Mycoparasites on the coffee rust in Mexico

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We surveyed coffee plantations for mycoparasites of the coffee rust (*Hemileia vastatrix*) in central Veracruz, México. We report the presence in natural conditions of six mycoparasites. Five are reported for the first time (*Acremonium byssoides*, *Calcarisporium arbuscula*, *C. ovalisporum*, *Sporothrix guttuliformis*, *Fusarium pallidoroserum*) as mycoparasites of *H. vastatrix*, the other species, *Verticillium lecanii*, had been previously reported.

Key words: coffee rust, *Hemileia vastatrix*, Hyphomycetous anamorphs, mycoparasites.

Introduction

A variety of fungicolous fungi (i.e. fungi associated to other fungi) have been found in nature, either as parasites, commensals or saprobes (Hawksworth *et al.*, 1995). The term hyperparasite is considered obsolete by some authors, however, it has served to describe the parasitic interaction between fungi (usually a primary parasite) (Issac, 1992). Mycoparasitism, which is quite common in nature, has received special attention due to the search for biological control alternatives for diseases such as powdery and downy mildews (Hijwegen, 1988, 1992; Hijwegen and Dirven, 1993).

The coffee rust *Hemileia vastatrix* Berk. & Br. has been the most devastating disease of coffee cultivars (*Coffea arabica*). It was first detected in the American Continent (Brazil) in 1971, reaching the México-Guatemala border ten years later (Schieber and Zentmyer, 1984), and, despite all the efforts to control its dispersal, it is now present throughout Mexico's coffee regions. The mycoparasitic fungi reported as parasites on the coffee rust are *Verticillium lecanii* (Zimm.) Viégas (Madagascar, Brazil), *V. psalliotae* Treschow (Congo, Malaysia), *Aphanocladium meliolae* (Hansf.) W. Gams (Ghana), and *Cladosporium hemileia* Steyaert (Congo) (Steyaert, 1930; Gams, 1971; Lim and Nik, 1983). The first report for Mexico of the coffee rust-*Verticillium lecanii* association was made in 1985, and it is mainly present

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during the Autumn and Winter months (Carrión, 1988). The efficiency of *V. lecanii* as a parasite of the coffee rust has been experimentally tested both in the laboratory and in the field (Carrión and Ruiz-Belin, 1988; Alarcón and Carrión, 1994; Romero and Carrión, 1995; Carrión *et al.*, 1999).

Here we present a description of the mycoparasites of *H. vastatrix* (Figs. 1, 2) found between the altitudes of 150 m and 1700 m in coffee plantations in central Veracruz, México. These mycoparasites are all Hyphomycetous anamorphs (*Acremonium*, *Calcarisporium*, *Fusarium*, *Sporothrix* and *Verticillium*). We evaluated the growth during 10 days of all species (5 repetitions) in PDA (agar, dextrose and potato), under room temperature (21 ± 3 °C). Samples of all fungi studied are deposited in the Herbarium XAL of Instituto de Ecología, A.C., and the strains obtained are deposited in the collection of the Departamento Hongos of Instituto de Ecología, A.C., which is registered in World Data Centre for Microorganism 782 (IE).

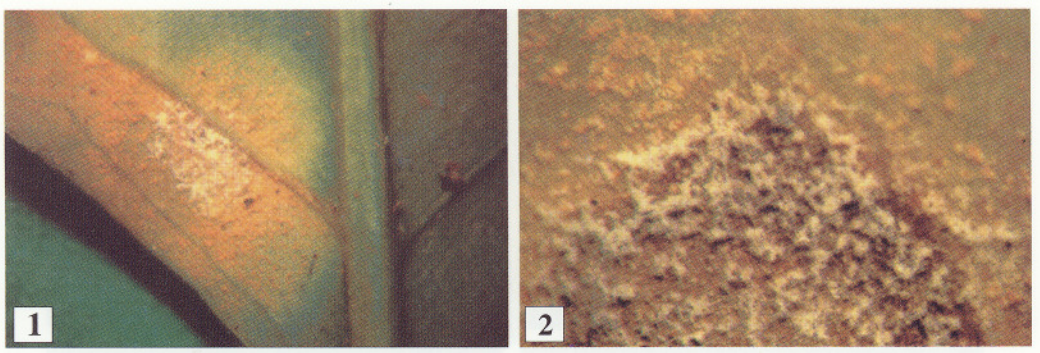
Taxonomy

Acremonium byssoides W. Gams & Lim, Transactions of the British Mycological Society 64: 389-404 (1975). (Figs. 3, 4)

Mycelium on groups of rust sori abundant, floccose, cottony-white when young and creamy when older, slightly raised at the centre, consistency slightly gelatinous to cartilaginous, deforming the PDA, growth rate 25-50 mm after 10 days. Vegetative hyphae thin-walled, fasciculate, chondroid 1.2 µm wide. Sporulation nematogenous to plectonematogenous. *Conidiogenous cells* simple or branched, septated, 16-31 µm long, at the base 1-1.6 µm and 0.4 µm at the tip, smooth wall. *Conidia* in slimy heads, hyaline greenish, ellipsoidal, apiculate base, apex slitghly rounded-truncate, irregularly guttulated 2-3.2 × 1-1.6 µm.

Material examined: MEXICO, Veracruz, Mpio. Coatepec, south of Coatepec, 26 Mar. 1987, Carrión 914b; Mpio. Emiliano Zapata, road Chavarrillo-Monte Oscuro, El Tizal, 25 Mar. 1998, Carrión 1997, strain IE-300; 23 Feb. 1999, Carrión 2082; Mar. 1999, Carrión 2095; Mpio. Xico, road to Cascada Texolo, 25 Mar. 1998, Carrión strain IE-301; Mpio. Catemaco, road Catemaco-Sontecomapam, 24 Nov. 1999, Carrión IE-377; around Laguna Escondida, 24 Nov. 1999, Carrión strain IE-378.

Acremonium byssoides is probably a ground dweller from where it then infects the uredinia of *H. vastatrix*. An *Acremonium* sp. has been isolated from coffee plantation soil in Nyasaland (Siddiqi, 1964); however, it was not found on roots, branches, leaves or fruits, and not reported as pathogenic on coffee. *Acremonium zonatum* has been reported as a parasite of coffee leaves, however, this species is clearly defined by its distinctive zonal leaf spot, which is not present on rust sori infected by *A. byssoides* (Hawksworth, 1976). Our



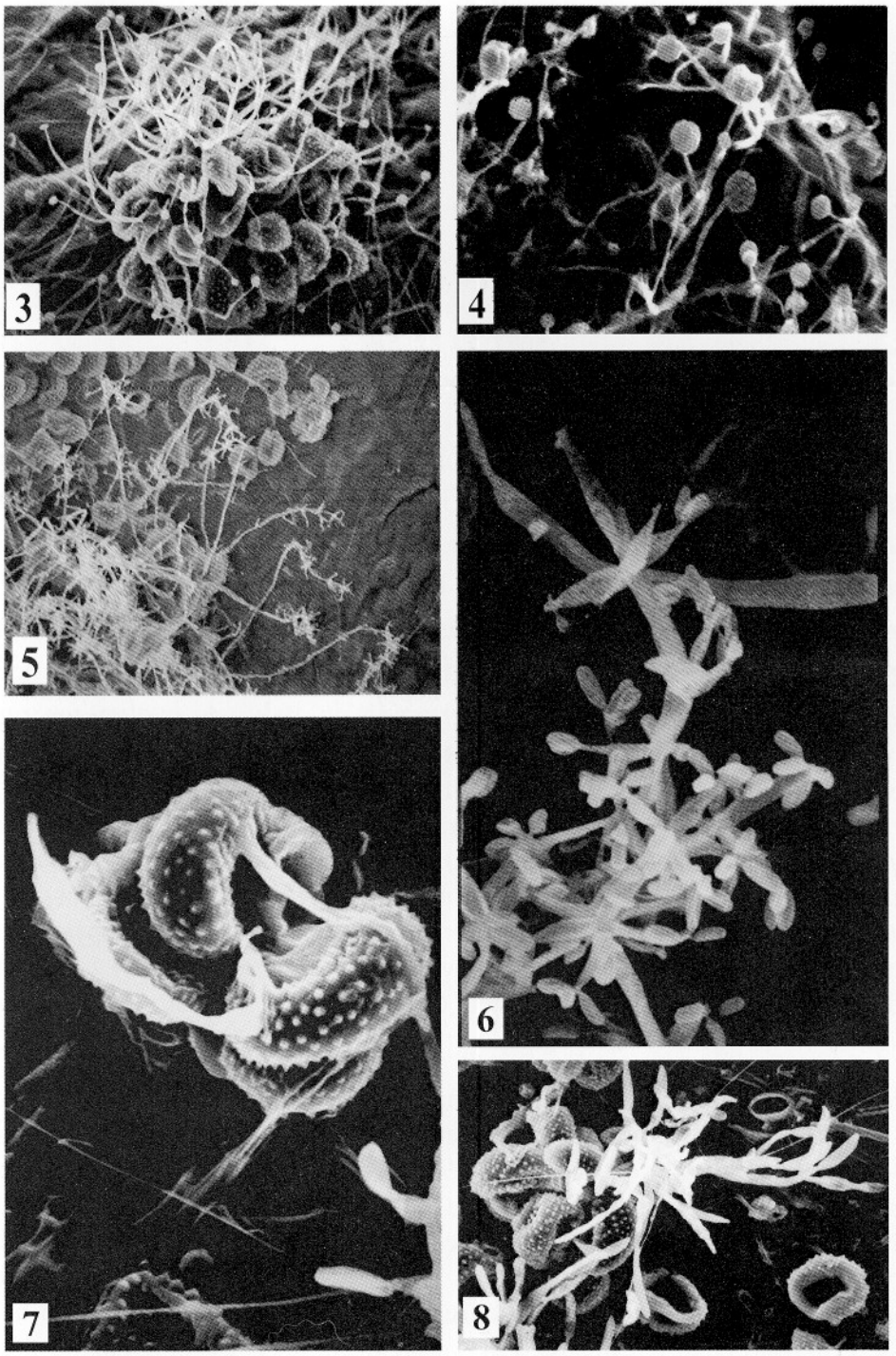
Figs. 1, 2. *Hemileia vastatrix*. **1, 2.** Sori with mycoparasites.

material is similar to that registered on *Oidium heveae*, a parasite of *Hevea brasiliensis* Muell.-Arg. in Malaysia (Gams, 1975). Other *Acremonium* species have also been reported on fungi, e.g., *A. acutatum* on *Cercospora atromarginali*, a parasite of *Solanum nigrum*, and *Acremonium ansfordii* on *Periconia cookei*, which lives on dead bamboo shoots in India. Several *Acremonium* species have been registered on Uredinales (Gams, 1971). *Acremonium terricola* on *Puccinia graminis* in Italy, *A. hyalinulum* on *P. heterospora* in the Philippines, and *A. sclerptogenum* on *P. rubigo-vera* in Braunschweig. Gams (1971) also reported 12 *Acremonium* species as mycoparasites of *Colletotrichum*, *Tubercularia* (Deuteromycetes), *Appendiculella* (= *Irenina*, Meliolales), *Ceratocystis*, *Corynespora*, *Daldinia*, *Diatrype*, *Hypoxylon*, *Nectria* and *Parodiella* (Ascomycetes), and *Armillariella*, *Fomes*, *Gymnopilus*, *Heterobasidion*, *Inonotus*, *Polyporus* and *Trametes* (Basidiomycetes). Finally, two *Acremonium* species, *A. alternatum* and *A. strictum*, have been reported on the powdery mildew *Sphaerotheca fuliginea* (Hijwegen, 1992).

Calcarisporium arbuscula Preuss, Linnaea 24: 124. 1851.

Mycelium white when young and greyish-pink when mature with a woolly-felty texture, growth rate 25-29 mm after 10 days. Vegetative hyphae hyaline 1.6-2.4 µm wide, thin-walled. Conidiophores erect, hyaline, 290-300 × 1-2 µm, verticillate with 3-9 verticil groups, distance between verticils variable, 10-20 µm, each verticil with (2-)4(-7) conidiogenous cells. *Conidiogenous cells* exhibiting progressive plagiotropic growth, wide at the base (10-)14-17 × 2 µm, with a variable number of denticles 4-8(-12), sympodial growth, denticles 2-3 µm long, when young and 6-13 µm long when mature. *Conidia* hyaline obovoidal to fusiform, thin-walled, smooth (3-)5(-7) × 2-3 µm.

Material examined: MEXICO, Veracruz, Mpio. Zongolica, road Zongolica-Nepopoalco, 23 Nov. 1999, Carrión strain IE-379.



Figs. 3-8. *Acremonium byssoides*. **3.** Coffee rust sorus covered by hyphae and conidophores, 500×. **4.** Conidiophores, 1500×. *Calcarisporium ovalisporum*. **5.** Conidiophores emerging from sorus 1000×. **6.** Conidiogenous cell showing traces of where spores are produced, 2000×. *Fusarium pallidoroseum*. **7.** Mycelium and the formation of a secondary conidium, 1500×. **8.** Rust sorus covered by the mycoparasite, 500×.

Two species are known for this genus, *Calcarisporium arbuscula* and *C. ovalisporum*, and both have been reported as parasites of higher Basidiomycetes and Ascomycetes. *Calcarisporium arbuscula* is the type species of the genus (de Hoog, 1974, 1978). Differences between both *Calcarisporium* species are based on the larger size of all structures in *C. arbuscula*. This fungus has been reported on *Sphaerotheca fuliginea* (cucumber powdery mildew), and its glycolytic activity has been studied in detail as it greatly affects the health of the conidiophores of *S. fuligenea* (Hijwegen, 1992; Hijwegen and Verhaar, 1993).

Calcarisporium ovalisporum (Petch) de Hoog, Persoonia 10: 76-77 (1978). (Figs. 5, 6)

≡ *Cladobotryum ovalisporum* Petch, in Transactions British Micologycal Society 16: 23 (1932).

Mycelium yellowish-white cottony, growth rate 33-49 mm after 10 days. It forms a cottony layer on the sori, which appear farinose at sporulation. Vegetative hyphae 2-3 µm wide. *Conidiophores* erect, hyaline 40-170 × 1-3 µm, verticillate with 2-4 verticil groups, distance between verticils variable 16-33 µm, each verticil with 1-4 conidiogenous cells. *Conidiogenous cells* (1-5), 6-12 × 1-1.5 µm, conidiogenous scars 2-2.5 µm. *Conidia* hyaline, unicellular, smooth, thin-walled, ovoid, navicular or fusiform, base acuminate, apex rounded (2-)3(-4) × (1-)2(-3) µm.

Material examined: MEXICO, Veracruz Mpio. Coatepec, coffee plantation at the south of Coatepec, 26 Mar. 1987, Carrión 914e; road Coatepec-Mahuixtlán, 3 Oct. 1995, Carrión strain IE-320; Mpio. Emiliano Zapata, road Chavarrillo-Monte Oscuro, El Tizal, 26 Feb. 1998, Carrión 1972; 25 Mar. 1999, Carrión strain IE-322; Mpio. Xico, road Cascada Texolo, 30 Oct. 1995, Carrión strain IE-321; 26 Jan. 1999, Carrión strain IE-326.

Even though both *Calcarisporium* species were found associated with the coffee rust, *C. ovalisporum* was more common. This species had not been reported previously as a mycoparasite of Uredinales, although it had been reported growing on *Hirsutella citriformis*, an entomopathogenic fungus growing on the brown planthopper, *Nilaparvata lugens* (Stål) brown (Rombach and Roberts, 1987).

Fusarium pallidoroseum (Cooke) Sacc. (Figs. 7, 8)

= *Fusarium semitectum* Berk. & Rav. in Berkeley, Grevillea 3: 98, 1875.

Mycelium growth rate 50 mm after 8 days, pinkish white under cultivation, sometimes reddish-white, changing from yellowish, peach, avellaneous to buff brown. Granulous texture on the sori, sometimes slightly pink. *Conidiomata* are sporodochia and are grouped in older cultures. *Conidiogenous cells* polyblastic, sympodial, 8-18 × 2.4-3.2 µm. *Conidia*

primary and secondary, curved, cuneiform, basal cell lacking pedicel, 3-7 septa, those with 3-5 septa 21-31 × 3-4 µm, those with 5-7 septa 36-48 × 3-4 µm. *Chlamydospores* intercalary, smooth or roughened, abundant, forming chains.

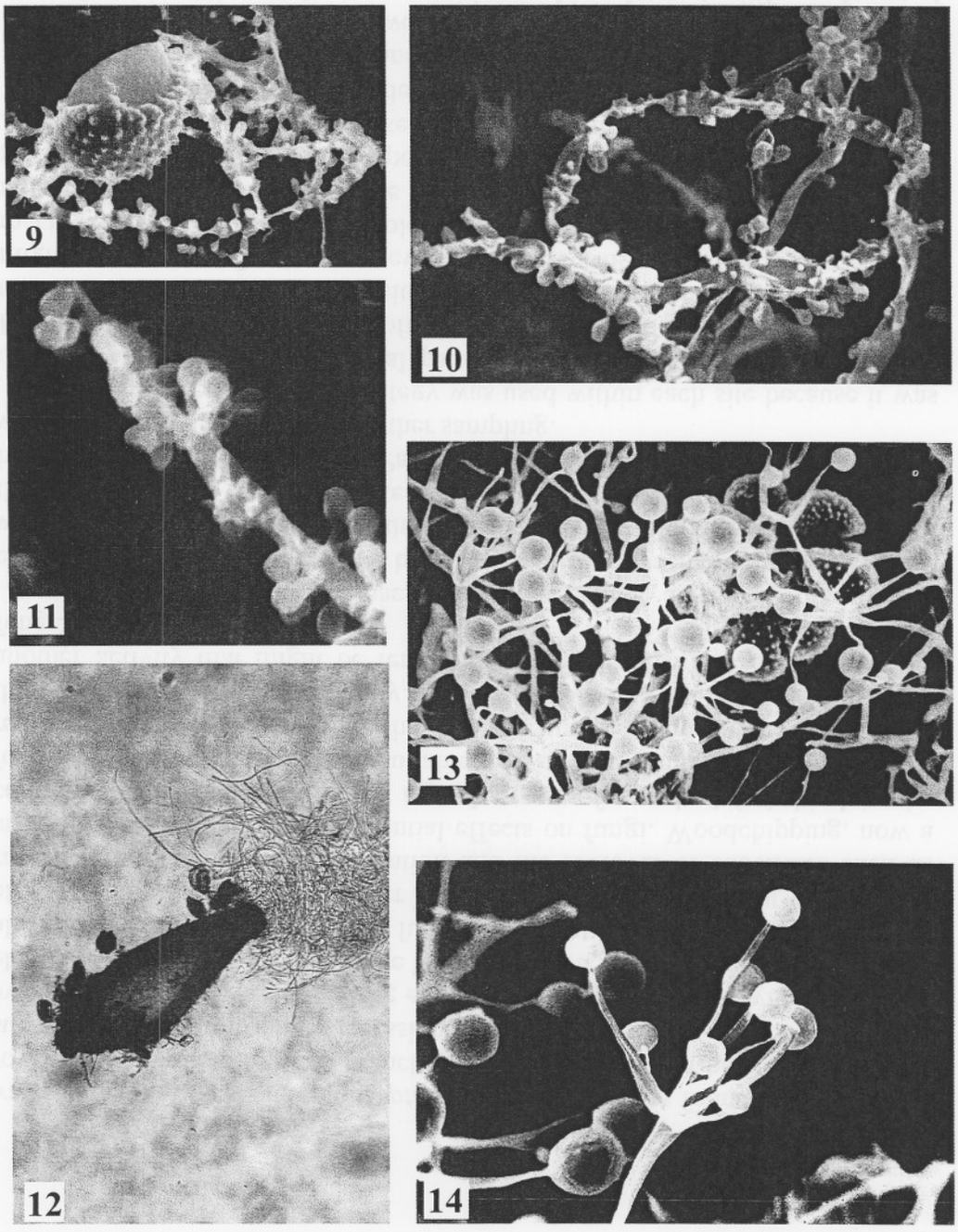
Material examined: MEXICO, Veracruz, Mpio. Coatepec, south of Coatepec, 26 Mar. 1987, Carrión 914c; Mahuixtlán, 30 Oct. 1995, Carrión strain IE-346; Mpio. Emiliano Zapata, road Chavarrillo-Monte Oscuro, El Tizal, 15 Mar. 1998, Carrión 1996; 23 Feb. 1999, Carrión strain IE-340, 25 Mar. 1999, Carrión 2092; Mpio. Xico, road Cascada Texolo, 26 Feb. 1998, Carrión 1973; 25 Mar. 1998, Carrión 1989b; 12 Nov. 1998, Carrión 2071.

This fungus has been recorded on leaves of *Chenopodium*, *Phytolacca* and the petioles of *Musa* (Booth and Sutton, 1984), on living leaves of *Brassica oleracea* var. *capitata* and *Mangifera indica*, on fallen leaves of *Pseudolmedia spuria*, on fruits of *Lycopersicon esculentus*, on basidiomata of *Pleurotus* sp., and as a parasite of *Phytium ultimum* (Castañeda Ruiz and Rodríguez de la Rosa, 1988; Hoch and Abawi, 1979). *Fusarium pallidoroseum* has recently been proposed as a biological control agent of *Mimosa invisa*, a weed of rice fields in the Philippines (Mabbayad and Watson, 2000). It had not been reported previously as a mycoparasite of Uredinales. The pink coloration is not evident on the sori when leaf necrosis begins. Species of *Fusarium* (Section Episphaeria, teleomorphs *Nectria*) had been found before associated with fungi (Booth, 1971) but not with rusts. The number of septa of *F. epistromum* (1-3) does not coincide with the description of this fungus and the spores differ in size (16-27 × 2.4-4 µm). The conidiophores of *F. merismoides* can be lateral phialides and polyphialides and spores of that species are very large (30-45) × (3.5-5) and 40-54 × 4-5 µm, with 3-4 septa.

Sporothrix guttuliformis de Hoog, Persoonia 10: 62-63 (1978). (Figs. 9-11)

Mycelium white, cottony-floccose, growth rate 30-40 mm after 10 days. Viewed from the bottom of the Petri dish, it is yellowish at the center. Exudate and odour absent. The mycelium is clearly defined as cottony-white marks on the sori of the coffee rust, making a striking contrast against the yellow of the uredinia. Vegetative hyphae hyaline. *Conidiophores* semi-macronematose, filiform, 36-124 × 1.5-2 µm. *Conidiogenous cells* integrated, polyblastic, intercalary or terminal, 2.5-5 × 1.5-2.5 µm, denticulate, scars 1-9 per cell, branching orthotropic, most frequently 3 scars, light when young, prominent when mature, less than 0.5-2 µm. *Conidia* guttuliform, smooth, thin-walled, hyaline, hilum inconspicuous, 1.5-2.5 × 1-2 µm, single, in short chains or ramo-conidia.

Material examined: MEXICO, Puebla, Mpio. Tlapacoya, Ahuacatlaya,14 Mar. 2000, Carrión 2165, strain IE-394; Mpio. Tlacuilotepec, San Pedro Petlacotla, road Huauchinango-Poza Rica, 15 Mar. 2000, Carrión 2176. Veracruz, Mpio, Coatepec, road Coatepec-Mahuixtlán, 7 Aug. 1995, Carrión strain IE-358, road Coatepec-San Marcos, 3 Oct. 1995, Carrión strain



Figs. 9-14. *Sporothrix guttuliformis*. **9.** Conidiogenous cells emerging of coffee rust spore, 1000×. **10.** Conidiogenous cells and conidia, 2000×. **11.** Conidiogenous cells with scars, 7500×. **12.** Perithecium of *Torrubiella* produced by the mycelium of *S. guttuliformis*, 400×. *Verticillium lecanii*. **13.** Sorus covered by mycelium and conidiophores, 500×. **14.** Verticillate conidiogenous cells, 1500×.

IE-361, Mahuixtlán; Mpio. Emiliano Zapata, road Chavarrillo-Monte Oscuro, 24 Mar. 1987, Carrión 913d; El Tizal, 25 Mar. 1998, Carrión 1998; 23 Feb. 1999, Carrión 2084 (presence of *Torrubiella*), strain IE-360; Mpio. Xico, road Cascada Texolo, 26 Feb. 1998, Carrión 1978; 25 Mar. 1998, Carrión 1989c; 12 Nov. 1998, Carrión strain IE-359; Mpio. Zongolica, road Zongolica-Xonamanca, 23 Nov. 1999, Carrión strain IE-380; Mpio. Catemaco, around Laguna Escondida, 24 Nov. 1999, Carrión 2159, strain IE-381.

The genus *Sporothrix* comprises more than 10 species, most associated with fungi such as *Cordyceps* and other entomopathogen species (de Hoog, 1974). *Sporothrix globuligera* was isolated from soil in Japan (Matsushima, 1995). *Aphanocladium meliolae*, a mycoparasite of the coffee rust in Ghana (Gams, 1971), can be mistaken for *Sporothrix guttuliformis*, however, the former differs because it lacks ramoconidia and the characteristic sympodial growth of the rachis of the genus *Sporothrix* (Gams, 1971; de Hoog, 1974, 1978). In *S. guttuliformis* the conidiogenous cells present only one scar when the mycelium is young, however, the number of scars increases during ageing. *Sporothrix guttuliformis* is similar to *S. curviconia* which differ however in that it has curved spores and very long conidiogenous cells, (6-)20-35(-60) × 1.2-2 µm (de Hoog, 1974, 1978). The development of some perithecia of *Torrubiella* was found in advanced parasitism states of *S. guttuliformis* on the rust (Fig. 12). Even though we observed the perithecia of *Torrubiella*, there are no report of a teleomorph for *Sporothrix*, however, de Hoog (1974) has reported that *Torrubiella* is a fungus associated with species of *Sporothrix*. Moreover, both fungi have not been linked as anamorph-teleomorph. This suggested association need to be tested in future research.

Verticillium lecanii (Zimm.) Viégas in Rev. Inst. Café Sâo Paulo 14: 754, 1939. (Figs. 13, 14)

Mycelium mass over the sori, with mycelium threads between sori, white, cottony. Growth rate 29-33 mm after 10 days, both aerial and immersed growth, and thus deforming the PDA. *Conidiophores* crystalline under the stereoscopic microscope, 4-10 groups of phialides in verticils, distance between verticils 24-40 µm. *Phialides* 4-8, arranged in whorls, slightly wide at the base and thinner at the apex, 9-40 × 0.8-2.4 µm. *Conidia* ellipsoidal to cylindrical arranged in heads, hyaline, 4-5.6 × 1.6-2.4 µm.

Material examined: MEXICO, Puebla, Mpio. Tlapacoya, Ahuacatlaya, 14 Mar. 2000, Carrión strain IE-393; coffee plantations Café Oro Verde, 14 Mar. 2000, Carrión 2173; Mpio. Tlacuilotepec, San Pedro Petlacotla, road Huauchinango-Poza Rica, 15 Mar. 2000, Carrión 2177 (teleomorph *Torrubiella*). VERACRUZ, Mpio. Coatepec, Mahuixtlán, 3 Oct. 1995, Carrión strain IE-362; Mpio. Emiliano Zapata, Chavarrillo, 15 Nov. 1995, Carrión strain IE-366; Monte Oscuro, 6 December 1995, Carrión strain IE-364, 24 Mar. 1987, Carrión 913a; El Tizal, road Chavarrillo-Monte Oscuro,Veracruz, 25 Mar. 1998, Carrión 1995; 23 Feb. 1999, Carrión 2080 (teleomorph *Torrubiella*); Mpio. Xico, road Xico-Texolo, 30 Oct. 1995, Carrión strain IE-363; 17 Jan. 1996, Carrión strain IE-365; 25 Mar. 1998, Carrión 1995; 5 Nov. 1998,

Carrión strain IE-367; Mpio. Zongolica, road Zongolica-Nepopoalco, 23 Nov. 1999, Carrión strain IE-388.

On quite old rust injuries, we found the development of a perithecia of *Torrubiella*, known teleomorph of *V. lecanii*, the latter has also been reported as a parasite of aphids, whiteflies, mealybugs and scales, and on several rust species (*Puccinia graminis tritici*, *P. coronata*, *Hemileia scholtzii* and *Uromyces laevigatus*) (Gams, 1971). Besides *V. lecanii*, *V. psalliotae* was recorded in Malaysia associated to the coffee rust (Lim and Nik, 1983). Over the past 10 years, *V. lecanii* has been used in greenhouses in Europe to control the white fly, and, recently, this species has been used to control such diseases as the cucumber powdery mildew, *Sphaerotheca fuliginea* (Samson *et al.*, 1988; Verhaar *et al.*, 1998). However, its use in the field is strongly limited by low relative humidity.

Discussion

The fungi described above, are reported for the first time as mycoparasites of the coffee rust, however, they had previously been reported as mycoparasites of other fungi in other regions of the world. *Sporothrix* spp. and *Calcarisporium ovalisporum* apparently prefer entomopathogenic fungi, like *Cordyceps* spp. or *Hirsutella* spp., as a substrate. *Acremonium* spp. are usually associated with a variety of fungus groups. *Sporothrix* spp. and *V. lecanii* prefer insects or fungi as hosts, and supposedly both coincide in the *Torrubiella* teleomorph. They probably originate in the soil and return to it after the fungal resource (coffee rust spores) is no longer available.

These species use their mycelia to form groups of rust spores and, at times, more than one species parasitises the rust's sori. Interestingly, these mycoparasitic fungi only develop on the spores of the coffee rust, but never on its mycelium, which is hidden within the plant. The coffee plantations visited exhibited the same species of fungi, suggesting that the mycobiota associated with coffee rust sori is similar throughout the coffee regions of México. The best collections were done between October and March, which is when the coffee rust and its parasites are abundant.

The coffee plant, an African species, was introduced in México in the nineteenth century, during more than one hundred years the plant was free of coffee rust. When the rust arrived in Mexico (1981) it occupied its niche as an obligate parasite of the coffee plant. This event generated a wealth of interactions with insect larvae and mycoparasites, which use rust spores as a substrate in the highly species-rich Mexican coffee plantations. In nature, interspecific interactions change both in space and time (Thompson, 1994), suggesting a highly variable environment that allows for new interactions among recently associated species. Parasitism is considered a pure form of

antagonistic interaction (Thompson, 1982), where the fitness of the parasite increases while the host's fitness decreases. The coffee rust can be considered as the second trophic level, while the five mycoparasites are the third trophic level, and, argueably, control the coffee rust population. These mycoparasites can colonize rust spores when they are being formed in the sori throughout their development, and up until they are ready for dispersion. Mycoparasites are considered necrotrophic when they kill the host's cells and use the liberated nutrients as substrate during the infection (Heath, 1987). They are considered biotrophic, rather than necrotrophic due to the absence of signs of damage, such as the breakage of uredospores at the onset of the infection. Examples of biotrophic micoparasites are *V. psalliotae* on the urediniospores of *H. vastatrix*, and *V. lecanii* on *U. dianthi* and *Puccinia recondita* (Spencer, 1980; Spencer and Atkey, 1981; Lim and Nik, 1983). The penetration of a fungal host by a biotrophic micoparasite is due both to mechanical and enzymatic mechanisms, the latter under strict control of lytic enzymes (Manocha and Balasubramanian, 1994).

The six mycoparasites reported here should be considered as good biological control agents, because they completely destroy the reproductive structures of the rust, decreasing the number of rust spores that can potentially infect new coffee plants. Fungicides are no longer used in the study region because this disease is of lesser importance, probably due to the activity of these mycoparasites. Detailed studies of these fungi and their interactions will be published elsewhere, as part of a large project on the ecology of mycoparasites and their potential as biological control agents of the coffee rust.

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References

Alarcón, R. and Carrión, G. (1994). Uso de *Verticillium lecanii* como control biológico de la roya del cafeto. Fitopatología 29: 82-85.

Booth, C. (1971). *The genus Fusarium*. Commonwealth Mycological Institute. Kew, Surrey, UK.

Booth, C. and Sutton, B.C. (1984). *Fusarium pallidoroseum* the correct name for *F. semitectum* Auct. Transactions of the British Mycological Society 83: 702-704.

Carrión, G. (1988). Estudio sobre el control biológico de la roya del cafeto mediante *Verticillium lecanii*. Micologia Neotroprical Aplicada 1: 79-86.

Carrión, G. and Ruiz-Belin, F. (1988). Inoculación en el laboratorio de *Verticillium lecanii* sobre la roya del café (*Hemileia vastatrix*). Revista Mexicana de Micologia 4: 317-321.

Carrión, G., Romero, A. and Rico-Gray, V. (1999). Use of *Verticillium lecanii* as biocontrol agent against bean rust (*Uromyces appendiculatus*). Fitopatologia 34: 214-219.

Castañeda Ruíz, R.F. and Rodríguez de la Rosa, N. (1988). Notas acerca del género *Fusarium* en Cuba. I. Revista del Jardín Botánico Nacional de Cuba 9: 89-96.

Gams, W. (1971). *Cephalosporium-artige Schimmelpilze (Hyphomycetes)*. Gustav Fischer Verlag, Stuttgart.

Gams, W. (1975). *Cephalosporium*-like hyphomycetes: some tropical species. Transactions of the British Mycological Society 64: 389-404.

Hawksworth, D.L. (1976). *Acremonium zonatum*. CMI Descriptions of Pathogenic Fungi and Bacteria 502.

Hawksworth, D.L., Kirk, P.M., Sutton, B.C. and Pegler, D.N. (1995). *Ainsworth & Bisby's Dictionary of the Fungi.* 8th edn. CAB International, Wallingford, UK.

Heath, M.C. (1987). Evolution of parasitism in the fungi. In: *Evolutionary Biology of the Fungi* (eds. A.D.H. Rayner, C.M. Grasier and D. Moon). Symposium of the British Mycological Society, Cambridge University Press, New York: 149-160.

Hijwegen, T. (1988). Effect of seventeen fungicolous fungi on sporulation of cucumber powdery mildew. Netherlands Journal of Plant Pathology 94: 185-190.

Hijwegen, T. (1992). Glycolitic activities in some fungicolous fungi. Netherlands Journal of Plant Pathology 98: 77-80.

Hijwegen, T. and Dirven, J.A.A.M. (1993). Mycoparasitism of Powdery and Mildews. In: *Biological Control of Foliar and Post-Harvest Diseases* (eds. N.J. Folhema, Y. Kohl and Y. Elad). 10BC WPRS Bulletin 16: 76-81.

Hijwegen, T. and Verhaar, M.A. (1993). Induced resistance to *Peronospora parasitica* in red cabbage. Netherlands Journal Plant Pathology 99: 103-107.

Hoch, H.C. and Abawi, G.S. (1979). Mycoparasitism of oospores of *Phythium ultimum* by *Fusarium merismoides*. Mycologia 71: 621-625.

Hoog, G.S. de (1974). The genera *Blastobotrys*, *Sporothrix*, *Calcarisporium* and *Calcarisporiella* gen. nov. Studies in Mycology 7: 1-84.

Hoog, G.S. de (1978). Notes on some fungicolous Hyphomycetes and their relatives. Persoonia 10: 33-81.

Isaac, S. (1992). *Fungal-Plant Interaction*. Chapman and Hall, London.

Lim, T.K. and Nik, W.Z. (1983). Mycoparasitism of the coffee rust pathogen, *Hemileia vastatrix*, by *Verticillium psalliotae* in Malaysia. Pertanika 6: 23-25.

Mabbayad, M.O. and Watson, A.K. (2000). Rejection of *Fusarium pallidoroseum* as a biological control agent of *Mimosa invisa* in upland rice. Biocontrol Science and Technology 10: 255-265.

Manocha, M.S. and Balasubramanian, R. (1994). Fungal chitinases: their properties and roles in morphogenesis, mycoparasitism and control of pathogenic fungi. In: *Host Wall Alterations by Parasitic Fungi* (eds. O. Petrini and G.B. Ouellette). APS Press, Saint Paul, Minnesota: 81-90.

Matsushima, T. (1995). *Matsushima Mycological Memoirs No. 8*. Published by the author, Kobe.

Rombach, M.C. and Roberts, D.W. (1987). *Calcarisporium ovalisporum*, symbiotic with the insect pathogen *Hirsutella citriformis*. Mycologia 79: 153-155.

Romero, A. and Carrión, G. (1995). Patogenicidad de *Verticillium lecanii* sobre la roya del frijol en condiciones de invernadero. Fitopatologia 30: 34-37.

Samson, R.A. Evans, H.C. and Latgé, J-P. (1988). *Atlas of Entomopathogenic Fungi*. Springer-Verlag, Berlin.

Schieber, E. and Zentmyer, G.A. (1984). Distribution and spread of coffee rust in Latin America. In: *Coffee Rust in the Americas* (ed. R.H. Fulton). American Phytophathological Society, Saint Paul, Minnesota: 1-14.

Siddiqi, M.A. (1964). Fungus flora of *Coffea arabica* in Nyasaland. Transactions of the British Mycological Society 47: 281-284.

Spencer, D.M. (1980). Parasitism of carnation rust (*Uromyces dianthi*) by *Verticillium lecanii*. Transactions of the British Mycological Society 74: 191-194.

Spencer, D.M. and Atkey, P.T. (1981). Parasitic effects of *Verticillium lecanii* on two rust fungi. Transactions of the British Mycological Society 77: 535-542.

Steyaert, R.L. (1930). *Cladosporium hemileiae* n. spec. un parasite de l'*Hemileia vastatrix* Berk. et Br. Bulletin de la Société Royale de Botanique de Belgique 63: 46-49.

Thompson, J.N. (1982). *Interaction and Coevolution*. John Wiley and Sons, New York.

Thompson, J.N. (1994). *The Coevolutionary Process*. University of Chicago Press, Chicago.

Verhaar, M.A. Hijwegen, T. and Zadocks, J.C. (1998). Selection of *Verticillium lecanii* isolates with high potential for biocontrol of cucumber powdery mildew by means of components analysis at different humidity regimes. Biocontrol Science and Technology 8: 465-477.

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