

Four new lichen-associated *Trimmatostroma* species (hyphomycetes)

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Abstract. Four new lichen-associated species of *Trimmatostroma* s. lat. are described. *T. dendrographae* is found on *Dendrographa* in California (U.S.A.), *T. hierrense* on cf. *Arthonia endlicheri* in El Hierro (Canary Islands), *T. lecanoricola* on saxicolous *Lecanora* in Peru; *T. quercicola* develops over bark of *Quercus* and is facultatively lichenicolous on degenerate lichen thalli in Belgium and Luxembourg. A key to the known lichenicolous species of *Trimmatostroma* is provided.

Key words. Anamorphic fungi, *Intralichen*, lichenicolous, *Taeniolella*.

1. Introduction

The genus *Trimmatostroma* Corda (1837), with *T. salicis* Corda as type species, was introduced for bark-inhabiting saprobic hyphomycetes. This genus is characterized by having simple, little differentiated conidiophores and conidiogenous cells as well as polymorphous conidia formed in irregular basipetal chains (Ellis 1971, 1976). *T. lichenicola* M.S. Christ. & D. Hawksw. (in Hawksworth 1979) was the first lichenicolous species assigned to this genus. Hawksworth & Cole (2002) revised and reassessed *T. lichenicola* and similar lichenicolous hyphomycetes and introduced the new genus *Intralichen* D. Hawksw. & M.S. Cole, mainly differentiated from *Trimmatostroma* by its lichenicolous habit, an immersed mycelium, entirely immersed micronematous conidiophores, and pale, smooth-walled conidia with few septa. Based on molecular sequence analyses, *Trimmatostroma* proved to be very heterogeneous and must probably be confined to *T. salicis* and a few closely allied species phylogenetically pertaining to the

Helotiales (Crous et al. 2007). Other species were transferred to the new genus *Catenulostroma* Crous & U. Braun (Crous et al. 2007). They are morphologically close to *Trimmatostroma* s. str., but belong to the Teratosphaeriaceae (Capnodiales). However, even *Catenulostroma* is in its current circumscription probably not monophyletic (Crous et al. 2009).

During the course of monographic studies on lichenicolous *Taeniolella* S. Hughes species, several collections provisionally named "*Taeniolella* sp." were encountered that turned out to be *Trimmatostroma*-like. Species of *Taeniolella* are easily distinguishable by having superficial, semimacronematous conidiophores, conidia formed in acropetal chains, and lacking multicellular aggregations of conidial cells, which are common in *Trimmatostroma*. As no sequence data are available for these species and as conidiomata are not stromatic (the type species *T. salicis* and related species have sporodochial conidiomata with a basal stroma), an inclusion in *Trimmatostroma* might be questionable. On the other hand, the formation of stromata

and conidiophores in sporodochia is often unreliable as distinctive generic character in hyphomycete genera. However, no other suitable genus is available. Therefore, we prefer to include the new licheni-

colous taxa tentatively in *Trimmatostroma* s. lat. The final generic position of lichenicolous *Trimmatostroma*-like hyphomycetes depends on the phylogenetic affinity of the taxa concerned.

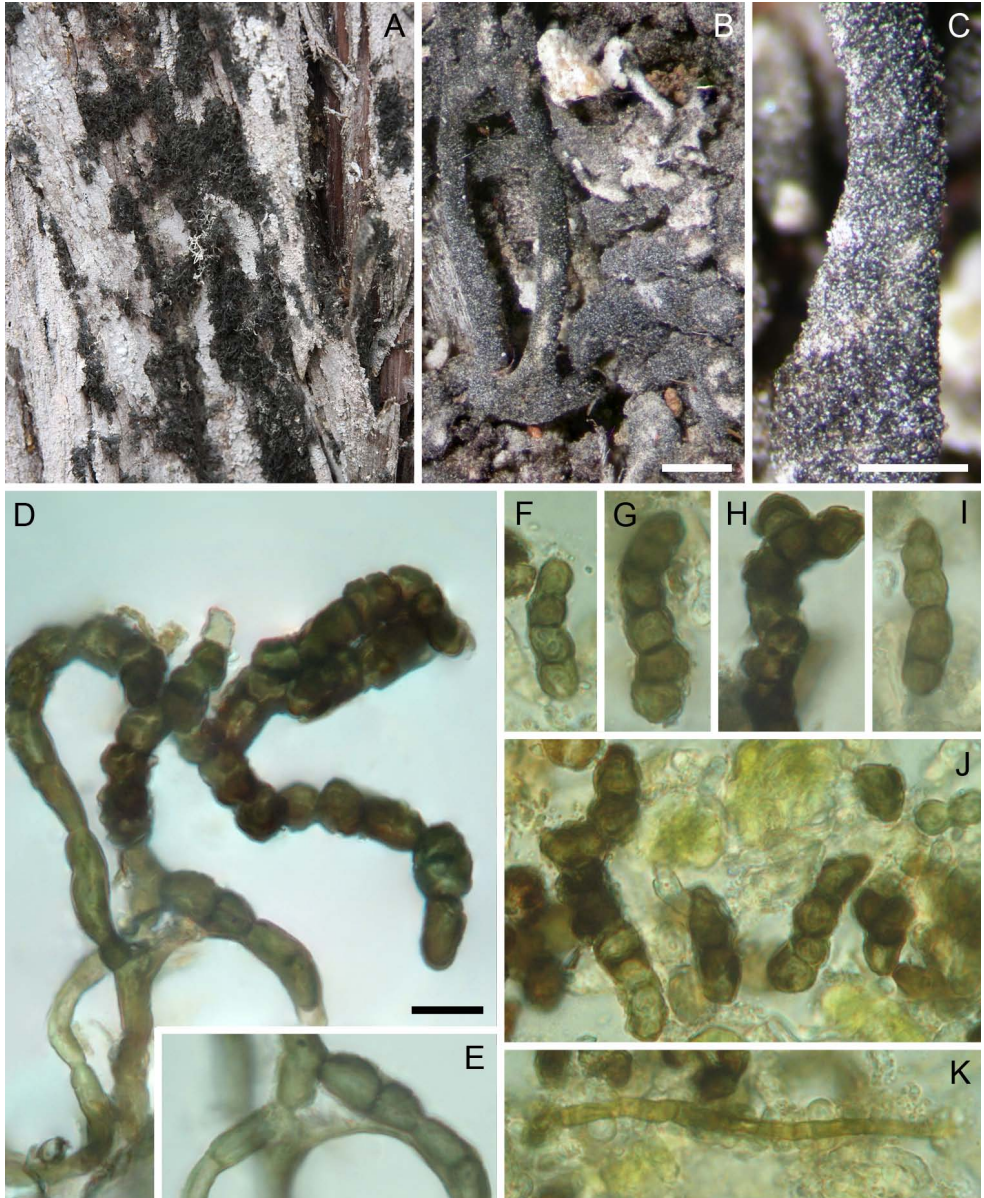


Fig. 1. *Trimmatostroma dendrographae*. A–C, Infected thalli of *Dendrographa*. D, Conidiophore with chains of conidia, in water. E, Same, in KOH. F–J, Chains of conidia, in water. K, Conidiophore, in water. A: California, Monterey, Crocker Grove; B–C, F–K: holotype; D–E: *Diederich* 16767. Scale bars: B = 1 mm, C = 0.5 mm, D–K (same scale bar) = 10 μ m.

2. Material and Methods

The specimens examined are deposited in B, BR, HAL, NY, UCR and UPS, and in the private herbarium of P. Diederich. For microscopical examination, small fragments were examined in water, after light pressure on the cover glass, and in 5% KOH.

3. Results

Trimmatostroma dendrographae Diederich, Ertz, U. Braun & Heuchert sp. nov. Fig. 1
Mycobank 518957.

Trimmatostromatis quercicolae simile, sed conidiorum macroscopice non distinctis, thallu hospitis plus minusve fuscescens, conidiis olivaceo-bruneis in aqua, intense olivaceis in KOH, 5.5–8.5 μm latis, pariete usque ad 1.2 μm crasso. Differt a *Trimmatostromate salicis* et *T. betulino* habitu lichenicola, stromatibus et sporodochiis nullis, coloniis dispersis supra thallos *Dendrographae*, conidiis olivaceo-bruneis, olivaceis in KOH, 0–pluriseptatis, 7–25 \times 5.5–8.5 μm , pariete rugoso-rimuloso.

Type: U.S.A., California, Monterey Co., Carmel, Point Lobos State Reserve, 30 m alt., on *Dendrographa* sp., on *Cupressus macrocarpa*, 18 Jul. 2008, P. Diederich 16789 & D. Ertz (BR – holotype; HAL, NY, UCR, herb. Diederich – isotypes).

Colonies lichenicolous over the thallus of *Dendrographa*, usually covering the entire surface of the host thallus, blackish, macroscopically appearing as a finely granular mixture of blackish conidia and white host hyphae, the whole appearing pale to dark greyish at a low magnification (e.g., in the field), individual chains of conidia hardly visible. *Mycelium* internal, hyphae sparingly branched, 2.5–3.5 μm wide, subhyaline to pale brown, septate, thin-walled, rugose. *Stroma* lacking. *Conidiophores* usually immersed, occasionally somewhat erumpent, micronematous, c. 20–70 \times 2.5–4 μm , hyphal filaments gradually developing into fertile threads by becoming somewhat wider and darker, with slightly thicker wall, but differentiation between hyphae and conidiophores very difficult, rugose. *Conidiogenous cells* integrated, terminal, monoblastic (i.e., the terminal cell functioning as conidiogenous cell), c. 5.5–9 \times 3.5–4 μm , conidiogenous loci undifferentiated,

subtruncate. *Conidia* in simple or rarely branched, irregular, rarely disarticulating, basipetal chains, shape and size very variable, mostly ellipsoid-ovoid to subcylindrical or oblong, transversely 0–pluriseptate, rarely dictyosporous, ends more or less rounded, c. 7–25 \times 5.5–8.5 μm , sometimes forming irregular aggregations, medium to dark brown or olivaceous-brown, distinctly olivaceous in KOH, wall 0.8–1.2 μm thick, wall rugose-rimulose.

This species is distinguished from *T. lecanoricola* by olivaceous conidia in KOH, from *T. hierrense* by rugose-rimulose conidia and from *T. quercicola* by narrower conidia that are not visible macroscopically. Attempts to culture freshly collected material failed.

Ecology, hosts and distribution: All known specimens are lichenicolous on epiphytic and saxicolous thalli of *Dendrographa*, including crustose, sorediate thalli that are considered to be the primary morph of the host, before the fruticose structures appear. In many specimens, fruticose thalli start growing, but are so heavily parasitized by this hyphomycete that they just reach up to 1 cm in length and then die. This species is known only from the coast of California, and it appears to be rather common in localities where the host *Dendrographa* is present.

Additional specimen examined (all on *Dendrographa*): USA, California, Monterey Co.: same locality as the type, on *Cupressus macrocarpa*, 2008, Ertz 12482, 12487 & Diederich (BR); *ibid.*, sheltered rock face near the sea, 2008, Ertz 12441, 12453 & Diederich (BR); SW of Monterey, 17 Mile Drive, Crocker Grove, alt. 15 m, on *C. macrocarpa*, 2008, Diederich 16767 & Ertz 12462 (BR, herb. Diederich); along coast S of Asilomar, China Rock, alt. 5 m, on rock outcrop on the beach, 2008, Ertz 12480 & Diederich (BR).

Trimmatostroma hierrense Diederich & Ertz sp. nov. Fig. 2

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Differt ab omnibus speciebus *Trimmatostromatis* conidiis transverse septatis et parietibus conidiorum unilateraliter incrassatis et fuscatis.

Type: Spain, Canary Islands, El Hierro, E of Frontera, trail between Frontera and 'mirador de Jinama' (part below 'Fuente de Tincos'), 27°45'29" N, 17°59'29" W, 'fayal brezal' forest and rocky outcrops, on a root under a rock along trail, on cf.

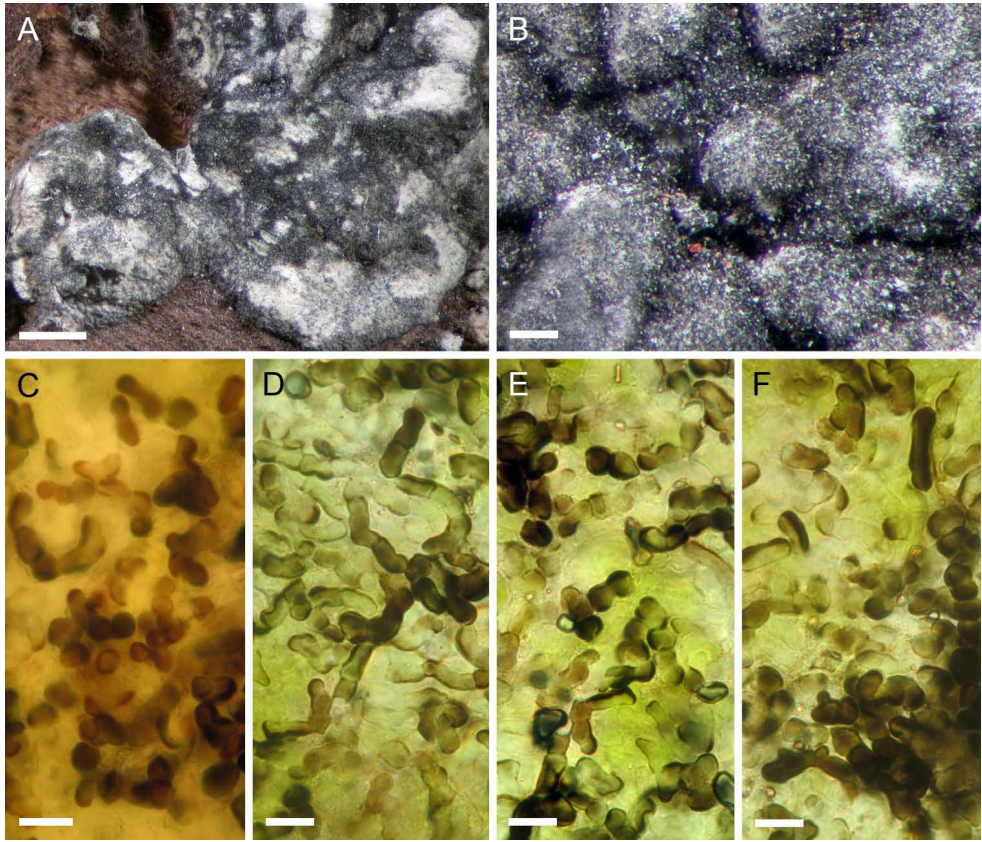


Fig. 2. *Trimmatostroma hierrense* (holotype). A–B, Infected thalli of cf. *Arthonia endlicheri*. C, Conidia and conidial chains, in water. D–F, Same, in KOH (conidiophores visible in D). Scale bars: A = 1 mm, B = 0.2 mm, C–F = 10 µm.

Arthonia endlicheri, 31 Aug. 2009, D. Ertz 13946 (BR – holotype; herb. Diederich – isotypes).

Colonies lichenicolous over the thallus of cf. *Arthonia endlicheri*, covering large parts of the host thallus, blackish, macroscopically appearing as a finely granular mixture of blackish conidia and white host hyphae, the whole appearing dark greyish to blackish at a low magnification (e.g., in the field), individual chains of conidia hardly visible. *Mycelium* internal, hyphae sparingly branched, 2–2.5 µm wide, subhyaline to pale brown, septate, thin-walled, smooth. *Stroma* lacking. *Conidiophores* usually immersed, occasionally somewhat erumpent, micronematous, up to 40 µm long and 2.5–3.5 µm wide, hyphal filaments gradually developing into fertile threads by becoming somewhat wider and darker, but differentiation between hyphae

and conidiophores very difficult, smooth. *Conidiogenous cells* integrated, terminal, monoblastic (i.e., the terminal cell functioning as conidiogenous cell), c. 5.5–10 × 3.5–4.5 µm, conidiogenous loci undifferentiated, subtruncate. *Conidia* in simple or rarely branched, irregular, often disarticulating, basipetal chains, shape and size very variable, mostly ellipsoid-ovoid to subcylindrical or oblong, often with irregular convex and concave regions, transversely 0–pauciseptate, ends more or less rounded, c. 7.5–15 × 3.5–6.5 µm, pale to medium brown, partly with thickened walls and then dark brown, olivaceous brown in KOH; wall c. 0.5 µm thick in pale areas, c. 1 µm in darker areas, smooth.

Macroscopically, the new species looks very similar to *Trimmatostroma dendrographae*, entirely darkening large areas of the host

thallus. Microscopically, it is distinguished by conidia frequently with a dark and thick outer wall limited to one side of the conidium (resembling conidia of *Milospium graphideorum*). Furthermore, conidia are usually smoother than in *T. dendrographae*, best seen in KOH. Because of the unevenly pigmented conidial wall, *T. hierrense* might be mistaken for a species of *Milospium*. However, conidia of the type species, *M. graphideorum* (Nyl.) D. Hawksw., have a very different shape, being irregularly lobed and aseptate, and they are never catenate. Conidia of *M. deslooveri* Diederich & Sérus. (Sérusiaux et al. 1999) and *M. planorbis* (Aptroot & Sipman 2001; holotype from B examined) are strongly curved, multicellular, often with incomplete septa, and never catenate; furthermore, both species are lichenized, not lichenicolous. The new species could also be confused with *Trimmatostroma scutellare* (Berk. & Broome) M.

B. Ellis, another species with an unevenly thickened and pigmented conidial wall, but in that species conidia are multicellular with transverse and longitudinal septa (Ellis 1976).

Ecology, hosts and distribution: The new species covers large parts of the thallus of a white crustose lichen with *Trentepohlia* reacting C+ red, that probably belongs to *Arthonia endlicheri*, growing on the root of a tree along a trail. Infected thalli become entirely dark greyish black. This species is known only from the type locality on the isle of El Hierro (Spain, Canary Islands).

Trimmatostroma lecanoricola Diederich, Etayo, U. Braun & Heuchert sp. nov. Fig. 3
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Trimmatostromatis dendrographae et *T. quercicola* simile, sed catenis conidorum disarticulantium aurantiaco-brunneis in KOH, nec umquam

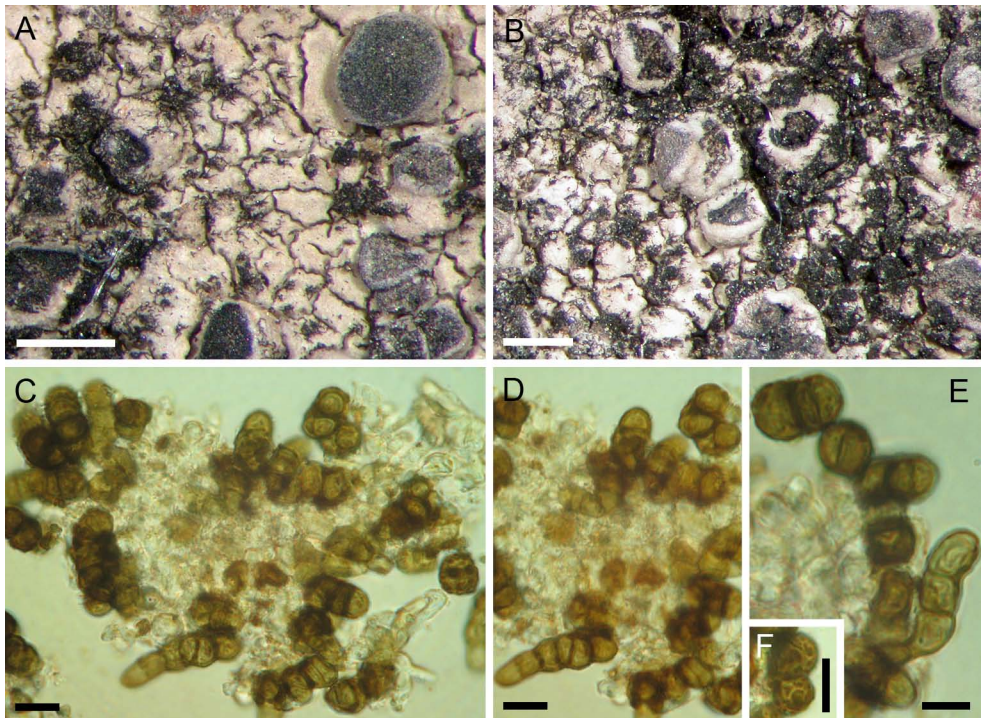


Fig. 3. *Trimmatostroma lecanoricola* (holotype). A, Thallus of saxicolous *Lecanora* with young infection. B, Thallus with older infection. C, Chains of conidia, in water. D, Same, in KOH. E, Disarticulating chain of conidia, in water. F, Conidium in surface view, showing verrucose, mosaic-like outer layer of conidial wall, in water. Scale bars: A–B = 0.5 mm, C–F = 10 µm.

olivaceo-brunneis, et partibus atrioribus paginae conidiorum minoribus in conidiis vetustioribus rimulosis.

Type: Peru, Dep. La Libertad, Prov. Trujillo, Cerro Malabrigo, SW of Puerto Chicama, on saxicolous *Lecanora*, 100–150 m alt., 9 Apr. 1981, R. Santesson & A. Tehler P128:1 (UPS – holotype).

Colonies lichenicolous, over the thallus and apothecia of a saxicolous *Lecanora*; when young, appearing as irregular, branched, blackish filaments (representing conidial chains), soon aggregating in very dense tufts of conidial chains, the infected parts of the host becoming entirely blackish. *Mycelium* internal, hyphae sparingly branched, 1.5–3 µm wide, subhyaline to pale brown, septate, thin-walled, smooth. *Stroma* lacking. *Conidiophores* usually immersed, occasionally somewhat erumpent, micronematous, c. 20–40 × 2–4 µm, hyphal filaments gradually developing into fertile threads by becoming somewhat wider and darker, with slightly thicker wall, but differentiation between hyphae and conidiophores very difficult. *Conidiogenous cells* integrated, terminal, monoblastic (i.e., the terminal cell functioning as conidiogenous cell), c. 4–7 × 3–4.5 µm, conidiogenous loci undifferentiated, subtruncate. *Conidia* in simple or rarely branched, irregular, easily disarticulating, basipetal chains, often subspherical and 1-septate, 6.5–10 × 6–8 µm, or oblong, transversely pluriseptate to dictyosporous, c. 11–24 × 5–9 µm, medium to dark brown, orange brown in KOH, wall 0.5–1.2 µm thick, rugose-rimulose to irregularly verrucose, ends more or less rounded.

This species is readily distinguished from the other taxa treated here by conidial chains becoming orange brown in KOH, never with an olivaceous tinge, and by chains of disarticulating conidia. Furthermore, when the outer layer of the conidial wall splits with age, the resulting darker patches are often smaller than in the other species, giving the conidial surface a mosaic-like appearance.

Ecology, host and distribution: This species is known only from the type collection made in Peru on an unidentified saxicolous *Lecanora*. Infected host thalli and apothecia are damaged, suggesting that the fungus is pathogenic.

Trimmatostroma quercicola Diederich, U. Braun & Heuchert sp. nov. Figs 4–5

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Trimmatostromatis dendrographae simile, sed catenis conidiorum macroscopice expedite conspicuis, irregulariter reticuloideis, conidiis badiis in aqua et olivaceo-brunneis in KOH, 5–15 µm latis, pariete usque ad 2 µm crasso. Differt a *T. lecanoricola* catenis conidiorum raro disarticulatis, conidiis olivaceo-brunneis in KOH, et strato exteriori conidiorum obscuriore in conidiis vetustioribus rimulosis.

Type: Luxembourg, Vogelsmühle, valley of Halerbaach, left side of river, on bark of *Quercus*, possibly associated with sterile crustose lichens, 9 Dec. 2007, P. Diederich 16723 (BR – holotype; HAL, herb. Diederich – isotypes).

Colonies over bark of *Quercus*, frequently overgrowing and probably parasitizing degenerate crustose lichen thalli or corticolous algae, effuse, loose to dense, fumose-black, macroscopically appearing as relatively short, prostrate, irregularly formed and branched, often agglomerated conidial chains. *Mycelium* internal, hyphae sparingly branched, 1–3.5 µm wide, subhyaline to pale brown, septate, thin-walled, smooth. *Stroma* lacking. *Conidiophores* usually immersed, occasionally somewhat erumpent, micronematous, c. 5–40 × 2–6 µm, hyphal filaments gradually developing into fertile threads by becoming somewhat wider and darker, with slightly thicker wall, but differentiation between hyphae and conidiophores very difficult. *Conidiogenous cells* integrated, terminal, monoblastic (i.e., the terminal cell functioning as conidiogenous cell), c. 5–10 × 3–4 µm, conidiogenous loci undifferentiated, subtruncate. *Conidia* in simple or rarely branched, irregular, occasionally disarticulating, basipetal chains, shape and size very variable, globose or subglobose, 0–1(–2)-septate, 4–9 µm diam., or ellipsoid-ovoid, subcylindrical, oblong, 1–4(–5)-septate, transversely septate to dictyosporous, c. 6–30 × 5–15 µm, sometimes forming irregular aggregations, medium to dark brown, olivaceous-brown in KOH, wall thick, up to 2 µm, occasionally distinctly two-layered, i.e., with a distinct, paler inner layer (but not distoseptate), wall rugose-rimulose to irregularly verrucose, ends more or less rounded.

Amongst the new species described here, *T. quercicola* is macroscopically rather distinct, as conidial chains are easily visible at a strong magnification ($\times 40$), appearing as an irregular, branched net of relatively thick hyphae overgrowing the substratum. Microscopically, the species has much thicker conidial chains than the three others. It is chemically distinct from *T. lecanoricola* by the K⁺ olivaceous conidial chains and differs slightly from *T. dendrographae* in having brown conidia (in water) without a distinct olivaceous tinge.

Trimmatostroma quercinum (Hoffm.) Höhn. (syn. *Phragmotrichum quercinum* Hoffm.) was described from rotten manufactured wood of *Quercus* in Germany. The species forms black, superficial, dispersed, orbicular, pulvinate stromata, and oblong, muricate, transversally septate to irregularly muriform, indistinctly catenate conidia $25\text{--}30 \times 12\text{--}15 \mu\text{m}$ (Migula 1921, Sutton &

Pirozynski 1965). Although the type of this species has never been restudied and the species never been reported after its original description, it seems to differ clearly from the new *T. quercicola* by the pulvinate, stromatic conidiomata, the different ecology (rotten wood, versus bark of *Quercus*) and the mostly larger conidia.

Ecology, hosts and distribution: The new species is known from two collections on the bark of old *Quercus*. As conidiophores at least occasionally overgrow and possibly parasitize reduced lichen thalli, the species may be considered as facultatively lichenicolous. It is probably widespread, but overlooked in similar habitats, and currently known from Belgium and Luxembourg.

Additional specimen examined: Belgium, SE of Buzenol, on bark of *Quercus*, possibly associated with sterile crustose lichens, 19 June 1984, P. Diederich 5576 (herb. Diederich).

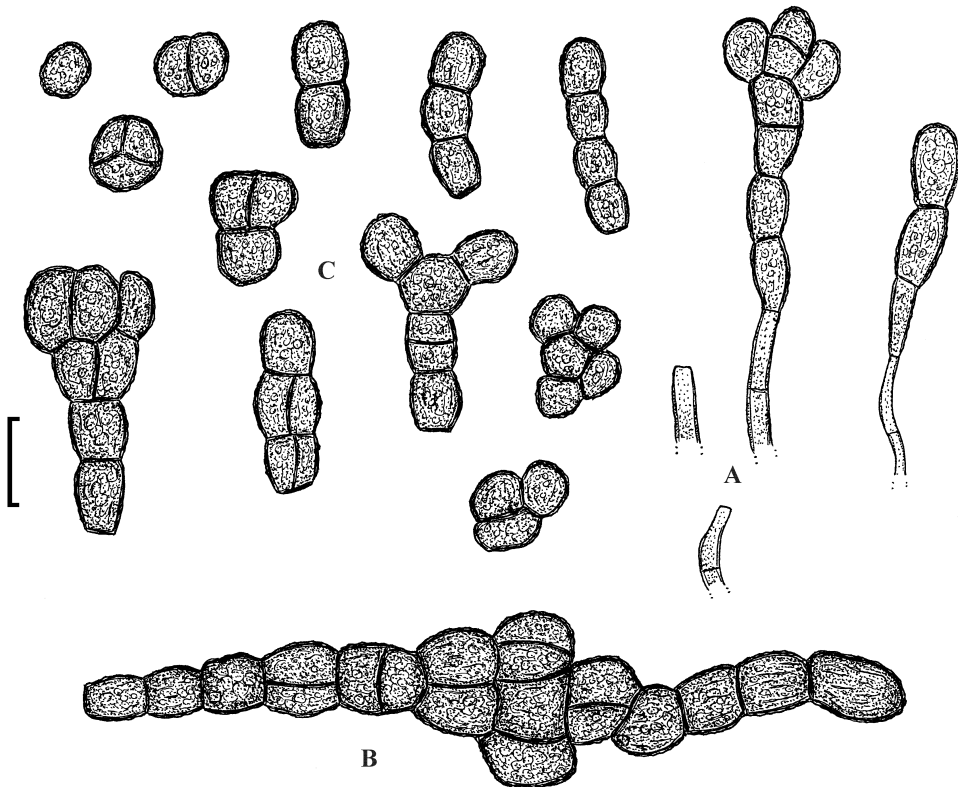


Fig. 4. *Trimmatostroma quercicola* (holotype). A, Conidiophores with and without conidia. B, Plagiotropous conidial chain. C, Conidia. Scale bar = $10 \mu\text{m}$. U. Braun del.

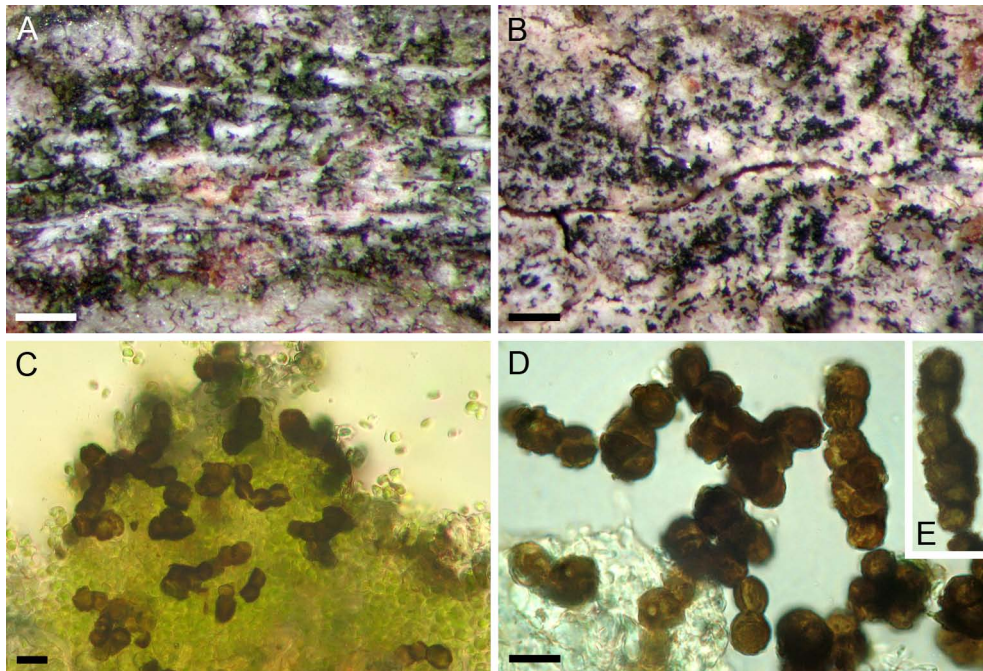


Fig. 5. *Trimmatostroma quercicola*. A, Overgrowing degenerate lichen thalli on *Quercus* bark. B, Saprobian over *Quercus* bark. C, Squash preparation of infected lichen thallus, in water. D, Chains of conidia, in water. E, Same, in KOH. A, C: holotype; B, D–E: *Diederich* 5576. Scale bars: A–B = 200 μ m, C–E = 10 μ m.

4. Discussion

Hawksworth (1979) described the lichenicolous *Trimmatostroma lichenicola* M.S.Christ. & D. Hawksw., intrahymenial in *Candelariella vitellina*. Later, Hawksworth & Cole (2002) introduced the new generic name *Intralichen* for this and several similar species, and no lichenicolous species was subsequently accepted in *Trimmatostroma*.

The four new species share a large number of characters. They all have dark, micronematous conidiophores not arranged in sporodochia, lack stromatic hyphal aggregations, have integrated conidiogenous cells, and conidia produced in simple or rarely branched basipetal chains, 1–pluriseptate, irregular in size and form, with an often rough surface, the outer layer of the wall often splitting with age, resulting in pale to medium brown conidia covered by dark brown remnants of the outer layer, or unevenly pigmented. Furthermore, they all obligately or facultatively parasitize lichen thalli.

Conidia are superficially similar to those of *Spilodochium* Syd. (Ellis 1971, 1976). However, the genus *Spilodochium* is easily distinguishable by its erumpent pseudoparenchymatic stromata, conidiophores arranged in sporodochia and conidia produced in branched acropetal chains. The entire habit of the new species is rather *Intralichen*-like. However, species of *Intralichen* have paler, smaller, smooth-walled, mostly 0–2-celled conidia, and conidiophores are usually entirely immersed in lichen thalli or apothecia, most commonly being intrahymenial, with only the mature conidia arising at the surface (Hawksworth & Cole 2002). On the other hand, the inclusion of these species in *Taeniolella* is no alternative, since species of this genus do not form dictyosporous conidia, and its conidial chains are acropetal.

Microscopically, the new species are similar to *Trimmatostroma salicis*, the type species, and *T. betulinum* (Corda) S.Hughes, from which they are distinguished by the absence of a basal stroma and lacking pulvinate spo-

rodochia (Crous et al. 2007). The latter two species have been shown to belong to the Helotiales (Crous et al. 2007). Many *Trimmatostroma*-like fungi have recently been transferred to the new genus *Catenulos-troma* in the Teratosphaeriaceae [Capnodiales] (Crous et al. 2007), which is, however, no alternative either, since this genus is also characterized by having stromatic conidiomata. The introduction of a new genus for the new lichenicolous species might be the best solution, but in the absence of molecular data, i.e., without knowledge of the phylogenetic affinity, we prefer to assign the new species tentatively to *Trimmatostroma* s. lat.

5. Identification key for the known lichenicolous species of *Trimmatostroma*

1. Conidia orange brown in KOH; conidial chains frequently disarticulating; outer layer of conidial wall splitting with age and then sometimes divided in many relatively small patches, looking mosaic-like (Fig. 3F); lichenicolous on saxicolous *Lecanora* ***T. lecanoricola***
1. Conidia olivaceous-brown in KOH; conidial chains rarely disarticulating; outer layer of conidial wall either smooth (Fig. 2) or splitting with age and then divided into several larger patches (Figs 1 & 5D) **2**
2. Conidial chains easily visible macroscopically ($\times 40$), appearing as an irregular net of blackish hyphae; conidia reddish brown in water, olivaceous-brown in KOH, 5–15 μm wide, wall up to 2 μm thick; saprobic on bark of *Quercus*, facultatively lichenicolous over degenerated lichen thalli ***T. quercicola***
2. Conidial chains indistinct macroscopically, almost entirely blackening large parts of the host thallus; conidia olivaceous-brown in water, more intensively olivaceous in KOH, 5.5–8.5 μm wide, wall up to 1.2 μm thick; obligately lichenicolous on lichens with *Trentepohlia* **3**
3. Conidia frequently with a dark outer wall limited to one side of the conidium (resembling conidia of *Milospium*), wall smooth; lichenicolous on cf. *Arthonia endlicheri* ***T. hierrense***

3. Conidia with a dark outer wall splitting with age, but more evenly surrounding the entire conidia, wall rugose; lichenicolous on *Dendrographa* ***T. dendrographae***

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