share highly similar phylotypes of *rpb2* with each other and with *T. asperellum* (>99%). In this case, the ambiguity of the final identification can be recorded as *T*. aff. *asperellum* if the query strain was isolated from Europe (for instance). If sampling was performed in the Chinese province Yunnan, then the strains can be identified as *T*. aff. *yunnanense* or *T*. aff. *kunmingense*, depending on other properties.

After the results of molecular identification become validated through the quality control of reference materials, the next important step is the biological verification of the identification result. Biological verification requires critical evaluation of such criteria as morphology, ecophysiology, biogeography, habitat, and occurrence. At this stage, the consideration of micromorphological features appears to be reasonable. For example, the three sister species *T. pleuroti*, *T. amazonicum*, and

T. pleuroticola have numerous common and sharply different morphological and ecophysiological features verifying their distinct taxonomic statuses. Cai and Druzhinina (2021) provide a detailed explanation of the verification stage of their protocol.

Finally, the "new species hypothesis" can be an unambiguous, accurate, and precise result of molecular identification. This case ultimately requires validation of reference materials, phylogenetic analysis, and biological verification. In this chapter, we avoid discussing the criteria applicable for the delineation of species in *Trichoderma* as Cai and Druzhinina (2021) had presented a comprehensive discussion of this topic. However, we would like to stress that the correct implementation of the genealogical concordance phylogenetic species recognition concept (Taylor et al. 2000) requires the analysis of single gene topologies. The common use of the single tree based on a combined multilocus alignment is insufficient for the new species proposal.

5 Conclusions

The identification of *Trichoderma* species is an intricate and laborious task that requires a background in mycology, molecular biological skills, training in molecular evolution, and in-depth knowledge of taxonomic literature (Cai and Druzhinina 2021). The contemporary diversity of *Trichoderma* spp. cannot be identified by automated sequence similarity searches (such as NCBI BLAST or MIST BLAST) or oligonucleotide DNA barcodes. All molecular identification results require in silico validation and biological verification. Similarly, *Trichoderma* spp. cannot be identified by phylogenetic analysis without considering the sequence similarity values relative to the complete set of closely related species. The complexity of the identification process points to the need for close interactions between *Trichoderma* taxonomy experts.

In this chapter, we used *Trichoderma* to address the modern taxonomic collision that can also occur in many other genera of common and well-investigated fungi. The taxonomy of these fungi was visited and revisited many times and seemingly progressed with the introduction of new species. The delineation of the cryptic species is considered to be a useful practice because it increases the accuracy and precision of property prediction. However, many of newly recognized species appear to be difficult to identify. Ultimately, the failure to identify species leads to ambiguity but, more dangerously, to the description of more new species that further complicate the identification. This loop has been already reported before and noticed that every single fungal species has been named 2.5 times on average (Hawksworth and Lucking 2017). The good taxonomic practice should include the verification of species identifiability. Even though this process appears to be implemented as a reverse operation to the species recognition, it is frequently obscured by the application of vague species criteria. In an unfortunate case, a species can be recognized based on a comparison with a taxonomically incomplete set of references or based on species criteria that do not correspond to the state of the art in this genus. Even now, the Code will allow the application of the morphological species concept or a description of a *Trichoderma* species based on the morphological characters and the analysis of any single locus, i.e., ITS.

In this chapter, we tried to emphasize that such cases will result in a valid species name, but this species will not be possible to identify because most sister species were delineated based on advanced molecular species criteria such as GCPSR or even an integrated polyphasic approach. The example above is an exaggeration, but the taxonomic reality of *Trichoderma* is highly ambiguous. We assume that this turbulent state was caused by the recent introduction of highly powerful molecular techniques in fungal taxonomy, and the situation will get its rational solution. However, we set a further warning related to the introduction of the whole genus genomic data in *Trichoderma* taxonomy. The whole genome sequences have a still unexplored inter- and intraspecific polymorphism and thus offer essentially more options for taxonomic splitting: Species within the genus may share only 75% similarity genome-wide (Kubicek et al. 2019) and genomes of the two strains of the same clonal species *T. harzianum* have up to 1000 unique genes each. Therefore, the discussion of the unified species concept suitable for such fungi as *Trichoderma* is an urgent task for *Trichoderma* researchers and fungal taxonomists.

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References

Atanasova L, Jaklitsch WM, Komoń-Zelazowska M, Kubicek CP, Druzhinina IS (2010) Clonal species *Trichoderma parareesei* sp. nov. likely resembles the ancestor of the cellulase producer *Hypocrea jecorina*/*T. reesei*. Appl Environ Microbiol 76(21):7259–7267. https://doi.org/10.1128/AEM.01184-10

Atanasova L, Druzhinina IS, Jaklitsch WM (2013) Two hundred *Trichoderma* species recognized on the basis of molecular phylogeny. CABI, Wallingford, pp 10–42. https://doi.org/10.1079/9781780642475.0010

Bissett J (1984) A revision of the genus *Trichoderma*. I. Section *Longibrachiatum* sect. nov. Can J Bot 62(5):924–931. https://doi.org/10.1139/b84-131

Bissett J (1991a) A revision of the genus *Trichoderma*. II. Infrageneric classification. Can J Bot 69(11):2357–2372. https://doi.org/10.1139/b91-297

Bissett J (1991b) A revision of the genus *Trichoderma*. III. Section Pachybasium. Can J Bot 69(11):2373–2417. https://doi.org/10.1139/b91-298

Bissett J (1991c) A revision of the genus *Trichoderma*. IV. Additional notes on section *Longibrachiatum*. Can J Bot 69(11):2418–2420. https://doi.org/10.1139/b91-299

Bissett J (1992) Trichoderma atroviride. Can J Bot 70(3):639–641

Bissett J, Gams W, Jaklitsch W, Samuels GJ (2015) Accepted *Trichoderma* names in the year 2015. IMA Fungus 6(2):263–295. https://doi.org/10.5598/imafungus.2015.06.02.02

Cai F, Druzhinina IS (2021) In honor of John Bissett: authoritative guidelines on molecular identification of *Trichoderma*. Fungal Divers. https://doi.org/10.1007/s13225-020-00464-4

Cai F, Gao R, Zhao Z, Ding M, Jiang S, Yagtu C, Zhu H, Zhang J, Ebner T, Mayrhofer-Reinhartshuber M, Kainz P, Chenthamara K, Akcapinar GB, Shen Q, Druzhinina IS (2020) Evolutionary compromises in fungal fitness: hydrophobins can hinder the adverse dispersal of conidiospores and challenge their survival. ISME J 14(10):2610–2624. https://doi.org/10.1038/s41396-020-0709-0

Carbone I, Kohn LM (1999) A method for designing primer sets for speciation studies in filamentous ascomycetes. Mycologia 91(3):553–556. https://doi.org/10.1080/00275514.1999.12061051

Chaverri P, Castlebury LA, Samuels GJ, Geiser DM (2003) Multilocus phylogenetic structure within the *Trichoderma harzianum/Hypocrea lixii* complex. Mol Phylogenet Evol 27(2):302–313. https://doi.org/10.1016/S1055-7903(02)00400-1

Chen P, Pang G, Cai F, Druzhinina IS (2021) Strain improvement and genetic engineering of *Trichoderma* for industrial applications. In: Zaragoza O, Casadevall A (eds) Encyclopedia of mycology. Elsevier, pp 505–517. https://doi.org/10.1016/B978-0-12-819990-9.00029-9

Chouaki T, Lavarde V, Lachaud L, Raccurt CP, Hennequin C (2002) Invasive infections due to *Trichoderma* species: report of 2 cases, findings of *in vitro* susceptibility testing, and review of the literature. Clin Infect Dis 35(11):1360–1367. https://doi.org/10.1086/344270

Ding MY, Chen W, Ma XC, Lv BW, Jiang SQ, Yu YN, Rahimi MJ, Gao RW, Zhao Z, Cai F, Druzhinina IS (2020) Emerging salt marshes as a source of *Trichoderma arenarium* sp. nov. and other fungal bioeffectors for biosaline agriculture. J Appl Microbiol n/a(n/a). https://doi.org/10.1111/jam.14751

Dou K, Lu Z, Wu Q, Ni M, Yu C, Wang M, Li Y, Wang X, Xie H, Chen J, Zhang C (2020) MIST: a multilocus identification system for *Trichoderma*. Appl Environ Microbiol 86(18):e01532–e01520. https://doi.org/10.1128/AEM.01532-20

Druzhinina I, Kubicek CP (2005) Species concepts and biodiversity in *Trichoderma* and *Hypocrea*: from aggregate species to species clusters? J Zhejiang Univ Sci B 6(2):100–112. https://doi.org/10.1631/jzus.2005.B0100

Druzhinina IS, Kubicek CP (2017) Genetic engineering of *Trichoderma reesei* cellulases and their production. Microb Biotechnol 10(6):1485–1499. https://doi.org/10.1111/1751-7915.12726

Druzhinina IS, Kopchinskiy AG, Komoń M, Bissett J, Szakacs G, Kubicek CP (2005) An oligonucleotide barcode for species identification in *Trichoderma* and *Hypocrea*. Fungal Genet Biol 42(10):813–828. https://doi.org/10.1016/j.fgb.2005.06.007

Druzhinina IS, Kopchinskiy AG, Kubicek CP (2006) The first 100 *Trichoderma* species characterized by molecular data. Mycoscience 47(2):55–64. https://doi.org/10.1007/S10267-006-0279-7

Druzhinina IS, Seidl-Seiboth V, Herrera-Estrella A, Horwitz BA, Kenerley CM, Monte E, Mukherjee PK, Zeilinger S, Grigoriev IV, Kubicek CP (2011) *Trichoderma*: the genomics of opportunistic success. Nat Rev Microbiol 9(10):749–759. https://doi.org/10.1038/nrmicro2637

Druzhinina IS, Komoń-Zelazowska M, Ismaiel A, Jaklitsch W, Mullaw T, Samuels GJ, Kubicek CP (2012) Molecular phylogeny and species delimitation in the section *Longibrachiatum* of *Trichoderma*. Fungal Genet Biol 49(5):358–368. https://doi.org/10.1016/j.fgb.2012.02.004

Druzhinina IS, Chenthamara K, Zhang J, Atanasova L, Yang D, Miao Y, Rahimi MJ, Grujic M, Cai F, Pourmehdi S, Salim KA, Pretzer C, Kopchinskiy AG, Henrissat B, Kuo A, Hundley H, Wang M, Aerts A, Salamov A, Lipzen A, LaButti K, Barry K, Grigoriev IV, Shen Q, Kubicek CP (2018) Massive lateral transfer of genes encoding plant cell wall-degrading enzymes to the mycoparasitic fungus *Trichoderma* from its plant-associated hosts. PLoS Genet 14(4):e1007322. https://doi.org/10.1371/journal.pgen.1007322

Gao R, Ding M, Jiang S, Zhao Z, Chenthamara K, Shen Q, Cai F, Druzhinina IS, Drake HL (2020) The evolutionary and functional paradox of cerato-platanins in fungi. Appl Environ Microbiol 86(13):e00696–e00620. https://doi.org/10.1128/AEM.00696-20

Gu X, Wang R, Sun Q, Wu B, Sun JZ (2020) Four new species of *Trichoderma* in the *Harzianum* clade from northern China. MycoKeys 73:109–132. https://doi.org/10.3897/mycokeys.73.51424

Harman GE, Howell CR, Viterbo A, Chet I, Lorito M (2004) *Trichoderma* species-opportunistic, avirulent plant symbionts. Nat Rev Microbiol 2(1):43–56. https://doi.org/10.1038/nrmicro797

Hawksworth DL, Lucking R (2017) Fungal diversity revisited: 2.2 to 3.8 million species. Microbiol Spectr 5(4). https://doi.org/10.1128/microbiolspec.FUNK-0052-2016

Inderbitzin P, Robbertse B, Schoch CL (2020) Species identification in plant-associated prokaryotes and fungi using DNA. Phytobiomes J 4(2):103–114. https://doi.org/10.1094/pbiomes-12-19-0067-rvw

Jaklitsch WM (2009a) European species of *Hypocrea* Part I. The green-spored species. Stud Mycol 63(0):1–91. https://doi.org/10.3114/sim.2009.63.01

Jaklitsch WM (2009b) European species of *Hypocrea* Part I. The green-spored species. Stud Mycol 63:1–91. https://doi.org/10.3114/sim.2009.63.01

Jaklitsch WM (2011) European species of *Hypocrea* part II: species with hyaline ascospores. Fungal Divers 48(1):1–250. https://doi.org/10.1007/s13225-011-0088-y

Jaklitsch WM, Komon M, Kubicek CP, Druzhinina IS (2005) *Hypocrea voglmayrii* sp. nov. from the Austrian Alps represents a new phylogenetic clade in *Hypocrea/Trichoderma*. Mycologia 97(6):1365–1378. https://doi.org/10.1080/15572536.2006.11832743

Jaklitsch WM, Lechat C, Voglmayr H (2014) The rise and fall of *Sarawakus* (Hypocreaceae, Ascomycota). Mycologia 106(1):133–144. https://doi.org/10.3852/13-117

Jiang S-Q, Yu Y-N, Gao R-W, Wang H, Zhang J, Li R, Long X-H, Shen Q-R, Chen W, Cai F (2019) High-throughput absolute quantification sequencing reveals the effect of different fertilizer applications on bacterial community in a tomato cultivated coastal saline soil. Sci Total Environ 687:601–609. https://doi.org/10.1016/j.scitotenv.2019.06.105

Kindermann J, El-Ayouti Y, Samuels GJ, Kubicek CP (1998) Phylogeny of the genus *Trichoderma* based on sequence analysis of the Internal Transcribed Spacer region 1 of the rDNA cluster. Fungal Genet Biol 24(3):298–309. https://doi.org/10.1006/fgbi.1998.1049

Komoń-Zelazowska M, Bissett J, Zafari D, Hatvani L, Manczinger L, Woo S, Lorito M, Kredics L, Kubicek CP, Druzhinina IS (2007) Genetically closely related but phenotypically divergent *Trichoderma* species cause green mold disease in Oyster mushroom farms worldwide. Appl Environ Microbiol 73(22):7415–7426. https://doi.org/10.1128/AEM.01059-07

Kopchinskiy A, Komon M, Kubicek CP, Druzhinina IS (2005) *Tricho*BLAST: a multilocus database for *Trichoderma* and *Hypocrea* identifications. Mycol Res 109(Pt 6):658–660. https://doi.org/10.1017/S0953756205233397

Kredics L, Antal Z, Dóczi I, Manczinger L, Kevei F, Nagy E (2003) Clinical importance of the genus *Trichoderma*. Acta Microbiol Immunol Hung 50(2–3):105–117. https://doi.org/10.1556/amicr.50.2003.2-3.1

Kredics L, Garcia Jimenez L, Naeimi S, Czifra D, Urbán P, Manczinger L, Vágvölgyi C, Hatvani L (2010) A challenge to mushroom growers: the green mould disease of cultivated champignons. In: Technology and education topics in applied microbiology and microbial biotechnology, pp 295–305

Kubicek CP, Steindorff AS, Chenthamara K, Manganiello G, Henrissat B, Zhang J, Cai F, Kopchinskiy AG, Kubicek EM, Kuo A, Baroncelli R, Sarrocco S, Noronha EF, Vannacci G, Shen Q, Grigoriev IV, Druzhinina IS (2019) Evolution and comparative genomics of the most common *Trichoderma* species. BMC Genomics 20(1):485. https://doi.org/10.1186/s12864-019-5680-7

Kuhls K, Lieckfeldt E, Samuels GJ, Meyer W, Kubicek CP, Börner T (1997) Revision of *Trichoderma* sect. *Longibrachiatum* including related teleomorphs based on analysis of ribosomal DNA internal transcribed spacer sequences. Mycologia 89(3):442–460. https://doi.org/10.1080/00275514.1997.12026803

Kullnig C, Szakacs G, Kubicek CP (2000) Molecular identification of *Trichoderma* species from Russia, Siberia and the Himalaya. Mycol Res 104(9):1117–1125. https://doi.org/10.1017/S0953756200002604

Kullnig-Gradinger CM, Szakacs G, Kubicek CP (2002) Phylogeny and evolution of the genus *Trichoderma*: a multigene approach. Mycol Res 106(7):757–767. https://doi.org/10.1017/S0953756202006172

Liu YJ, Whelen S, Hall BD (1999) Phylogenetic relationships among ascomycetes: evidence from an RNA polymerase II subunit. Mol Biol Evol 16(12):1799–1808. https://doi.org/10.1093/oxfordjournals.molbev.a026092

Lücking R, Aime MC, Robbertse B, Miller AN, Ariyawansa HA, Aoki T, Cardinali G, Crous PW, Druzhinina IS, Geiser DM, Hawksworth DL, Hyde KD, Irinyi L, Jeewon R, Johnston PR, Kirk PM, Malosso E, May TW, Meyer W, Öpik M, Robert V, Stadler M, Thines M, Vu D, Yurkov AM, Zhang N, Schoch CL (2020) Unambiguous identification of fungi: where do we stand and how accurate and precise is fungal DNA barcoding? IMA Fungus 11(1):14. https://doi.org/10.1186/s43008-020-00033-z

Lutzoni F, Kauff F, Cox C, McLaughlin D, Celio G, Dentinger B, Padamsee M, Hibbett D, James T, Baloch E (2004) Where are we in assembling the fungal tree of life, classifying the fungi, and understanding the evolution of their subcellular traits. Am J Bot 91:1446–1480

Marra R, Lombardi N, d'Errico G, Troisi J, Scala G, Vinale F, Woo SL, Bonanomi G, Lorito M (2019) Application of *Trichoderma* strains and metabolites enhances soybean productivity and nutrient content. J Agric Food Chem 67(7):1814–1822. https://doi.org/10.1021/acs.jafc.8b06503

May TW, Redhead SA, Bensch K, Hawksworth DL, Lendemer J, Lombard L, Turland NJ (2019) Chapter F of the International Code of Nomenclature for algae, fungi, and plants as approved by the 11th International Mycological Congress, San Juan, Puerto Rico, July 2018. IMA Fungus 10(1):21. https://doi.org/10.1186/s43008-019-0019-1

Migheli Q, Balmas V, Komoñ-Zelazowska M, Scherm B, Fiori S, Kopchinskiy AG, Kubicek CP, Druzhinina IS (2009) Soils of a Mediterranean hot spot of biodiversity and endemism (Sardinia, Tyrrhenian Islands) are inhabited by pan-European, invasive species of *Hypocrea/Trichoderma*. Environ Microbiol 11(1):35–46. https://doi.org/10.1111/j.1462-2920.2008.01736.x

Myoken Y, Sugata T, Fujita Y, Asaoku H, Fujihara M, Mikami Y (2002) Fatal necrotizing stomatitis due to *Trichoderma longibrachiatum* in a neutropenic patient with malignant lymphoma: a case report. Int J Oral Maxillofac Surg 31(6):688–691. https://doi.org/10.1054/ijom.2001.0211

Pang G, Sun T, Yu Z, Yuan T, Liu W, Zhu H, Gao Q, Yang D, Kubicek CP, Zhang J, Shen Q (2020) Azaphilones biosynthesis complements the defence mechanism of *Trichoderma guizhouense* against oxidative stress. Environ Microbiol 22(11):4808–4824. https://doi.org/10.1111/1462-2920.15246

Persoon CH (1794) Disposita methodical fungorum. Romers Neues Mag Bot 1:81–128

Rahimi MJ, Cai F, Grujic M, Chenthamara K, Druzhinina IS (2021) Molecular identification of *Trichoderma reesei*. In: Mach-Aigner AR, Martzy R (eds) *Trichoderma reesei*: methods and protocols. Springer US, New York, pp 157–175. https://doi.org/10.1007/978-1-0716-1048-0_14

Rifai MA (1969) A revision of the genus *Trichoderma*. Mycol Pap 116:1–56

Rivera-Méndez W, Obregón M, Morán-Diez ME, Hermosa R, Monte E (2020) *Trichoderma asperellum* biocontrol activity and induction of systemic defenses against *Sclerotium cepivorum* in onion plants under tropical climate conditions. Biol Control 141:104145. https://doi.org/10.1016/j.biocontrol.2019.104145

Schoch CL, Seifert KA, Huhndorf S, Robert V, Spouge JL, Levesque CA, Chen W, List FBCA (2012) Nuclear ribosomal internal transcribed spacer (ITS) region as a universal DNA barcode marker for *fungi*. Proc Natl Acad Sci U S A 109(16):6241–6246. https://doi.org/10.1073/pnas.1117018109

Steenkamp ET, Wingfield MJ, McTaggart AR, Wingfield BD (2018) Fungal species and their boundaries matter – definitions, mechanisms and practical implications. Fungal Biol Rev 32(2):104–116. https://doi.org/10.1016/j.fbr.2017.11.002

Sun J, Yuan X, Li Y, Wang X, Chen J (2019) The pathway of 2,2-dichlorovinyl dimethyl phosphate (DDVP) degradation by *Trichoderma atroviride* strain T23 and characterization of a paraoxonase-like enzyme. Appl Microbiol Biotechnol 103(21):8947–8962. https://doi.org/10.1007/s00253-019-10136-2

Taylor JW (2011) One Fungus = One Name: DNA and fungal nomenclature twenty years after PCR. IMA Fungus 2(2):113–120. https://doi.org/10.5598/imafungus.2011.02.02.01

Taylor JW, Jacobson DJ, Kroken S, Kasuga T, Geiser DM, Hibbett DS, Fisher MC (2000) Phylogenetic species recognition and species concepts in fungi. Fungal Genet Biol 31(1):21–32. https://doi.org/10.1006/fgbi.2000.1228

Turland N, Wiersema J, Barrie F, Greuter W, Hawksworth D, Herendeen P, Knapp S, Kusber W-H, Li D-Z, Marhold K, May T, McNeill J, Monro A, Prado J, Price M, Smith G (2018) International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017. Regnum Vegetabile Volume 159. Koeltz Botanical Books. doi:https://doi.org/10.12705/Code.2018

White TJ, Bruns T, Lee S, Taylor J (1990) 38 - Amplification and direct sequencing of fungal ribosomal rna genes for phylogenetics. In: Innis MA, Gelfand DH, Sninsky JJ, White TJ (eds) PCR protocols. Academic Press, San Diego, pp 315–322. https://doi.org/10.1016/B978-0-12-372180-8.50042-1

Wu Q, Ni M, Dou K, Tang J, Ren J, Yu C, Chen J (2018) Co-culture of *Bacillus amyloliquefaciens* ACCC11060 and *Trichoderma asperellum* GDFS1009 enhanced pathogen-inhibition and amino acid yield. Microb Cell Factories 17(1):155. https://doi.org/10.1186/s12934-018-1004-x

Zachow C, Berg C, Müller H, Meincke R, Komon-Zelazowska M, Druzhinina IS, Kubicek CP, Berg G (2009) Fungal diversity in the rhizosphere of endemic plant species of Tenerife (Canary Islands): relationship to vegetation zones and environmental factors. ISME J 3(1):79–92. https://doi.org/10.1038/ismej.2008.87

Zhang J, Bayram Akcapinar G, Atanasova L, Rahimi MJ, Przylucka A, Yang D, Kubicek CP, Zhang R, Shen Q, Druzhinina IS (2016) The neutral metallopeptidase NMP1 of *Trichoderma guizhouense* is required for mycotrophy and self-defence. Environ Microbiol 18(2):580–597. https://doi.org/10.1111/1462-2920.12966

Zhang J, Miao Y, Rahimi MJ, Zhu H, Steindorff A, Schiessler S, Cai F, Pang G, Chenthamara K, Xu Y, Kubicek CP, Shen Q, Druzhinina IS (2019) Guttation capsules containing hydrogen peroxide: an evolutionarily conserved NADPH oxidase gains a role in wars between related fungi. Environ Microbiol 21(8):2644–2658. https://doi.org/10.1111/1462-2920.14575

Zhao Z, Cai F, Gao R, Ding M, Jiang S, Chen P, Pang G, Chenthamara K, Shen Q, Bayram Akcapinar G, Druzhinina IS (2021) At least three families of hyphosphere small secreted cysteine-rich proteins can optimize surface properties to a moderately hydrophilic state suitable for fungal attachment. Environ Microbiol. https://doi.org/10.1111/1462-2920.15413