

The Nature and Application of Biocontrol Microbes II: *Trichoderma* spp.***Trichoderma*: Systematics, the Sexual State, and Ecology**

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ABSTRACT

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A chronology is presented that charts the development of a genus and species concept in *Trichoderma*. Eighty-nine species of *Trichoderma* have been named, and several species of *Hypocrea* have been linked to unnamed *Trichoderma* anamorphs. Eighty-three taxa of *Trichoderma* and their teleomorphs, *Hypocrea* spp., have been included in phylogenetic analyses, including 11 species of *Hypocrea* with unnamed *Trichoderma* anamorphs. Phylogenetic analyses show that *Trichoderma* and *Hypocrea* are congeneric. *Trichoderma* species not linked to *Hypocrea* teleomorphs are derived from among species that are linked to teleomorphs, indicating sexual and asexual lineages are not independent of each other. Many more species remain to be discovered and described. Molecular phylogenetic analyses have revealed the existence of more species than have been recognized on the basis of morphology alone. A suggestion is made to modify the International Code of Botanical Nomenclature to enable

adoption of a single generic name for *Trichoderma/Hypocrea*, with *Trichoderma* being the older and more utilitarian name. As increasing numbers of species are studied, the few morphological characters of anamorph and teleomorph have reached their limit for defining species. DNA-based characters have assumed an indispensable role. Exploration of new niches, such as within tree trunks and new geographic locations, have resulted in a substantial increase in the number of species of *Trichoderma*. *Trichoderma* is usually considered a genus of free-living soil fungi but evidence suggests that *Trichoderma* species may be opportunistic, avirulent plant symbionts as well as parasites of other fungi. Members of the genus *Trichoderma* are universally present in soils, although individual species may be either cosmopolitan (e.g., *T. harzianum*) or limited (e.g., *T. viride*) in their geographic distribution. To facilitate identification of species, a list of correctly identified strains of *Trichoderma* and their GenBank numbers for sequences of translation-elongation factor EF-1 α and internal transcribed spacer rDNA is provided.

The *Trichoderma* chronology. Identification of *Trichoderma* species is notoriously difficult. The few morphological characters available are variable to some degree, leading to overlap among species; this could explain why so few species have been described over most of the life of the genus. An unfortunate result of the failure of taxonomists, until recently, to provide the basics for species identification is that strains reported in the literature may have been misidentified. Kullnig et al. (63) reidentified several strains as *Trichoderma harzianum* that had been reported in the literature under different names. How have we come to this state of species recognition, and what are we doing to improve the situation? To understand this, it is essential to review how the taxonomy of *Trichoderma* has developed. The appreciation of what constitutes a species of *Trichoderma*, or even of what constitutes the genus, has been incremental and free of a plethora of names that cannot be pinned down, or competing taxonomic systems, both of which have plagued taxonomy of other economically important genera such as *Fusarium*. Following is a summary of the highlights in this development.

Trichoderma was first proposed as a genus by Persoon in 1794 (77) on the basis of material collected in Germany. Persoon included four species and evidently had difficulty recognizing his own genus because, of the four species originally included in the genus, only one—*T. viride*—remains in *Trichoderma*. In 1865, the Tulasne brothers (99), in France, elegantly illustrated a link be-

tween *T. viride* and a sexual stage, *Hypocrea rufa*. Their illustrations are the standard of identification for this holomorph. Prior to 1969, few species were added to *Trichoderma*. Over time a few genera, each including one or a few species, were synonymized with *Trichoderma* thereby expanding the concept of the genus to include species that produced hairs and colorless (white in mass) conidia as well as characteristic species with green conidia. With this expansion in generic concept one might think that the flood gates for description of new species would have been opened, but that was not the case. In 1927, Abbott (1) only recognized four well-defined groups among the intergrading *Trichoderma* isolates from soil but distinguished only three species in a key; two of them are now considered to be synonyms of *T. viride*. In 1939, Bisby (8) expressed what probably most people feel even today: they all look the same! He was not able to distinguish between *H. rufa*, a species with colorless ascospores, and *H. gelatinosa*, a species with green ascospores. One would not think it difficult to distinguish between these two species because of the difference in ascospore colors, and the anamorph of *H. gelatinosa*, *T. gelatinosum*, is easily distinguished from that of true *H. rufa*, *T. viride*. For whatever reason, Bisby could not see the differences and the practical result was a taxonomy that reduced most of *Trichoderma* to a single species, *T. viride*. This system was in place until 1969. Needless to say, this single-species system was very popular; certainly no special skills were required to reach an identification, and only few species were added until 1969. In 1957, Dingley (31), characterizing the *Trichoderma* anamorphs of several species of *Hypocrea* in New Zealand, identified all of the anamorphs as typical of *T. viride*.

Bisby's one-species system prompted John Webster and student Mein Rifai to review taxonomy of *Trichoderma* and *Hypocrea* by examining life cycles of identified *Hypocrea* species (81,82,102,

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103). They took the approach that the addition of characters from a teleomorph would help to define *Trichoderma*. Their work culminated in the 1969 publication of Rifai's thesis (80), a groundbreaking monograph of *Trichoderma*. In this work he recognized nine aggregate species, some of which were isolated from *Hypocrea* specimens. He emphasized that his was not the last word but was rather a preliminary attempt to establish a natural and workable system based on patterns of variation in *Trichoderma* isolates, especially those derived from *Hypocrea* specimens of unquestionable identity. Further, he acknowledged that each of the "aggregate" species could comprise two or more cryptic species—a small but important detail that was largely overlooked as Rifai's work quickly became, and then remained, the unchallenged authority for *Trichoderma* for 15 years. Significantly, Rifai excluded *Gliocladium virens* from *Trichoderma* while noting that it was not *T. viride*; *G. virens*, now *T. virens*, was the name used in the first publications describing the fungistatic compounds gliotoxin and viridin in the mid-1940s (15–17).

Between 1972 and 1989, Doi monographed *Hypocrea* for Japan and published several papers describing the life cycles of tropical species of *Hypocrea*. He (36) proposed subdivisions of *Hypocrea* based on anatomy of the stroma and on the anamorph. This work remains the only overall study of *Hypocrea* and its closest relatives for a geographic region, although individual species and groups of species have been monographed recently (21,22,24–27, 32,33,68–71,89).

Between 1984 and 1992, Bissett (9–13) undertook a revision of *Trichoderma* using Rifai's work as the foundation. Essentially, Bissett viewed some of Rifai's aggregate species to be sections and, within those sections, Bissett recognized biological species. In place of nine aggregate species, Bissett (10) formally recognized four sections, of which he monographed two. Bissett rarely considered teleomorphs in his work.

In about 1995, the use of DNA sequence analysis became the new paradigm in fungal systematics and *Trichoderma* workers quickly incorporated sequence data to the developing taxonomy of *Trichoderma* and *Hypocrea*. The early work is reviewed by Lieckfeldt et al. (66). Most significant among the early publications is the demonstration that the genus *Gliocladium* is paraphyletic, comprising at least three phylogenetically and morphologically distinct groups, and that *G. virens* is a species of *Trichoderma* not *Gliocladium* (78), confirming the largely ignored new combination proposed by von Arx in 1987 (5). In 1995, Rehner and Samuels (79) demonstrated the derivation of apparently asexual fungi from within clades that include sexual fungi and that *Trichoderma* is phylogenetically indistinguishable from *Hypocrea*. Christian Kubicek and his group explored the generic phylogeny of *Trichoderma* using, first the internal transcribed spacer (ITS) region of rDNA (55), and later used multiple genes (64).

***Trichoderma*: A definition of a genus and its species and a discussion of sex.** Prior to the mid-1990s the course of evolution in fungi—phylogeny—was plotted from phenotype, cytology, physiology, ultrastructure and to a small extent fossils and so on. Cladistic analysis of phenotype data provided a powerful tool for reconstructing phylogenies in character-rich groups such as arthropods, but was slow to be adopted by mycologists because of the paucity of characters (104). DNA sequencing, which became routine in the mid-1990s, provided the great number of characters, in the form of diverging base pairs, which invite cladistic analysis. Regarding microfungi, traditional phylogenetic schemes were supported mainly by the new, independently derived sequence data (90). Before long the analysis of DNA characters came to be synonymous with phylogenetic analysis. Today, sequences of multiple genes are used to infer phylogenies of taxa at all levels and also to infer the evolution of physical traits (72). The reigning species concept, which relies on the comparison of more than one gene genealogy, is known as Genealogical Concordance Phylogenetic Species Recognition (GCPSR; 97).

The fundamental questions—what is *Trichoderma*? what are its relatives? what are its limits? how many species?—could not be answered satisfactorily with classical methods. Thanks to DNA sequencing, these questions can be answered. Of course, the link between *Trichoderma* and *Hypocrea* was known since at least the mid-19th century (99), but Rehner and Samuels (79) and subsequent authors (22,64) revealed that even *Trichoderma* species, and members of other genera not known to be linked to teleomorphs, are not distinguishable from their sexually reproducing counterparts. With additional fieldwork, a growing number of named *Trichoderma* species have been linked to *Hypocrea* teleomorphs, such as *T. harzianum*, the anamorph of *H. lixii* (24), or *T. virens*, the anamorph of *H. virens* (26). However, some common and important species such as *T. asperellum* have not been linked to a teleomorph and are apparently clonal.

A phylogenetic concept has been developed that is highly consistent with the "typical" *Trichoderma* phenotype. Most *Trichoderma* do not look very different from the stereotype of the genus: lots of powdery green conidia in fast-growing colonies. However, not all species that fall within the phylogenetic concept of the genus are morphologically typical. *T. virens* was included in *Gliocladium* because of its gliocladium-like aspect: phialides held in a penicillus, conidia held in drops of clear green, watery liquid. No true species of *Gliocladium* can be included in *Trichoderma* so *G. virens* is *T. virens* (5,78). True *Gliocladium* is a genus of fungi that occurs on bracket fungi and that has teleomorphs in *Sphaerostilbella* (92). One phylogenetic lineage within *Trichoderma* is characterized by the production of white conidia from conidiophores typical of the genus *Pachybasium* Sacc. *T. hamatum* (Link:Fr.) Rifai, the type species of *Pachybasium* is also derived from within *Trichoderma* (71). Several *Hypocrea* species have anamorphs that are anything but typical of *Trichoderma*, being acremonium- or verticillium-like with colorless conidia. *H. citrina* and its relatives, a phenotypically and phylogenetically homogeneous assemblage of species (75), are derived from within *Trichoderma* but their anamorphs are acremonium- and verticillium-like; this group includes *T. lactea* and other members of *Trichoderma* sect. *Hypocreanum*. The possibility exists that these *Hypocrea* species have lost the typical *Trichoderma* morph but have retained a spermatial morph. In at least one species of *Hypocrea*, both typical *Trichoderma* and acremonium-like morphs form (87). *H. avellanea*, a parasite of the mushroom *Collybia subnuda* in forests of eastern North America, produces a verticillium-like anamorph (20). *H. flavovirens* has a *Stilbella* anamorph (93). The common soil fungus *G. viride* (with the better known name *G. deliquescens* as a later synonym) is the anamorph of *H. lutea*, which is an undoubted species of *Hypocrea* (25). Although the anamorph of this species would not be confused with a true *Gliocladium*, it is very un-*Trichoderma*-like, and despite its phylogenetic unity with *Trichoderma*, it has never been placed nomenclaturally in the genus. Similarly, the anamorphs of *H. cinereo-flava* (*Stilbella flavipes* [93] and *H. pallida* [*Gliocladium*]) are completely inconsistent with any morphological concept of *Trichoderma*. Phylogenetic analysis shows that *H. pallida* is, in fact, not a species of *Hypocrea* and requires a new genus (78). *H. cinereo-flava* has not been included in any phylogenetic analysis, but the divergent phenotype of its anamorph suggests that it also should be excluded from *Hypocrea*.

Trichoderma is typically thought of as producing only one form of asexual spores, viz. green conidia from a single kind of conidiophore. We now know that some species produce chlamydoconidia (11,26), which are very abundant and conspicuous in *T. virens*. Chaverri et al. (22) described synanamorphs for several species of *Trichoderma* that produce their conidia from pustules. These synanamorphs form their conidia on verticillium-like or gliocladium-like conidiophores in aerial mycelium; these are morphologically quite different from the typical *Trichoderma* conidiophores that form in the same cultures. The conidia are held in drops of clear,

green liquid. When the synanamorph is formed in abundance, one could even think that the culture had become contaminated. As above, a spermatial (?vestigial) function for the synanamorphs is suggested (87).

There are few examples of *Trichoderma/Hypocrea* species undergoing sexual reproduction in vitro and, in my experience, this is a rare thing. One very well-known example, however, is of what is known in the literature as *Chromocrea spinulosa* (= *H. spinulosa*). In this species, half of the ascospore progeny were self sterile and the other half were self fertile but when the self-sterile spore progeny were paired with the self-fertile progeny, perithecia formed along a strong line contact, indicating that the two sterility types were of opposite mating types as well (73). This was explained by a mutation of nuclei in the mycelial hyphae of the self-fertile strains to the mating type of the self-sterile strains, leading to the self fertility; this phenomenon is known as mating-type switching and has been observed to occur in other unrelated fungi (76). *H. citrina* var. *citrina* and *H. citrina* var. *americana* readily produce perithecia in culture and appear to have the same type of mating system as is seen in *H. spinulosa* (18), but the mating system in these two taxa has not been studied in detail. Similarly, *H. poronioidea* produces self-fertile and self-sterile spore progeny in the ascus but perithecia did not form when self-fertile and self-sterile progeny were mated, moreover hyaline—possibly spermatial—conidia formed in close association with developing perithecia (87). The tropical species *H. jecorina*, the teleomorph of *T. reesei*, manifests a typical bipolar heterothallism with the two mating types segregating in the ascus in a 4:4 ratio (67); it is the only species known to behave this way.

Molecular phylogenetic methods have been used to test competing hypotheses about the number of species in *Trichoderma* and it is now clear that there are more rather than fewer. To date, 83 taxa (species, forms, and varieties) of *Trichoderma* and *Hypocrea* have been included in phylogenetic analyses. These include 72 named species of *Trichoderma*, 19 of which have not been linked to *Hypocrea* teleomorphs (Table 1). A summary phylogram is shown in Figure 1. Important anamorph/teleomorph links include *T. reesei*/*H. jecorina* (62), which is a primary source of cellulase enzymes, and three biological control species: *T. virens*/*H. virens* (26), *T. harzianum*/*H. lixii* (24), and *T. stromaticum*/*H. stromatica* (7). It should be noted that about 400 species of *Hypocrea* have been described in the past 200 years and only very few of them have been grown in pure culture. Doi (34–39) linked many species of *Hypocrea* to unnamed *Trichoderma* anamorphs, but his original cultures are no longer viable.

At this time a single gene is not considered sufficient to characterize species of *Trichoderma* and *Hypocrea* and new species are resolved using multiple genes, including actin, calmodulin, endochitinase, and translation-elongation factor (14,22,71). Each of the 83 species is represented in GenBank by sequences of at least the ITS region of rDNA, and most are represented by sequences of the protein-coding gene translation-elongation factor 1- α (*tef*). Although generally the ITS region is species specific, identifications based on ITS sequences must be used with caution because sometimes closely related species cannot be distinguished using this gene. This is especially true of *Trichoderma* sect. *Trichoderma*, which includes *T. viride*, where more than one species can share the same ITS sequence (70; G. J. Samuels, unpublished data). Because *tef* is more variable than the ITS rDNA, it is better able to reflect species differences within and among groups of closely related species. Unfortunately, at least three different primers have been used in *tef* studies in *Trichoderma*, making it impossible to identify unknowns by BLAST searching using a single primer (contrast 22,64,85). In our laboratory, we use the primers *efl*-728 (19) and *tef*1 rev (85), which results in a polymerase chain reaction product of approximately 600 bp, which is sequenced in both directions.

A further problem with identifying isolates by BLAST searching GenBank is the number of sequences deposited for misidentified strains. Table 1 lists correctly identified strains and their corresponding GenBank numbers for *tef* and ITS sequences. An interactive key to identification of several *Trichoderma* species based on ITS and multiple genes, including a short part of *tef*, can be found online by the International Subcommittee on *Trichoderma* and *Hypocrea* (ISTH) (41,42). Traditional keys to the most common species are available in Gams and Bissett (44), and most species are illustrated in an interactive key provided online by the Systematic Botany & Mycology Laboratory, USDA-ARS (84).

The molecular studies essentially support the morphologically based taxonomy proposed by Bissett (9–13), although the arrangement of species in morphologically defined sections is not supported and individual species may be too broadly conceived. Two of the sections that he proposed, sects. *Longibrachiatum*, which includes *T. reesei*, and *Hypocreanum*, are phylogenetically and morphologically homogeneous. Sect. *Saturnisporum* has been amalgamated with sect. *Longibrachiatum* (61,89). Sect. *Pachybasium*, which includes *T. hamatum*, *T. harzianum*, and *T. virens* along with most other species in the genus, is paraphyletic (25, 55,64), and many of the species in sect. *Pachybasium* now join *T. viride* and *T. koningii* in sect. *Trichoderma*. As more species are included in phylogenetic analyses, the sectional definitions lose their meaning and, although closely related species are typically morphologically similar, species in the same clade may have quite different morphology. Moreover, as additional species are studied, new clades are discovered (53). Currently, there is no acceptable formal subdivision of *Trichoderma* or *Hypocrea*, and as new species are added, the genus appears to become more complex. Today, only sect. *Longibrachiatum* (including sect. *Saturnisporum*) is monophyletic. Jaklitsch et al. (53) have essentially dropped reference to sections and instead have adopted a reasonable approach of giving informal names to clades and lineages.

Commonly reported species have been evaluated using molecular phylogenetic techniques. DNA sequence analysis has revealed the existence of morphological species, that is, morphologically cryptic species within phylogenetic species. Rifai (80) recognized that what he referred to as a species was often an amalgam of two or more biological species. The truth of this statement is revealed in the DNA sequence analyses. For example, the widely reported *T. viride* was known to be the only species to have warted, subglobose conidia, but now we know that at least three species share this conidial character (70,86); searching for characters beyond the conidia has revealed differences in the conidiophore that have been overlooked previously. *T. koningii* represents a conserved morphology in *Trichoderma* sect. *Trichoderma*. Phylogenetic analysis reveals that true *T. koningii* is limited in distribution. From this complex, so far two species have been described (*T. ovalisporum* and *H. stilbohypoxyli* [50]); both share the *T. koningii* morphology but differ from that species in subtle morphological characters and in characters of colonies. At least nine more species that would have been identified as *T. koningii* are known to form monophyletic lineages and remain to be described (G. J. Samuels, unpublished data). Each of these lineages shows a strong geographic bias. On the other hand, Grondona et al. (46) and Hermosa et al. (49) questioned whether *T. harzianum* represents more than one species. In response, Chaverri et al. (23) studied a wide morphological and geographic diversity of isolates using four genes. They concluded that this common, cosmopolitan species is a species complex with distinct, partly geographically defined phylogenetic lineages that lacked diagnostic morphological characters.

The subdivisions of *Hypocrea*, the teleomorph, based on the anatomy of the stroma proposed by Doi (36), have not held up either, although there is a tendency for closely related species to share sexual state to such an extent that the species can only be

TABLE 1. Correctly identified *Trichoderma/Hypocrea* species and their translation/elongation factor 1- α (EF-1 α) and internal transcribed spacer (ITS) rDNA GenBank numbers^a

Taxon (<i>T</i> = <i>Trichoderma</i> , <i>H</i> = <i>Hypocrea</i>)	DNA sequence	
	EF-1 α GenBank/strain	ITS 1+2 +5.8S GenBank/strain
<i>T. aggressivum</i> f. <i>aggressivum</i>	AF348094 ⁸⁵ : G.J.S. 99-29 AF348109 ⁸⁵ : G.J.S. 99-30	AF345950 ⁸⁵ : G.J.S. 99-29 AF345949 ⁸⁵ : G.J.S. 99-30
<i>T. aggressivum</i> f. <i>europaeum</i>	AF348098 ⁸⁵ : CBS 689.94 AF348095 ⁸⁵ : CBS 100525	AF057600 ²³ : CBS 100525
<i>H. albocornea</i>	AY937440*: G.J.S. 97-28	DQ018116*: G.J.S. 97-28
<i>H. andinensis</i>	AY956321*: G.J.S. 90-140	X93957 ⁶⁹ : G.J.S. 90-140
<i>T. asperellum</i>	AY376058 ⁵⁰ : CBS 433.97 = Tr3	AJ230669 ⁸⁶ : TR31, TR32, Tr48, TR50, G.J.S. 90-14, G.J.S. 91-1 AJ230680 ⁸⁶ : BBA 68646R AJ230668 ⁸⁶ : TR3, CBS 433.97, CBS 983.97, CBS 984.97, TR44, G.J.S. 94-81, BBA 68543, G.J.S. 91-160, G.J.S. 90-7, G.J.S. 91-162, G.J.S. 91-24 AY380912 ⁵⁰ : CBS 433.97
<i>H. atrogelatinosa</i>	AY937417*: G.J.S. 00-162	DQ023302*: G.J.S. 00-162
<i>T. atroviride</i> / <i>H. atroviridis</i>	AF348112 ³² : G.J.S. 90-134 AF348113 ³² : G.J.S. 95-108 AF348114 ³² : G.J.S. 95-10 AY376051 ⁵⁰ : CBS 142.95	AJ230666 ³² : G.J.S. 09-134 AF055212 ³² : G.J.S. 95-10 AY380906 ⁵⁰ : CBS 142.95
<i>T. aureoviride</i> / <i>H. aureoviridis</i>	AY956322*: CBS 245.63	Z48819 ⁶⁸ : CBS 245.63 AF191040 ⁶⁸ : CBS 525.63 AF194004 ⁶⁸ : CBS 103.69 AF194005 ⁶⁸ : CBS 138.79 AF194021 ⁶⁸ : IMI 138258 AF194006 ⁶⁸ : CBS 628.77 AF194016 ⁶⁸ : IMI 355906 AF194018 ⁶⁸ : IMI 311745 DQ020000*: CTR 77-155 DQ000635*: G.J.S. 04-381 AY737757*: P.C. 59
<i>H. avellanea</i>	AY937453*: G.J.S. 04-381	DQ000635*: G.J.S. 04-381
<i>T. brevicompactum</i>	AY737742*: P.C. 59	AY737757*: P.C. 59
<i>T. candidum</i> / <i>H. candida</i>	AY737726*: G.J.S. 02-76	AY737766*: G.J.S. 02-76
<i>T. catoptron</i> / <i>H. catoptron</i>	AY737738*: G.J.S. 88-70	AY737764*: G.J.S. 88-70
<i>T. ceramicum</i> / <i>H. ceramica</i>	AY937443*: DAOM 230012	AF149869 ¹⁴ : TUB F778
<i>T. cerinum</i>	AY737737*: G.J.S. 98-1	AY737762*: G.J.S. 98-1
<i>T. chlorosporum</i> / <i>H. chlorospora</i>	AY737728*: G.J.S. 94-67	AY737774*: G.J.S. 94-67
<i>T. chromospermum</i> / <i>H. chromosperma</i>	AY737732*: G.J.S. 97-237	AY737759*: G.J.S. 97-237
<i>T. cinnamomeum</i> / <i>H. cinnamomea</i>	DQ005525*: G.J.S. 95-183	AF400254 ⁶⁴ : CBS 977.69 DQ000622*: G.J.S. 89-145 DQ000623*: G.J.S. 95-96 DQ000624*: G.J.S. 95-183
<i>H. citrina</i> var. <i>americana</i>	DQ005522*: G.J.S. 94-79 DQ005523*: G.J.S. 96-191	AF400255 ⁶⁴ : CBS 976.69 DQ000626*: G.J.S. 94-79 DQ000636*: G.J.S. 96-191
<i>T. citrinoviride</i> / <i>H. schweinitzii</i>	AY937422*: DAOM 145647	Z31017 ⁶¹ : CBS 258.85 X93939 ⁶¹ : DAOM 145647 X93958 ⁶¹ : DAOM 167676 X93940 ⁶¹ : DAOM 1 ⁸⁶¹⁵² X93941 ⁶¹ : DAOM 191523 X93942 ⁶¹ : TR 85 Z82905 ⁶¹ : CBS 931.69 X48949 ⁶¹ : ATCC 24961 X93943 ⁶¹ : IMI 288111 X93944 ⁶¹ : IMI 91793 X93945 ⁶¹ : TR 98 X93959 ⁶¹ : TR 106 X93946 ⁶¹ : MVHC 6587 X93960 ⁶¹ : CBS 817.91 Z31013 ⁶¹ : CBS 818.91 X93962 ⁶¹ : G.J.S. 93-1 Z82906 ⁶¹ : G.J.S. 90-111 Z82907 ⁶¹ : IMI 235065 X93963 ⁶¹ : G.J.S. 92-8 AY737754*: P.C. 21
<i>H. costaricensis</i>	AY737741*: P.C. 21	AY737754*: P.C. 21
<i>T. crassum</i> / <i>H. crassa</i>	AY750879*: DAOM 167068 AY750892*: DAOM 167063	DQ083026*: DAOM 167068 AF011946 ⁵⁵ : CBS 336.93 AF011947 ⁵⁵ : DAOM 167063 AF011946 ⁵⁵ : DAOM 167068 AY737760*: G.J.S. 91-125 AY737763*: G.J.S. 91-93
<i>T. cremeum</i> / <i>H. cremea</i>	AY737736*: G.J.S. 91-125	AY737760*: G.J.S. 91-125
<i>T. cuneisporum</i> / <i>H. cuneispora</i>	AY737727*: G.J.S. 91-93	AY737763*: G.J.S. 91-93

(Continued on following page)

^a Superscript numbers refer to publications in which the GenBank number is cited. * Indicates new sequences deposited here using the primers *ef1*-728 (19) and *tef1* rev (⁸⁵), which results in a polymerase chain reaction product of approximately 600 bp, which is sequenced in both directions.

TABLE 1. (Continued from preceding page)

Taxon (<i>T</i> = <i>Trichoderma</i> , <i>H</i> = <i>Hypocrea</i>)	DNA sequence	
	EF-1 α GenBank/strain	ITS 1+2 +5.8S GenBank/strain
<i>T. effusum</i>	AY937419*: DAOM 230007	AF149858 ¹⁴ : DAOM 230007
<i>T. erinaceus</i>	AY750879*: DAOM 230019	DQ083009*: DAOM 230019
<i>T. estonicum/H. estonica</i>	AY737733*: G.J.S. 96-129	AY737767*: G.J.S. 96-129
<i>T. fasciculatum</i>	AY750895*: DAOM 167646	DQ087258*: DAOM 167646
<i>T. fertile</i>	AY750881*: DAOM 167161	DQ083018*: DAOM 167161
		AF011952 ⁵⁵ : DAOM 167070
		AF012002 ⁵⁵ : DAOM 195118
<i>H. flaviconidia</i>	DQ020001*: G.J.S. 99-49	DQ023301*: G.J.S. 99-49
<i>T. gelatinosus/H. gelatinosa</i>	AY737740*: G.J.S. 88-17	AY737775*: G.J.S. 88-17
<i>T. ghanense</i> including <i>T. parceramosum</i>	AY937423*: G.J.S. 95-137	Z69588 ⁶¹ : TNS-F 237181
	AY937420*: G.J.S. 99-38	Z31015 ⁶¹ : ATCC 28019 = CBS 259.85
		Z48936 ⁶¹ : DAOM 165776
		X93961 ⁶¹ : DAOM 190843
		X93947 ⁶¹ : CBS 135.79
		Z48727 ⁶¹ : NRRL 3091
<i>T. hamatum</i>	AY750893*: DAOM 167057	DQ083017*: G.J.S. 99-198
	DQ151582*: T-382 = G.J.S. 04-368	DQ151583*: T-382 = G.J.S. 04-368
<i>T. harzianum/H. lixii</i> including <i>T. inhamatum</i>	AY737729*: G.J.S. 90-22	AY737761*: G.J.S. 90-22
	AF348100 ⁸⁵ : CBS 227.95	Z68187 ⁶⁹ : CBS 273.78
	AF348101 ⁸⁵ : CBS 226.95	AJ222720 ⁸⁵ : CBS 226.95
	AF348099 ⁸⁵ : CBS 273.78	AF345948 ⁸⁵ : G.J.S. 95-81
	AF348102 ⁸⁵ : G.J.S. 95-81	AF194010 ⁸⁵ : G.J.S. 97-263
	AF348091 ⁸⁵ : G.J.S. 97-263	AF194011 ⁸⁵ : G.J.S. 97-264
	AF348103 ⁸⁵ : G.J.S. 97-264	AF194013 ⁸⁵ : G.J.S. 97-266
	AF348090 ⁸⁵ : G.J.S. 97-266	AF194015 ⁸⁵ : G.J.S. 97-268
	AF348105 ⁸⁵ : G.J.S. 97-268	AY027780 ⁸⁵ : G.J.S. 99-230
	AF348092 ⁸⁵ : IMI 359823	AY027783 ⁸⁵ : G.J.S. 99-231
	AF348107 ⁸⁵ : G.J.S. 99-230	AY027784 ⁸⁵ : G.J.S. 99-227
	AF348108 ⁸⁵ : G.J.S. 99-231	AY027781 ⁸⁵ : G.J.S. 97-265, G.J.S. 99-225
	AF348093 ⁸⁵ : G.J.S. 99-227	Z68187 ⁸⁵ : CBS 273.78
	AF348104 ⁸⁵ : G.J.S. 97-265	AF275330 ²³ : G.J.S. 98-183
		AF443919 ²³ : G.J.S. 92-100
		AF443916 ²³ : G.J.S. 94-53
		AF443925 ²³ : G.J.S. 92-61
		AF194012 ⁸⁵ : G.J.S. 97-265
		AF443914 ²³ : G.J.S. 00-06
		AF443914 ²³ : G.J.S. 00-08
		AF443913 ²³ : G.J.S. 00-18
		AF443928 ²³ : G.J.S. 00-21
		AF443912 ²³ : G.J.S. 00-22
		AF443922 ²³ : G.J.S. 00-24
		AF469188 ²³ : Harman 129522
		AF443911 ²³ : DAOM 222136
<i>T. helicum</i>	AY937416*: DAOM 230016	DQ083022*: DAOM 230016
	AY937433*: DAOM 230017	AF486021 ¹⁴ : TUB F293
		AF486021 ¹⁴ : TUB F 922
		AF486020 ¹⁴ : TUB F902
		AF486020 ¹⁴ : TUB F903
<i>T. konilangbra</i>	AY937425*: G.J.S. 96-147	DQ083021*: G.J.S. 96-147
		AF400261 ⁶⁴ : G.J.S. 96-146
<i>T. koningii/H. koningii</i>	AY376045 ⁵⁰ : G.J.S. 89-122	Z79628 ⁶⁹ : ATCC 64262, CBS 457.96, CBS 458.96, CBS 459.96, CBS 460.96, CBS 979.70, CBS 988.97, CBS 987.97, CBS 989.97
		AY380902 ⁵⁰ : G.J.S. 89-122
<i>H. lacuwombatensis</i>	AY937452*: G.J.S. 99-198	DQ083017*: G.J.S. 99-198
<i>T. longibrachiatum</i>	AY937412*: ATCC 18648 = TR 97 = CBS 816.68	Z31019 ⁶⁹ : ATCC 18648
<i>T. longipile</i>	AY937430*: DAOM 177227	AF011975 ⁷¹ , AF398493 ⁷¹ : DAOM 177227
<i>Gliocladium viride/H. lutea</i>	AY737731*: G.J.S. 89-129	AY737773*: G.J.S. 89-129
<i>T. melanomagnum/H. melanomagna</i>	AY737751*: G.J.S. 99-153	AY737770*: G.J.S. 99-153
<i>T. minutisporum/H. minutispora</i>	AY750883*: DAOM 167069	DQ083015*: DAOM 167069
<i>H. neurufa</i>	AF487670 ³³ : G.J.S. 96-135	AF487653 ³³ : G.J.S. 96-132
	AF487672 ³³ : G.J.S. 96-143	AF487654 ³³ : G.J.S. 96-143
	AF487671 ³³ : G.J.S. 87-72	
<i>T. nigrovirens/H. nigrovirens</i>	AY737744*: G.J.S. 99-64	AY737777*: G.J.S. 99-64
<i>H. novaезelandiae</i>	AY937448*: G.J.S. 81-265	DQ083019*: G.J.S. 81-265
		X93969 ⁶¹ : CBS 496.97
		X93967 ⁶¹ : ICMP 1694
		X93968 ⁶¹ : CBS 472.97
<i>T. oblongisporum</i>	AY750884*: DAOM 167085	DQ083020*: DAOM 167085
<i>H. orientalis</i>	AY937421*: CBS 243.63	X93964 ^{61,89} : G.J.S. 88-81
		X93966 ^{61,89} : ICMP 5426
		Z48935 ^{61,89} : ATCC 52326

(Continued on following page)

TABLE 1. (Continued from preceding page)

Taxon (<i>T</i> = <i>Trichoderma</i> , <i>H</i> = <i>Hypocrea</i>)	DNA sequence	
	EF-1 α GenBank/strain	ITS 1+2 +5.8S GenBank/strain
		X93965 ^{61,89} : CBS 243.63 X93929 ^{61,89} : CECT 2606
<i>T. ovalisporum</i>	AY387660 ⁵⁰ : DIS 172h = CBS 113300 AY376037 ⁵⁰ : DIS 70a = CBS 113299	AY380896 ⁵⁰ : DIS 172h = CBS 113300 AY376671 ⁵⁰ : DIS 70a = CBS 113299
<i>H. parapilulifera</i>	AY937444*: G.J.S. 91-60 AY937444*: DAOM 231930	AY241587 ⁷¹ : G.J.S. 91-60
<i>H. patella</i> f. <i>patella</i>	AY937427*: G.J.S. 91-141	AF487660 ³³ : G.J.S. 91-146 AF487658 ³³ : G.J.S. 91-141 AF487659 ³³ : G.J.S. 95-178 AF487661 ³³ : G.J.S. 96-198
<i>H. patella</i> f. <i>tropica</i>	AY937428*: G.J.S. 96-198	DQ000632*: G.J.S. 01-257
<i>H. pezizoides</i>	AY937438*: G.J.S. 01-257	AY737755*: G.J.S. 92-123
<i>T. phyllostachydis</i> / <i>H. phyllostachydis</i>	AY737745*: G.J.S. 92-123 AY391983*: G.J.S. 98-184	AY737755*: G.J.S. 92-123
<i>T. piluliferum</i> / <i>H. pilulifera</i>	AY737747*: CBS 814.68	Z488137 ¹ : CBS 814.68
<i>T. polysporum</i> / <i>H. pachybasioides</i> including <i>T. croceum</i>	AY750885*: Tr 46, DAOM 167068 AY750886*: TR 100	DQ083026*: DAOM 167068 Z488157 ¹ : CBS 860.68 AY240839 ⁷¹ : G.J.S. 86-540 AY240841 ⁷¹ : G.J.S. 80-135 AY240840 ⁷¹ : G.J.S. 88-59 AY240842 ⁷¹ : G.J.S. 90-63 AY240841 ⁷¹ : G.J.S. 89-135 AY240842 ⁷¹ : G.J.S. 90-63 AY240843 ⁷¹ : G.J.S. 90-116 AY240844 ⁷¹ : G.J.S. 90-126
<i>T. pseudokoningii</i> / <i>H. pseudokoningii</i>	AY937429*: G.J.S. 81-300	DQ083025*: G.J.S. 81-300 Z82908 ⁶¹ : DAOM 210151 X93985 ⁶¹ : ATCC 18646 X93971 ⁶¹ : CBS 432.97 X93970 ⁶¹ : CBS 583.92 X93972 ⁶¹ : ICMP 5421
<i>H. psychrophila</i>	AY737752*: Hy 8	AY74468*: Hy 8
<i>T. pubescens</i>	AY750887*: DAOM 166162	DQ083016*: DAOM 166162
<i>H. pulvinata</i>	DQ005520*: G.J.S. 91-55a DQ005524*: G.J.S. 92-127 DQ005526*: G.J.S. 92-128	DQ000627*: G.J.S. 92-128 DQ000629*: G.J.S. 91-55A DQ000631*: G.J.S. 92-127
<i>T. reesei</i> / <i>H. jecorina</i>	DQ025754*: ATCC 24449	Z31016 ⁶¹ : QM 6a Z31018 ⁶¹ : CBS 822.91, CBS 816.91 Z93950 ⁶¹ : G.J.S. 85-249 Z93951 ⁶¹ : CBS 836.91 X93952 ⁶¹ : CBS 815.91 X93953 ⁶¹ : G.J.S. 93-19 X93954 ⁶¹ : G.J.S. 93-22 X93955 ⁶¹ : G.J.S. 93-23 X93956 ⁶¹ : G.J.S. 93-24 DQ000625*: ATCC 24449
<i>T. rossicum</i>	AY937441*: DAOM 230011 AY937424*: DAOM 230010	DQ083024*: DAOM 230010 AF149857 ¹⁴ : TUB F752 AF149856 ¹⁴ : TUB F698 AF149857 ¹⁴ : TUB F718
<i>T. saturnisporum</i>	AY937414*: CBS 886.72	Z48726 ⁶¹ : CBS 330.70 X93977 ⁶¹ : ATCC 28023 X93973 ⁶¹ : CBS 335.72 X93974 ⁶¹ : CBS 886.72
<i>H. semiorbis</i>	AY737750*: DAOM 167636	AY737758*: DAOM 167636 AF011937 ⁵⁵ : CBS 244.63 AF011938 ⁵⁵ : G.J.S. 73-48
<i>T. sinensis</i>	AY750888*: DAOM 230005 AY750889*: DAOM 230004	AF486014 ¹⁴ : TUB F1058 AF486014 ¹⁴ : TUB F1047 DQ083012*: DAOM 230005 AY737771*: P.C. 8 DQ083014*: DAOM 183974
<i>T. sinuosum</i> / <i>H. sinuosa</i>	AY737743*: P.C. 8	DQ083011*: G.J.S. 99-222
<i>T. spirale</i>	AY750896*: DAOM 177714 AY750890*: DAOM 183974	Z95924 ⁶⁹ : CBS 992.97, G.J.S. 96-32 AY380915 ⁵⁰ : G.J.S. 96-32 AY380914 ⁵⁰ : G.J.S. 96-42a AY380916 ⁵⁰ : G.J.S. 96-30a
<i>H. stellata</i>	AY937445*: G.J.S. 99-222	AY737765*: G.J.S. 02-84
<i>H. stilbohypoxyli</i>	AY376061 ⁵⁰ : G.J.S. 96-42a AY376062 ⁵⁰ : G.J.S. 96-32 AY376063 ⁵⁰ : G.J.S. 96-30a	AF400263 ⁶⁴ : CBS 347.93
<i>T. stramineum</i> / <i>H. straminea</i>	AY737746*: G.J.S. 02-84	
<i>T. strictipile</i> / <i>H. strictipilosa</i>	AY937450*: DAOM 167072 AY937451*: DAOM 172827	
<i>T. strigosum</i>	AY376057 ⁵⁰ : DAOM 166121 = CBS 348.93	DQ083027*: DAOM 166121 = CBS 348.93

(Continued on following page)

distinguished on the basis of the phenotype of cultures or of the anamorph.

The phylogenetic tree for *Trichoderma* is growing. The tree shown in Figure 1, which is modified from Chaverri and Samuels (25), shows representative species. With some modification, the names of the clades follow Jaklitsch et al. (53). With this tree, one is able to see the distribution of biological properties. For example, the most common, medically important *Trichoderma* species are found in sect. *Longibrachiatum*; it is in this section where species produce cellulase in high titre (59) and only in this section are species found that can grow and sporulate at 40°C. Many biological control species are found in the harzianum-virens and viride clades, and although the production of the antifungal antibiotic 6-pentyl- α -pyrone may be widespread in *Trichoderma* (30,45,54), the characteristic coconut odor may be produced only by members of the viride clade, most notably *T. atroviride*. Trichothecene mycotoxins, which may be involved in mycotoxicoses of farm animals, are reportedly produced by a number of *Trichoderma* species (94); however, it is difficult to evaluate the reports in taxonomic terms because some of the names are of uncertain application (e.g., *T. sporulosum* and *T. lignorum*). *T. harzianum* ATCC 90237, reported to produce T2 toxin harzianum A (94), is *T. brevicompactum* and unrelated to *T. harzianum*. According to Nielsen et al. (74), the strain originally described as producing trichodermin is also *T. brevicompactum*. In a limited survey of *Trichoderma* species, they found trichothecene production only in *T. brevicompactum*, whose closest relative is *H. lutea*/G. viride (Fig. 1). Their study suffers from not having investigated *T. polysporum*, strains of which are reported to produce both trichodermin and trichodermol.

Geographic distribution of *Trichoderma* species. Although the genus *Trichoderma* is represented in soils and other organic matter

collected at all latitudes, some species are widely distributed while other species are geographically limited in their distribution. Based on my own observations, *T. polysporum* and *T. minutisporum* are species of cooler lands. The name *T. viride*, as mentioned above, refers to a morphological species; true *T. viride* is a rather uncommon species of cooler northern regions. The same can be said for the widely reported *T. aureoviride*, which seems to be limited to the United Kingdom and northern Europe (68). The numerous reports of *T. pseudokoningii* in the literature imply a wide distribution for the species but Turner et al. (100) found it to be an Australasian species. *T. reesei*, the species best known for the commercial production of cellulase enzymes, was until recently known only from a single culture isolated from canvas material in the Solomon Islands of the Pacific region. We now know that this is the anamorph of *H. jecorina* (62), a species that is limited in its distribution to a narrow Equatorial band, and we have isolated it directly from natural substrata in Brazil and French Guiana (67). *T. stromaticum* (88) has perhaps the most restricted distribution of any species in the genus; it is found only in tropical America and then in association with cacao (*Theobroma cacao*) trees or with the pathogen that causes witches' broom of cacao, *Crinipellis perniciosus* (= *Moniliophthora*; 2). *T. stromaticum* is effective in control of this disease (91). Turner et al. (100) observed that *T. longibrachiatum* was found in North and South America, Europe, Africa, and India but not in Southeast Asia or Australasia, while the closely related *T. citrinoviride* is found in North and South America, Europe, Southeast Asia, and Australasia but not in Africa and India. Some species of *Trichoderma* such as *T. harzianum* (23) and *T. asperellum* (G. J. Samuels, personal observation) are truly cosmopolitan.

***Trichoderma* in the environment.** The ecology of *Trichoderma* was reviewed in Klein and Eveleigh (56). *Trichoderma*

TABLE 1. (Continued from preceding page)

Taxon (<i>T</i> = <i>Trichoderma</i> , <i>H</i> = <i>Hypocrea</i>)	DNA sequence	
	EF-1 α GenBank/strain	ITS 1+2 +5.8S GenBank/strain
<i>T. stromaticum</i> / <i>H. stromatica</i>	AY937418*: G.J.S. 97-183	Z95926 ⁶⁹ : TR75
	AY937434*: G.J.S. 97-179	Z95926 ⁶⁹ : CBS 993.97
	AY937436*: G.J.S. 00-108	AF098287 ⁸⁸ : G.J.S. 97-179
	AY937447*: G.J.S. 97-181	AF097913 ⁸⁸ : G.J.S. 97-183
		AF097910 ⁸⁸ : G.J.S. 97-181
<i>H. sulawesensis</i>	AY737730*: G.J.S. 85-228	AF097912 ⁸⁸ : G.J.S. 97-182
	AY737734*: G.J.S. 88-73	AF097911 ⁸⁸ : G.J.S. 97-180
	AY737739*: G.J.S. 97-174	AF098287 ⁶⁴ : CBS 101875
	AY737748*: G.J.S. 97-61	DQ083013*: G.J.S. 00-108
	AY737735*: G.J.S. 95-135	AY737753*: G.J.S. 85-228
	AY750882*: DAOM 178713a	AY737769*: G.J.S. 88-73
	AY937415*: DAOM 230013	AY737756*: G.J.S. 97-174
	AY937446*: DAOM 230014	AY737772*: G.J.S. 97-61
		AY737776*: G.J.S. 95-135
		DQ085432*: DAOM 178713a
<i>T. virens</i> / <i>H. virens</i> including <i>T. flavofuscum</i>	AY750894*: G.J.S. 01-287	AF149873 ¹⁴ : TUB F784
	AY750891*: DAOM 167652	AF149873 ¹⁴ : TUB F801
		DQ083010*: DAOM 230014
		DQ083023*: G.J.S. 01-287
		AF099006 ⁶⁴ : Gli 3
		AF099007 ⁶⁴ : Gli 20
		AF099005 ⁶⁴ : AF222865, CBS 249.59
		AF328552 ²⁶ : G.J.S. 95-194
		AF099008 ⁶⁴ : Gli 21
		AY737768*: P.C. 278
<i>H. virescentiflava</i>	AY376052 ⁵⁰ : CBS 240.63	AJ230678 ⁸⁶ : ATCC 28020
	AY376053 ⁵⁰ : CBS 101526	X93986 ⁸⁶ : TR 8
	AY376054 ⁵⁰ : ATCC 28038	X93978 ⁸⁶ : AF127150, ATCC 18652
	AY937413*: CBS 439.95	AJ230678 ⁸⁶ : G.J.S. 91-62, BBA 770238, G.J.S. 92-14,
	AY937449*: ATCC 28020	G.J.S. 92-15
		X93980 ⁸⁶ : G.J.S. 89-127
		AY376052 ⁵⁰ : CBS 240.63
		AY380908 ⁵⁰ : CBS 202526
		AY380909 ⁵⁰ : ATCC 28038

species have long been known to be soil fungi, and they are certainly common in all soils (47,83,105–107). More recently, they have been found in water-damaged building materials or indoor dust (98) and in hospitals (29), and may adversely affect human health (65,96). *Trichoderma* species have been involved in several cases of invasive infections of immunocompromised

humans (29,57,60) and in allergic reactions (52), the most common being *T. longibrachiatum* (29) and *T. citrinoviride* (60). *T. longibrachiatum* and *T. citrinoviride* are closely related members of *Trichoderma* sect. *Longibrachiatum* and are able to grow and sporulate well at 40°C (89), which may explain their dominance in clinical settings.

Neighbor-Joining
RPB2 + TEF

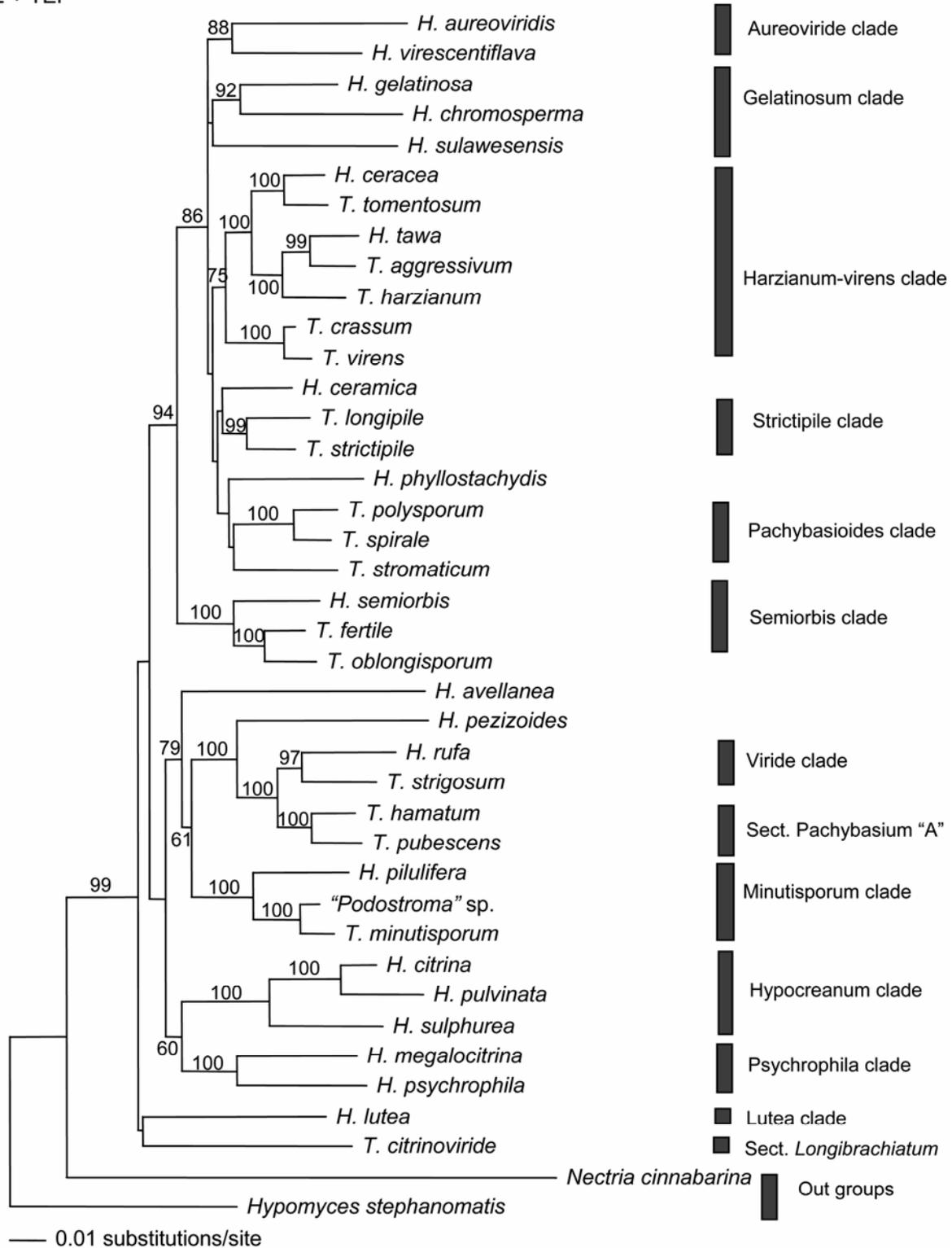


Fig. 1. Neighbor-joining tree with combined RPB2 and EF-1 α data sets. Numbers at branches represent bootstrap values based on 1,000 replicates.

Trichoderma species are considered now to be opportunistic, avirulent plant symbionts (48). These fungi may invade the first few layers of the root hairs and stimulate resistance to attack by pathogens either locally, in the roots, or at a distance. The ability of some *Trichoderma* species to induce resistance to fungal parasites in crops considerably augments their arsenal, beyond mycoparasitism (28), antibiosis (51), and plant-growth stimulation in general (6).

Typically, *Trichoderma* species are thought of as being soil fungi, but Evans et al. (43) discovered many *Trichoderma* species and other soil fungi such as *Clonostachys*, *Fusarium*, and *Cylindrocarpon* as well as unidentified basidiomycetes existing as endophytes in healthy tree bolls and pods of the cacao relative *Theobroma gileri*. This contrasts to the endophytes of leaves of *Theobroma cacao*, and other tropical tree species, which are dominated by ascomycetous fungi that sporulate on above-ground parts of plants such as *Xylariaceae*, *Colletotrichum*, *Botryosphaeria* (3), and many others (see references in Evans et al. [43]). The only study that I know of that enumerates specifically stem endophytes of a tree is Evans et al. (43). On the basis of this one report, it is impossible to say that there is a general trend among plants for soil fungi to occur as endophytes in stems and for foliar/twig fungi to occur as endophytes in leaves, but the possibility is intriguing. The species of *Trichoderma* most commonly isolated from stems of *Theobroma* species is *T. harzianum*, which is also the most common species in the genus. Smaller numbers of named *Trichoderma* species, such as *T. spirale* have been found too, but several endophytic species remain to be described (G. J. Samuels, unpublished data).

Can endophytic fungi be utilized in biological control against plant disease? There is a wealth of literature affirming this possibility in grasses but little work has been done with other types of plants. A mixture of foliar endophytes introduced into mature leaves of cacao (*Theobroma cacao*) gave localized protection from infection by a *Phytophthora* species, but there was no evidence of systemic resistance to the pathogen (4). Bryan Bailey and Ron Collins (*personal communication*) have established endophytic colonization of shoots and leaves of tomato and cacao seedlings with the cosmopolitan soil species *T. asperellum*; early results suggest that those seedlings resist infection by the cacao pathogen *Crinipellis pernicioso*. It also has been possible to reintroduce *Trichoderma* stem endophytes into cacao seedlings (43,50; T. Gianfagna, *personal communication*). Two of them, both undescribed species, inhibit *in vitro* growth of the serious cacao pathogen, *Moniliophthora roreri* (the cause of frosty pod rot disease of cacao; K. Holmes, T. Gianfagna, and C. Suarez, *personal communication*); *in vitro* and in planta both produce nonanoic acid and 6-pentyl- α -pyrone (M. Aneja and T. Gianfagna, *personal communication*), compounds known to inhibit germination of spores of plant-pathogenic fungi (95,101). The production of these metabolites in plants must contribute to induced host resistance to disease. Two additional endophytic species, *T. ovalisporum* (50) and *Trichoderma* sp. nov. (G. J. Samuels, R. Bateman, K. Holmes, and C. Suarez, unpublished data), have demonstrated *in vitro* ability to parasitize the pseudostroma of *M. roreri*. The first field trials with *T. ovalisporum* indicate promise in protecting pods of *Theobroma cacao* from infection by *M. roreri* (K. Holmes and R. Bateman, *personal communication*).

Most species of *Trichoderma* are not specific as to substratum, although some *Hypocrea* species are, including *H. latizonata* on birds nest fungi, *H. pulvinata* on bracket fungi, and *H. avellanea* on *Collybia subnuda*. These *Hypocrea* species, however, do not produce typical *Trichoderma* anamorphs. *T. stromaticum* and its teleomorph, *H. stromatica*, mentioned above, are unusual in that they are found only in association with *Theobroma* species in tropical America. *T. stromaticum* was originally found on brooms on *Theobroma cacao* caused by *Crinipellis pernicioso* (88). Since

then it has been isolated as an endophyte of *Theobroma cacao* (G. J. Samuels, unpublished data). No doubt additional host-specific species will be found.

Some things to expect. The discovery of *Trichoderma* species as endophytes of cacao and cacao relatives suggests a potential for protecting crop plants against attack by pathogens through induced resistance, antibiosis, or both. In addition, endophytic fungi will be found to produce many novel, biochemically and medically important metabolites.

Many *Trichoderma* species are known under two names, viz. the name of the *Trichoderma* anamorph and that of the *Hypocrea* teleomorph (e.g., *H. lixii*, the teleomorph of *T. harzianum*; Table 1). That these two names represent a single life cycle, one organism, is obvious and one might question whether two names for one organism are necessary. With the use of molecular tools, it is possible to recognize the relationship between anamorphs and teleomorphs to combine morphologically disparate parts of a single life-cycle. Because *Trichoderma* with and without *Hypocrea* teleomorphs consistently cluster in a single, well-supported clade, there is no doubt that they are the same genus (25). There is a movement in the taxonomic mycology community to adopt "one fungus/one name", but the mechanism for achieving that goal is not clear. Under the current International Code of Botanical Nomenclature (Art. 59), the correct name for the whole organism (the "holomorph" under any single-name scheme) would be *Hypocrea*, the name of the sexual stage. One way would be to modify or delete Art. 59, so as to enable the names of anamorph and teleomorph to compete on priority (date of publication). Under this scenario, *Trichoderma* (1794) is older than *Hypocrea* (1825) and would thus be the accepted name of the holomorph regardless of whether a sexual stage was produced or not. In 6 years, when the next botanical congress will take place and changes to the International Code of Botanical Nomenclature will be considered, it is likely that moves toward one fungus/one name will be made.

Over the past 35 years, the number of named *Trichoderma* species has increased from nine aggregate species to about 80 phylogenetic species. *Trichoderma* is now in a discovery phase; as new niches and new geographical regions are explored, many new species of *Trichoderma* will be discovered (58). The development of molecular tools has enabled the positive identification of any strain and the development of a phylogenetic tree. We are now able to account taxonomically for a significant component of the biological diversity of soil, predict biological activity, and communicate results through the use of accurately determined names. Identification of *Trichoderma* species, and most likely species in other economically important and species-rich genera, will rely on DNA sequence data as the limits of phenotype to distinguish species are reached.

Many activities of humankind interface with *Trichoderma*. The genus is widely regarded as completely benign, but the negative aspects of some members of this genus in human and animal health are significant and should not be overlooked—as is the case with any mold. For example, one should consider seriously whether it is safe to use *T. longibrachiatum* in biological control because this species can grow and sporulate at human body temperature and thus may pose a risk to individuals who apply it. However, most species and activities of *Trichoderma* species are beneficial for the enzymes that they produce, for their plant growth promoting activities, and in biological control of plant diseases. *Trichoderma* species represent a major component of the diversity of Life on Earth. The numbers, diversity, roles, and interactions of *Trichoderma* species in the environment are only now being revealed. Many new species will be found, and processes will be unraveled for well-known and those yet-to-be-discovered members of this fascinating genus of molds.

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Errata

Corrections to the following errors or deletions were made to this manuscript on March 16, 2006. On page 196, the type of *Pachybasium* is *T. hamatum*. On page 201, it is *Trichoderma pseudokoningii* that has an Australasian distribution, not *T. koningii*; *T. koningii*, a species reported to have a wide geographic distribution actually has a limited, north temperate distribution. On page 201, the incomplete sentence has been corrected as follows: “*T. reesei*, the species best known for the commercial production of cellulase enzymes, was until recently known only from a single culture isolated from canvas material in the Solomon Islands of the Pacific region. We now know that this is the anamorph of *H. jecorina* (62), a species that is limited in its distribution to a narrow Equatorial band, and we have isolated it directly from natural substrata in Brazil and French Guiana (67).” On page 203, the genus *Trichoderma* was first published by Persoon in 1794.