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Xylariaceous Fungi as Endophytes

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1. Introduction

Although a great number of papers has been dedicated to the Xylariaceae, the activities of most fungi belonging to this group are still very obscure. Most of them are collected from dead angiospermous plants and only a few from gymnosperms; others fruit on angiospermous remains in dung and soil. Xylariaceae are known to be mainly saprobes, although some species are considered to be weak parasites and can cause considerable damage (Rogers, 1979a). However, many routine isolations from living tissues (wood, fruits, seeds) as well as from soil yield hyphomycetes that are xylariaceous (Basham & Anderson, 1977; Rogers, 1979b; Barron, 1968). Therefore, it was not surprising that fungi belonging to the Xylariaceae could be isolated from living needles of European conifers (Carroll & al., 1977). The low incidence of infection by these fungi, however, led to the assumption that their occurrence in healthy plant tissues had to be considered as rather casual. The extensive investigations on endophytic fungi which were carried out in the following years revealed that Xylariaceae are common inhabitants of apparently healthy, living plant tissues. Carroll & Carroll (1978) and Petrini & Mueller (1979) regularly isolated hyphomycetes that could be linked to a perfect state belonging in the Xylariaceae by cultural characters and conidiophore morphology. Luginbuehl & Mueller (1980) reported the occurrence of Xylariaceae in the green leaves of evergreen angiospermous shrubs. These results were confirmed by the studies of several other authors (summarized in Petrini, 1984). Thus, xylariaceous fungi assumed an unexpected ecological significance, and stimulated detailed studies on the relationship of these fungi with their hosts and substrates.

The identification of these xylariaceous endophytes, however, proved to be extremely difficult. While the teleomorphs were comparatively rare in culture and could be easily identified by means of

existing keys and descriptions, the more frequently isolated anamorphs could be named mostly only to the genus; no further identification was possible, because so far the cultural characters of only a limited number of xylariaceous species have been described (GREENHALGH & CHESTERS, 1968; JONG & ROGERS, 1972). This problem can be overcome by careful investigation and description of the cultural characters of single ascospore isolates from freshly collected xylariaceous teleomorphs and by the use of biochemical methods.

The aim of this study is to provide a key to the identification of some European Xylariaceae in culture, to document the information available on their occurrence and distribution as endophytes and to discuss their ecological significance.

2. Methods

Cultural studies were carried out with single ascospore isolates obtained by the methods described by SAMUELS (1979). Most cultures formed conidiophores and conidia within 3–5 weeks at room temperature under irregular illumination on 2% malt extract agar (MA) plates. A few members of the Primocinerea section in the genus *Hypoxylon* and some species of *Rosellinia* DE NOT. developed their teleomorphs in the single ascospore isolates (PETRINI & MUELLER, 1986); the production of ascomata, however, was very slow and required sometimes up to 6 months incubation, mostly at rather low temperatures (see below).

Endophytes were isolated from living plant tissues according to the methods already described by different authors (e. g. CARROLL et al., 1977; summarized in PERTINI, 1984). The resulting cultures were incubated either at room temperature with irregular illumination or at 16°–20° C in darkness on MA plates.

Conidiophores and conidia in endophyte and single ascospore isolates are usually formed after a few weeks incubation at 16°–21° C. Endophytic Xylariaceae very often produce only their anamorphs in culture. Incubation at low temperatures sometimes induced the production of asci and ascospores in several species. *Anthostomella* SACC. usually forms its ascomata at room temperature, but the sporulation is enhanced after exposure of the cultures at 8° C under fluorescent light with a 12 h dark-light cycle or after incubation at 4° C in the darkness. The sporulation occurs mostly very slowly, taking place sometimes only after two – three months.

3. Taxonomy

3.1. General considerations

The identification of the form-genera is comparatively easy; on the other hand, the conidiophore morphology and the size and shape of conidia are of little diagnostic significance and cannot be used alone to describe and to delimit xylariaceous species in culture.

Microscopical features such as conidiophore morphology (fig. 1), shape and size of conidia, as well as the formation of particular structures like stromatic elements (fig. 2), hyphal strands or stromata can be effectively combined with cultural characters to describe species of the Xylariaceae. Growth rates, colours and the

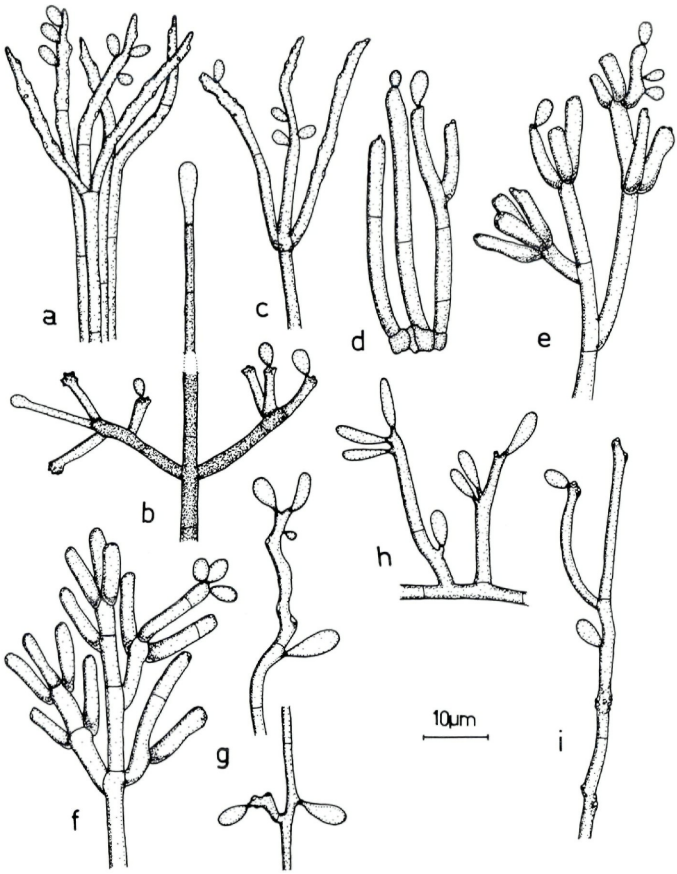

Fig. 1: Form-genera of xylariaceous anamorphs. – a. *Dematophora* sp. – b. *Dicyma* cf. *olivacea*, after DREYFUSS & PETRINI, 1984. – c. *Geniculosporium* sp. – d. *Hadrotrichum* anamorph of *Hypoxylon deustum*. – e. *Nodulisporium* anamorph of *H. fragiforme*. – f. *Periconiella* anamorph of *Biscogniauxia nummularia*. – g. *Rhinocladiella* anamorph of *Rosellinia diathrausta*. – h. *Sporothrix* anamorph of *R. limoniispora*. – i. *Virgariella* anamorph of *H. julianii*.

formation of peculiar structures (pustules, stromatic structures hyphal strands) are rather stable characters within a species and vary very little. Therefore, a careful comparison of suspected endophytic xylariaceous colonies with single ascospore isolates allows a number of them to be named to the species level. The anamorphs of some Pezizales can be confused with xylariaceous anamorphs and then wrongly placed in form-genera so far known to be tied to the Xylariaceae. PADEN (1984) discusses the major features which enables their separation from the xylariaceous ones.

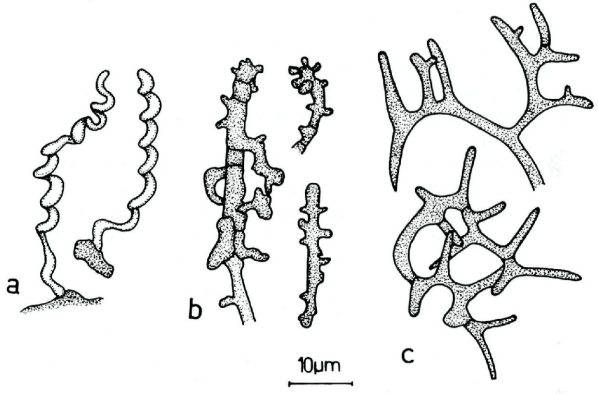

Fig. 2: – a. coiled hyphae of *Hypoxylon deustum*. – b. stromatic structures of *H. unitum*. – c. stromatic structures of *Daldinia* spp.

On the other hand, some form-genera can also accommodate the anamorphs of ascomycetes belonging to other families (e. g. *Sporothrix* is also the anamorph of *Ophiostoma* spp.): these possibilities are considered in the following key, but no attempt is made to discuss them further, little information existing on such borderline cases.

While all genera so far known to live endophytically are considered in the key, particular emphasis is placed on the cultures of species in the genera *Hypoxylon* and *Daldinia* CES. & DE NOT. The key is far from being exhaustive as, apart from a few exceptions, only European representatives of the family have been studied in detail.

3.2. Conidiophore morphology and conidiogenesis in the anamorphs of xylariaceous fungi

The anamorphs of the Xylariaceae treated in this study can be accommodated in the form-genera *Dematophora* HARTIG, *Dicyma* BOULANGER sensu von ARX (1982) (= *Hansfordia* S. HUGHES), *Geniculosporium* CHESTERS & GREENHALGH, *Hadrotrichum* FUCKEL, *Nodulisporium* PREUSS (= *Acrostaphylus* ARNAUD ex SUBRAMANIAN), *Periconiella* SACC., *Rhinocladiella* NANNF., *Sporothrix* HEKTOEN & PERKINS, and *Virgariella* S. HUGHES (Fig. 1).

Five more genera, viz. *Achroomyces* BONORDEN, *Lindquistia* SUBRAMANIAN, *Padixonia* SUBRAMANIAN, *Xylocladium* SYD. ex LINDAU (= *Basidiobotrys* v. HOEHNEL), and *Xylocoremium* J. D. ROGERS are known to be related to xylariaceous teleomorphs. These genera, however, have never been isolated as endophytes, nor were they produced by single ascospore isolates of species investigated during this study. Therefore, they are not considered here, although they may possibly be found in the course of further investigations on endophytic fungi.

The conidiophore morphology is distinctive for each form genus. All xylariaceous anamorphs usually have hyaline to light brown conidiophores, but the branching, the position of the conidiogenous cells, and the arrangement of the conidiogenous loci within the conidiogenous cells form good differential characters.

On the other hand, conidial morphology is not helpful in delimiting species or even genera: the conidia are hyaline to light brown, ovoid to nearly globose, with a truncate base, apart from the conidia of *Geniculosporium,* which possess a distinctive frill.

It is probable that some anamorphic form-genera can be linked to definite morphological types of teleomorphs. For example, species in the *Hypoxylon* section Primo-cinerea constantly exhibit anamorphs belonging to *Geniculosporium* and *Periconiella* has so far been reported for species of *Biscogniauxia* and *Hypoxylon* in the section Applanata.

Conidiogenesis is usually holoblastic on sympodially arranged conidiogenous loci (COLE & SAMSON, 1979). In *Xylaria longipes* NITSCHKE and in *Daldinia occidentalis* CHILD, however, percurrently proliferating conidiogenous cells were also observed (ROGERS, 1983; PETRINI & MUELLER, 1986); the parallel occurrence of sympodial, holoblastic conidiogenesis and percurrent proliferation has been reported in other groups of Ascomycetes (e. g. *Eutypa*, GLAWE & ROGERS 1982). The anamorphs of the two species mentioned above do not differ significantly in conidiophore morphology from already known form-genera. Therefore, no new form-genus is required. It is assumed that within xylariaceous anamorphs both forms of conidiogenesis can occur.

3.3. Key for the identification of some xylariaceous fungi in culture.*

a: further identification not possible.

1 Teleomorph and sometimes also anamorph produced in culture . . . . . (key I)
1* Anamorph only produced in culture, or culture sterile 2
2 Culture sterile . . . . . (key II)
2* Culture fertile 3
3 Conidiophores not differentiated, conidia formed on morphologically undifferentiated hyphae 4
3* Conidiophores differentiated 5
4 Conidiogenous cells with short denticles, conidia often clustered (De Hoog, 1974) . . . . . *Sporothrix* (a)
4* Conidiogenous cells with scar-like, small denticles; conidia not clustered . . . . . *Rhinocladiella* (key VII)
5 Conidiophores compactly aggregated, arranged in a palisade, branched only at the base, arising from a basal tissue of variable texture or from a filiform stroma . . . . . *Hadrotrichum* (key IV)
5* Conidiophores scattered, branched over their whole length, arising from loosely aggregated hyphae or from single stromatic cells 6
6 Conidiophores with verticillately arranged conidiogenous cells, conidiogenous loci not, or seldom, intercalar 7
6* Conidiophores with superimposed conidiogenous cells, conidiogenous loci apical and intercalar 10
7 Conidiogenous cells with denticles, conidiophores sometimes with sterile tips (see *Ascotricha* for further references, key I) . . . . . *Dicyma* (a)
7* Conidiogenous cells with scars, conidiophores always with fertile tips 8
8 Conidia in mucoid masses, conidiophores perfectly hyaline; anamorph of Pezizales (Paden, 1984) . . . . . *Molliardiomyces* Paden (a)
8* Conidia dry, conidiophores hyaline to light brown 9
9 Conidiophores without a main axis . . . . *Nodulisporium* (key V)
9* Conidiophores with a main axis . . . . . *Periconiella* (key VI)
10 Conidiogenous loci crowded, densely aggregated on short, thickened nodules, separated by sterile segments . . . . . *Virgariella* (key VIII)
10* Conidiogenous loci separated, arranged in a rachis, sometimes interrupted by sterile segments 11

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* This key is intended for 3–5 weeks old cultures, grown in daylight at room temperature on 2% malt extract agar.

11 Conidiophores synnematous on the host, in culture often not synnematous and then hardly distinguishable from the following genus (ELLIS, 1971). . . . . *Dematophora* (a)
11* Conidiophores not synnematous either on the host or in culture. . . . . *Geniculosporium* (key III)

Key I: Teleomorph and sometimes anamorph produced in culture

1 Ascomata not in a stroma, less than 0,8 mm in diameter 2
1* Ascomata immersed in a stroma, stroma usually more than 0,8 mm in diameter 3
2 Ascomata hairy, anamorph present, growing mostly on the fruit-body, belonging to the form-genus *Dicyma* (HAWKSWORTH, 1971; DE HOOG, 1977; von ARX, 1982; DREYFUSS & PETRINI, 1984). . . . . *Ascotricha* BERK. (a)
2* Ascomata smooth, anamorph rarely present and then not belonging to *Dicyma* (FRANCIS, 1975) . . . . *Anthostomella* SACC. (a)
3 Ascomata in up to 50–70 mm long, filiform to cylindrical, black stromata with white tips, production of conidia mostly on the tips (OBERHOLZER, 1982; ROGERS, 1985) . *Xylaria* HILL ex GREV. (a)
3* Ascomata in sessile, globose, black stromata 4
4 Mature ascospores with one cellular appendage at each end, with or without a gelatinous sheath 5
4* Mature ascospores without appendages and without a gelatinous sheath 6
5 Appendages up to 10 µm long, pointed, ascospores 17–23 × 5,5–7,5 µm, without gelatinous sheath, culture dark brown. – Anamorph: *Nodulisporium* . . . . 22. *Rosellinia thelena*
5* Appendages up to 5 µm long, rounded, ascospores (21) 24–27 (30) × 9–13 µm, with a conspicuous gelatinous sheath, culture white to yellow, primordia after 6 months, teleomorph formed usually at 3–6° C after 18 (!) months. Anamorph: *Rhinocladiella*. . . . . 20. *R. diathrausta*
6 Ascospores lemon-shaped, dark brown, 13–20 × 8–10 µm. Anamorph produced on old stromata only, belonging to the form-genus *Sporothrix* . . . . . 21. *R. limoniispora*
6* Ascospores asymmetrical, ellipsoidal to cylindrical, light brown, 6–29 × 3–10 µm. – Anamorph produced in young cultures and belonging to the form-genus *Geniculosporium*. 7
7 Ascospores 6–8 × 3 – 4,5 µm . . . . . 6. *Hypoxylon effusum*
7* Ascospores 9–29 × 3–10 µm 8
8 Ascospores 19–29 × 7 – 10 µm (WHALLEY & al., 1983) . . . . . *Hypoxylon gwyneddii* WHALLEY et al.
8* Ascospores 9–13 (15) × 3–6 µm 9

9 Ascospores 9–13 × 3–6 µm, asymmetrical, ellipsoidal, germ slit short, easily seen ..... 9. *Hypoxylon irregulare*
9* Ascospores 10–13 (15) × 3,5–5,5 µm, ellipsoidal to cylindrical, germ slit as long as the spore, faintly visible ..... 13. *Hypoxylon serpens*

Key II: Culture sterile

1 Culture only 20 mm in diameter after four weeks, grey brown, surface with densely aggregated brown-grey pustules, margin and reverse of culture orange ..... 17. *H. udum*
1* Above characters not combined 2
2 Culture with filiform to narrowly cylindrical, black stromata, these often with a white tip..... *Xylaria* spp. (a)
2* Culture without such stromata..... 3
3 Culture with radiate, white hyphal strands, with infolded, black stromatic structures and scattered hyaline, spiral hyphae on its surface (fig. 2a) ..... 5. *H. deustum*
3* Above characters not combined 4
4 Young stromatic structures composed of long elements with short protuberances (fig. 2b)..... 18. *H. unitum*
4* Culture lacking the above mentioned features ..... sterile Deuteromycete

Key III: Anamorph belonging to the form-genus *Geniculosporium*

1 Culture with radiate mycelial strands, cream-coloured, production of conidiophores restricted to small grey areas ..... 9. *H. irregulare*
1* Above characters not combined 2
2 Culture only 20 mm in diameter after four weeks, grey-brown, surface with densely aggregated, brown-grey pustules, margin and reverse of culture orange ..... 17. *H. udum*
2* Above characters not combined 3
3 Culture showing concentric rings, white or orange, production of conidiophores scanty ..... 4. *H. confluens*
3* Above caracters not combined 4
4 Culture in daylight strongly orange, without concentric rings, surface felty, aerial mycelium absent, production of conidiophores restricted to small areas ..... 14. *H. serpens* var. *macrosporum*
4* Above characters not combined 5
5 Culture with stromatic structures composed of long elements with short protuberances (fig. 2b) ..... 18. *H. unitum*
5* Above characters not combined ..... *Geniculosporium* spp.

Key IV: Anamorph belonging to the form genus *Hadrotrichum* (the genus *Xylocoremium* ROGERS (1984) is keyed out here)

1 Culture white, grey to black with filiform to narrow cylindrical, black stromata, these often with a white tip; production of conidiophores usually restricted to the tip but sometimes distributed over the whole length of the stroma, agar not coloured ... . Anamorph of *Xylaria* spp. (includes *Xylocoremium*) (a)
1* Above characters not combined 2
2 Culture white, with yellow and brown spots, felty, production of conidiophores scanty, restricted to small areas, agar dark brown coloured ..... 11. *H. moravicum*
2* Above characters not combined ..... *Hadrotrichum* spp. (a)

Key V: Anamorph belonging to the form genus *Nodulisporium*

1 Agar not coloured, culture white to dark grey 2
1* Agar brown, dark brown to green-brown coloured, culture with pale to dark brown-colours 3
2 Culture dark grey, sometimes when old with pink to grey sectors, surface velvety, with grey aerial mycelium ..... 15. *H. terricola*
2* Culture white, grey to brown .. anamorph of *Rosellinia* spp. (a)
3 Culture grey-green, with scattered, small, green to black pustules, composed of reticulated dark brown stromatic structures (fig. 2c) 4
3* Culture not grey-green, reticulate stromatic structures absent 5
4 Conidiogenesis annellidic, production of conidiophores restricted to some pustular areas ..... 3. *Daldinia occidentalis*
4* Conidiogenesis holoblastic, sympodial, production of conidiophores scattered over the whole mycelium ..... anamorph of *Daldinia* spp. (a)
5 Young culture with yellow-orange, later, brown pustules, on which conidiophores develop, rusty brown, to brown, mycelial strands sometimes at the margin, reverse of young culture dark green ..... 7. *Hypoxylon fragiforme*
5* Above characters not combined 6
6 Culture white, light brown to reddish brown, surface pellicular, production of conidiophores scanty, restricted to small areas ... . 8. *H. howeianum*
6* Above characters not combined 7
7 Culture evenly yellow-brown to light brown coloured, aerial mycelium scanty ..... 19. *H. vogesiacum* s. l.

7* Above characters not combined 8
8 Culture white with yellow and brown spots, felty, production of conidiophores scanty, restricted to small areas . . . . . 11. *H. moravicum*
8* Above characters not combined . . . . . *Nodulisporium* spp. (a)

Key VI: Anamorph belonging to the form genus *Periconiella*

1 Conidiophores covering the surface of the substrate with the appearance of white to cream granules, culture light brown, with white, abundant aerial mycelium, agar reddish brown coloured . . . . . 2. *Biscogniauxia nummularia*
1* Above characters not combined 2
2 Conidiophores upright, scattered over the mycelium, culture yellow-brown, with scanty, white aerial mycelium, brown when old, agar reddish brown coloured . . . . . 1. *B. marginata*
2* Above characters not combined . . . . . *Periconiella spp.* (a)

Key VII: Anamorph belonging to the form genus *Rhinocladiella*

This key refers only to the anamorphs of Xylariaceous genera. For an exhaustive treatment of this form genus with discussion of other anamorph-teleomorph connections see DE HOOG (1977).

1 Culture white to yellow, aerial mycelium scanty, greyish to cream, production of conidiogenous cells restricted to small brown areas, agar not coloured; primordia after 6 months, teleomorph formed at 3–6° C after 18 (!) months . . . . . 20. *Rosellinia diathrausta*
1* Above characters not combined 2
2 Culture rusty brown to brown-yellow, production of chlamydospores and later of conidiogenous cells at the margin of older cultures, agar coloured dark brown . . 16. *Hypoxylon ticinense*
2* Above characters not combined . . . . . *Rhinocladiella* spp. (a)

Key VIII: Anamorph belonging to the form genus *Virgariella*

1 Culture white, yellow to light brown, aerial mycelium scanty, felty, areas of conidiophore production light brown, conidiophores not, or rarely, dichotomously branched . . . . . 10. *Hypoxylon julianii*
1* Above characters not combined 2
2 Culture brown-grey to black, regularly covered with grey areal myelium, areas of conidiophore production white to grey . . . . . 12. *H. multiforme*
2* Above characters not combined . . . . . *Virgariella* spp. (a)

4. Description of cultures

1. *Biscogniauxia marginata* (Fr.) Z. Pouzar

Illustrations: Petrini & Mueller (1986).

Culture yellow to brown, aerial mycelium scanty, initially white, when old becoming brown and felty, production of conidiophores restricted to white to yellow mycelial areas, reverse of the culture dark brown, agar stained reddish brown. – Conidiophores up to 450 × 5 µm. – Conidia 5–7 × 1,5–2 µm.

2. *Biscogniauxia nummularia* (Bull.) O. Kuntze

Description and Illustrations: Greenhalgh & Chesters (1968).

Culture white to light brown with abundant loose aerial mycelium, production of conidiophores on the substrate with the appearance of white to cream granules, reverse of the culture dark brown, agar stained reddish brown. – Conidiophores up to 100 × 5 µm. – Conidia hyaline, 4–6 × 2,5–4 µm.

3. *Daldinia occidentalis* Child

Illustrations: Petrini & Mueller (1986).

Culture grey-green to green-brown, with small mycelial pustules composed of reticulate, dark brown stromatic structures (fig. 2c). Production of conidiophores restricted to dense, velvety, brown to pink pustules, reverse of the culture yellow-green to dark brown, agar stained slightly brown. – Conidiophores up to 100 × 4 µm. – Conidiogenesis annellidic. – Conidia 5,5–8,5 × 3–5,5 µm.

4. *Hypoxylon confluens* (Tode: Fr.) West.

Description and Illustrations: Chesters & Greenhalgh (1964).

Culture cream to grey, sometimes orange, reverse of the culture cream, agar not stained. Aerial mycelium scanty, often growing in concentric rings.

5. *Hypoxylon deustum* (Hoffm.: Fr.) Grev.

Descriptions and Illustrations: Jong & Rogers (1972).

Culture white, with radiate mycelial strands and a black, infolded stromatic layer with scattered coiled hyphae on its surface (fig. 2a); agar not stained. Culture almost always sterile.

6. *Hypoxylon effusum* NITSCHKE

Culture white, aerial mycelium woolly to velvety, reverse of the culture cream to brown, agar not stained. – Ascospores 6–8 × 3–4.5 µm.

7. *Hypoxylon fragiforme* (PERS.: FR.) KICKX

Descriptions and Illustrations: GREENHALGH & CHESTERS (1968), JONG & ROGERS (1972).

Culture rusty brown to brown, with mycelial strands and veins; conidiophores produced on yellow-orange pustules. Reverse of the culture initially dark green, later brown; agar dark brown stained. – Conidiophores up to 150 × 3 µm. – Conidia 3–5,5 × 2–3 µm.

8. *Hypoxylon howeianum* PECK

Description and Illustrations: GREENHALGH & CHESTERS (1968).

Culture white, light brown to reddish brown, surface pellicular, reverse of the culture dark brown, agar brown stained. – Conidiophores when old incrusted with warts, up to 150 × 2 µm. – Conidia 4,5–5,5 × 2 µm.

9. *Hypoxylon irregulare* CKE

Illustrations: PETRINI & MUELLER (1986).

Culture white, felty; aerial mycelium scanty, with radiate hyphal strands and small pustules at the margin; production of conidiophores restricted to small, gray areas, reverse of the culture white, agar not stained. – Conidiophores variable in length, up to 2,5 µm wide. – Conidia 2–5 × 2–4 µm.

10. *Hypoxylon julianii* L. PETRINI

Illustrations: PETRINI & MUELLER (1986).

Culture white, yellow to light brown, surface felty, aerial mycelium absent; areas of conidiophore production yellow to light brown. Reverse of the culture light yellow-brown, agar stained yellow-brown. – Conidiophores up to 75 × 2 µm, not or rarely dichotomously branched. – Conidia 4–5,5 × 2–2,5 µm.

11. *Hypoxylon moravicum* Z. POUZAR

Description and illustrations: PETRINI & CANDOUSSAU (1983).

Culture white with brown and yellow spots, white aerial mycelium initially scanty, later abundant; areas of conidiophore

production yellow to brown; reverse of the culture dark brown, agar stained dark brown. – Conidiophores up to 65 × 3 µm. – Conidia 4,5–6,5 × 3,5–4,5 µm.

12. *Hypoxylon multiforme* (Fr.) Fr.

Descriptions and Illustrations: Greenhalgh & Chesters (1968), Jong & Rogers (1972).

Culture brown-grey to black, area of conidiophore production white to grey, reverse of the culture dark brown to black, agar stained dark brown to black. – Conidiophores 30–100 × 2,5 µm, when old incrusted with warts. – Conidia 3,5–5,5 × 2–3,5 µm.

13. *Hypoxylon serpens* (Pers.: Fr.) Kickx

Descriptions and Illustrations: Chesters & Greenhalgh (1964), Jong & Rogers (1972).

Culture initially white, later becoming uniformly grey over the whole surface due to the production of conidiophores. Reverse of the culture white, agar not stained. – Conidiophores variable in length, up to 2 µm wide. – Conidia 2,5–4,5 × 2–3 µm.

14. *Hypoxylon serpens* var. *macrosporum* J. H. Miller

Illustrations: Jong & Rogers (1972).

Culture 30 mm in diameter after three weeks, orange in light, surface felty, aerial mycelium scanty; production of conidiophores restricted to small, dark grey areas, reverse of the culture orange, agar not stained. – Conidiophores variable in length, up to 2 µm wide. – Conidia 3,5 – 4,5 × 1,5–2 µm.

15. *Hypoxylon terricola* J. H. Miller

Illustrations: Petrini & Mueller (1986).

Culture dark grey, sometimes when old with pink to grey sectors, surface velvety with grey aerial mycelium, areas of conidiophore production white to grey, restricted to mycelial clusters, reverse of the culture brown to pink, later, dark brown, agar not stained. – Conidiophores up to 120 × 3 µm. – Conidia 4–5 × 2,5–3 µm.

16. *Hypoxylon ticinense* L. Petrini

Illustrations: Petrini & Mueller (1986).

Culture orange brown to grey brown, areas of chlamydospore and conidiophore production orange and mostly restricted to the margin; reverse of the culture light brown, later black, agar at the

beginning stained green brown, later, dark brown. – Chlamydospores hyaline to light brown, one-celled, 3–6 µm in diameter. – Conidiophores not differentiated. – Conidia 2,5–4 × 1,5–2 µm.

17. *Hypoxylon udum* (Pers.: Fr.) Fr.

Description and Illustrations: Whalley (1976).

Culture 20 mm in diameter after four weeks, grey to brown, margin of the culture white orange, surface densely covered with pustules, reverse of the culture orange, agar not stained. Some cultures sometimes remain sterile. – Conidiophores variable in length, up to 2,5 µm wide. – Conidia 3–5 × 2,5–3,5 µm.

18. *Hypoxylon unitum* (Fr.) Nitschke

Illustrations: Petrini & Mueller (1986).

Culture white, with black, stromatic structures composed of long hyphae with short protuberances (fig. 2b), sometimes with radiate mycelial strands; aerial mycelium abundant, reverse of the culture dark brown, agar not stained. Some cultures often remain sterile. – Conidiophores variable in length, up to 2,5 µm wide. – Conidia 3,5–5,5 × 2,5–3,5 µm.

19. *Hypoxylon vogesiacum* (Pers.) Sacc. s. l.

Description and Illustrations: Whalley & Petrini (1984).

Culture homogeneously yellow brown to light brown, aerial mycelium scanty, conidiophore production at first restricted to small light brown areas, in older cultures scattered over the whole surface, reverse of the culture light brown, agar at the beginning stained yellow-brown, later brown. – Conidiophores 150–210 × 2 µm. – Conidia 3,5–4,5 × 2–2,5 µm.

20. *Rosellinia diathrausta* (Rehm) L. Petrini

Description and Illustrations: Jong & Rogers (1972).

Culture 15 mm in diameter after four weeks, white to yellow, aerial mycelium grey to cream, scanty, reverse of the culture yellow to white, agar not stained. – Conidiophores not differentiated. – Conidia 6 – 15(20) × 2,5–4,5 µm. – Anamorph: *Rhinocladiella.*

21. *Rosellinia limoniispora* Ellis & Everhart

Description and Illustrations: Jong (1970).

Culture white with abundant, woolly aerial mycelium, reverse of the culture white to cream or even brown, agar not stained. – Ascospores lemon-shaped, 13–20 × 8–10 µm. – Anamorph: *Sporothrix.*

22. *Rosellinia thelena* (Fr.) Rabh.

Illustrations of the teleomorph: Dargan & Thind (1979).

Culture brown grey, aerial mycelium scanty, with radiate, dark brown hyphal strands, reverse of the culture light to dark brown, agar not stained. – Ascospores 17–23 × 5.5–7.5 µm. – Anamorph: *Nodulisporium*.

5. Ecological significance of Xylariaceae

Miller (1961) lists three *Hypoxylon* species on gymnosperms, five species on monocotyledons and none on cryptogams: the remaining known *Hypoxylon* species occur on woody dicotyledons. The degree of host specificity for other xylariaceous genera has not been investigated thoroughly. On the basis of the known occurrence of *Hypoxylon* species, however, Rogers (1979a) came to the conclusion that *Hypoxylon* has to be considered as associate of relatively advanced dicotyledons.

An analysis of table 1 raises some doubts about this conclusion. As we have so far considered only an arbitrary selection of hosts, and the host-fungus lists were compiled on the base of isolations performed by slightly different methods, we shall not attempt to evaluate the table in detail nor shall we draw any inference as to the effective host specificity of the individual species; however, the presence of endophytic Xylariaceae in mosses, lichens and ferns is noteworthy. Also, some species which were reported to fruit on only one host (e. g. *Hypoxylon fragiforme, Biscogniauxia nummularia*) have been isolated from a number of plants belonging to different families. Thus, although most Xylariaceae can grow endophytically in many hosts, the physiological conditions required for the formation of the teleomorphs are fulfilled only on determinate hosts. This pattern of host induced fructification has already been observed for other endophytic fungi (Widler & Mueller, 1984).

Endophytic Xylariaceae can be divided roughly into two groups. Representatives of the genus *Anthostomella*, for instance, and a few from *Hypoxylon* (e. g. *H. terricola*) and *Rosellinia* seem to be confined only to members of a single plant family.

Xylaria spp. and *Hypoxylon* spp., on the other hand, are widely distributed within the plant kingdom; for instance, members of the *H. serpens* complex (*H. effusum, H. irregulare, H. serpens* s. str., *H. unitum*) are apparently quite unspecific.

The microclimatic conditions appear to be of paramount importance for the occurrence of fungi belonging to the *H. serpens*-complex. Our investigations on endophytic fungi of Ericaceae suggest that *H. deustum* and *H. unitum* are likely to prefer host plants growing in shady, humid sites (Petrini O., unpublished). This obser-

Tabelle 1: Occurrence of Xylariaceae as endophytes. This list summarizes the results of personal investigations as well as published data. For a more detailed account see PETRINI (1984). In brackets: number of plant species studied in each family or group. T: teleomorph; A: only anamorph produced in culture.

	Araceae (5)	Bromeliaceae (5)	Bryophyta (1)	Coniferae (41)	Ericaceae (15)	Lichenes (3)	Orchidaceae (16)	Poaceae (4)	Pteridophyta (8)	Others (33)
Anthostomella aracearum (T)	+						+		+	+
Anthostomella clypeoides (T)					+					
Anthostomella formosa (T)*)				+	+					
Anthostomella sepelibilis (T)					+					
Anthostomella tomicoides (T)					+					
Anthostomella tomicum (T)				+	+					
Biscogniauxia nummularia (A)	+				+		+	+		
Daldinia spp. (A)				+	+		+	+		+
Geniculosporium spp. (A)**)			+	+	+	+		+		+
Hypoxylon aureoluteum (A)								+		
Hypoxylon deustum			+		+	+		+		+
Hypoxylon effusum (T)										+
Hypoxylon fragiforme (A)	+	+		+	+		+	+	+	+
Hypoxylon fuscum (A)		+		+						+
Hypoxylon irregulare (T)					+	+		+	+	+
Hypoxylon rubiginosum (A)					+					+
Hypoxylon serpens (T)				+				+		
Hypoxylon terricola (A)				+						
Hypoxylon unitum (A)			+		+	+		+		+
Nodulisporium spp.	+			+	+	+	+	+	+	+
Rosellinia limoniispora (T)								+		
Rosellinia thelena (T)				+				+		
Xylaria cf. *bulbosa* (T)				+						
Xylaria hypoxylon (T)					+					
Xylaria spp. (A)	+	+	+	+	+	+	+	+	+	+

*) includes some isolates of uncertain affinity
**) uncludes *G. serpens* CHESTERS & GREENHALGH

vation correlates well with the reports by other authors on the teleomorphs of Xylariaceae and supports the hypothesis of a host – fungus co-evolution as observed for other fungal groups (PARLEVLIET, 1979).

The limited number of investigations on endophytic fungi does not allow any conclusions to be drawn about the geographical distribution of xylariaceous endophytes. Nevertheless, the frequent isolations of *Xylaria* spp. from tropical Araceae, Bromeliaceae, Orchidaceae and Pteridophyta (PETRINI & DREYFUSS, 1981; DREYFUSS & PETRINI, 1984), compared to the rather rare isolations from hosts in the temperate regions, indicate the tropical distribution of species belonging to this genus, a feature already known for the teleomorphs (e. g. DENNIS, 1956; 1957).

The significance of the Xylariaceae for their hosts cannot be easily explained. CARROLL & PETRINI (1983) reported that endophytic Xylariaceae can utilise both cellulose and lignin and suggested that they could be latent pathogens or decomposers after leaf fall. On the other hand, *Geniculosporium serpens* CHESTERS & GREENHALGH seems to exert a control on the flowering process of young plants of *Nicotiana tabacum* (STROTZ, pers. comm.). Xylariaceae are thus certainly not only saprobes; their symbiosis, however, cannot be described by known models, and needs further investigation.

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