Life History Studies of Brazilian Ascomycetes 8 [1]). — *Thamnomyces chordalis* (anam.: *Nodulisporium*) and *Camillea bacillum* (anam.: *Geniculosporium*) with notes on taxonomy of the Xylariaceae

G. J. Samuels
Plant Diseases Division,
Department of Scientific and Industrial Research,
Private Bag, Auckland, New Zealand

and

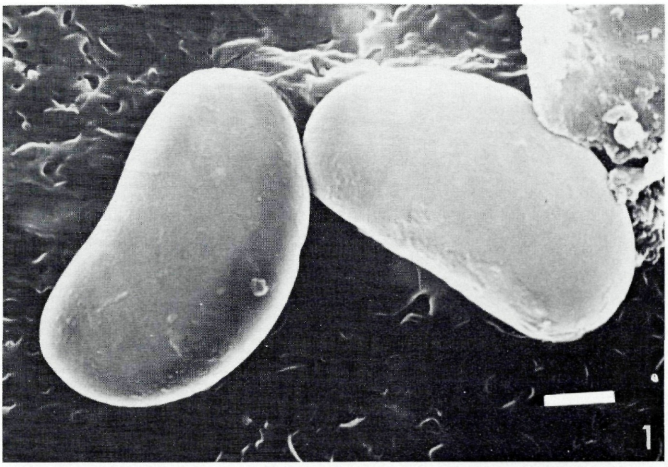
E. Müller
Eidg. Technische Hochschule,
Mikrobiologisches Institut, Zürich
CH-8092, Schweiz

Introduction

Thamnomyces Ehrenberg and *Camillea* Fries, genera of the Xylariaceae, are two of the most conspicuous and spectacular of the ascomycetous fungi. Stromata of *Thamnomyces* are black, wiry-filamentous, unbranched or dichotomously branched at the tips. They are up to 15 cm long but only 1.5 mm in diameter. Stromata of *Camillea* are black, cylindrical, either short and squat or long, up to 4 cm, and slender and with ascomata embedded just below the tip. Both are genera of the warm, dry tropics where they are found on recently killed hard-wood trees. According to Dennis (1957, 1961; see also Lloyd, 1917, for somewhat different generic concepts) who has monographed the genera, there are approximately five species in each genus. *Thamnomyces chordalis* Fries and *Camillea leprieuri* (Montagne) Montagne are common in the Amazon region of Brazil. Other species of *Thamnomyces* and *Camillea*, including *C. bacillum* (Montagne) Montagne, are less common.

Apart from their distinctive stromatal morphology, *Thamnomyces chordalis* and *C. bacillum* are noteworthy because the asci of these xylariaceous fungi lack an apical discharge apparatus and deliquesce soon after the delimitation of ascospores. In spite of the lack of one of the most distinctive features of the Xylariaceae, amyloid apical rings (Rogers, 1979), there is no doubt that these species are members of the family because of their black ascospores which have a germ slit and

[1]) Part 7 in Sydowia 32: 277—292. 1979.



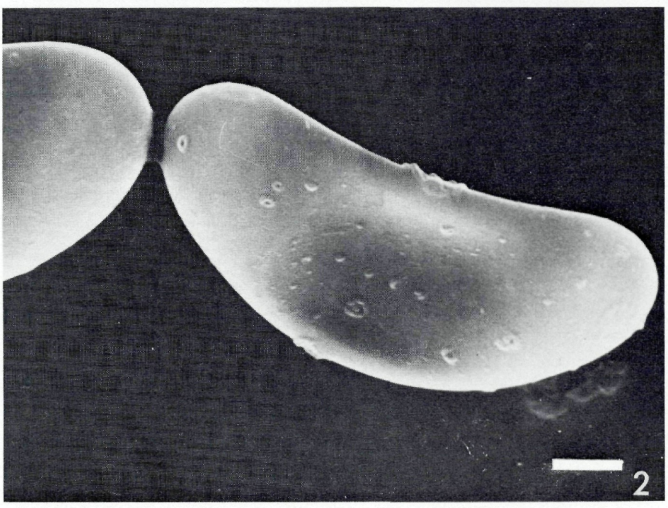


Fig. 1. *Camillea bacillum*. Ascospores. Scanning electron microscope, line = 1 μm
Fig. 2. *Thamnomyces chordalis*. Ascospores. Scanning electron microscope, line = 1 μm

because of the presence of true paraphyses, carbonized stromata and holoblastic denticulate or geniculate conidiogenesis.

The amyloid ascal apex is such an obvious feature of the Xylariaceae that its absence has been the basis for taxa at various levels. At least three genera, *Ascotricha* BERKELEY, *Phylacia* LÉVEILLE and *Rhopalostroma* HAWKSWORTH (HAWKSWORTH, 1977) are maintained in large part because of their fugacious asci. DENNIS (1961) and MÜLLER & ARX (1973) recognized the subfamily Thamnomycetoideae for stromatic genera whose asci are fugaceous. There is, however, a tendency within the Xylariaceae for asci to become simplified. Apical rings of some species are large while in others they are small and inconspicuous. In some species the ring is consistently inamyloid while in other species it is iodine positive or iodine negative depending upon the collection (ROGERS, 1979). DENNIS (1957) described typically xylariaceous asci for several species of *Camillea* but asci of *C. bacillum*, an undoubted member of the genus, have simple apices and are deliquescent. Conversely, asci of most species of *Ascotricha* (HAWKSWORTH, 1971), including the type, lack a ring and are deliquescent but in at least one species, *A. erinacea* ZAMBETTAKIS (KHAN & CAIN, 1977), they have an amyloid ring. A further step in ascal reduction is seen in the monotypic genus *Pulveria* MALLOCH & ROGERSON (1977) whose asci are reduced to spheres that lack a discharge mechanism and that are borne in chains.

Within the Xylariaceae, species whose asci deliquesce belong to different developmental lines and are not necessarily closely related. *Ascotricha*, a non-stromatic genus, is not related to *Phylacia* or *Rhopalostroma*, which are probably derivatives of *Kretzschmaria* FRIES and have little to do with either *Thamnomyces* or *Camillea*. Because the phenomenon of ascal deliquescence is found throughout the family (as it is in other families, e. g. the Hypocreaceae), a separate subfamily for species having such asci serves no useful purpose. Genera based on ascal deliquescence are also of dubious value because, as is shown above, some species of a genus may have an apical ring while in others the ring is lacking.

Relationships of *Camillea* and *Thamnomyces*

Anatomically, stromata of *Thamnomyces chordalis* and *Camillea bacillum* are similar, consisting of a white, fibro central core and a brittle outer sheath that is formed by deposition of black, amorphous material that eventually obliterates cellular structure. Ascomata of both species are embedded within the stroma and they do not rupture the brittle, outer layer. Ascomata of *T. chordalis* appear superficial but actually have a covering that is continuous with the surrounding stromal tissue. The stroma of *Thamnomyces* is not a single ascoma with scattered areas of ascal production as was suggested by LLOYD (1917).

Ascomata of both *Thamnomyces* and *Camillea* are delimited from surrounding stromal tissue by a thin, discrete wall that can be revealed by chipping away the overlying carbonaceous tissue with the tip of a scalpel.

Morphologically, stromata of *Thamnomyces* resemble stromata of some species of *Xylaria* HILL ex GREVILLE [cfr. *X. carpophila* (PERSOON) FRIES and *X. filiformis* (FRIES) FRIES] but the similarity may be only superficial. The composition of the outer layer of the stroma and the arrangement of ascomata within the stroma is far more reminiscent of *Hypoxylon* and *Rosellinia* than of *Xylaria*. In *Xylaria* the stromal surface is usually thin and soft; ascomata are partially to completely erumpent through the stromal surface while in *Hypoxylon* and *Rosellinia* the stromal surface is continuous over the ascomata and is often hard and lacks discernable cellular structure.

The *Nodulisporium*-like anamorph found in cultures of *T. chordalis* indicates little about relationships of *Thamnomyces* to other genera within the Xylariaceae. According to ROGERS (1979) *Nodulisporium* PREUSS anamorphs are found in *Daldinia* CESATI & NOTARIS and some sections of *Hypoxylon*. Denticulate-sympodial conidiogenesis is found in the few known anamorphs of *Xylaria*, but unlike *T. chordalis*, the conidiophores in those species are united into a tight palisade (= *Xylocladium* SYDOW; MORGAN-JONES & HASHMI, 1973, ROGERS, 1979). We do not know whether the anamorph of *T. chordalis* is more complex when found in nature. MÖLLER (1901) germinated ascospores of *T. chamissionis* EHRENBERG but conidia did not from in culture. BREFELD & TAVEL (1891) had the same experience with a *Thamnomyces* sp. sent to them by HENNINGS from Brazil.

DENNIS (1970), without comment, placed *Thamnomyces* in the Diatrypaceae. Although the Diatrypaceae and the Xylariaceae share many features, including method of conidiogenesis, the morphology of ascospores in *Thamnomyces* and the *Nodulisporium*-like anamorph found for *T. chordalis* do not support such a rearrangement. Inasmuch as *Nodulisporium*-like anamorphs are found in *Hypoxylon* and stromatal anatomy of *Thamnomyces* is similar to that of *Hypoxylon* or *Rosellinia*, we believe that the affinities of *Thamnomyces* lie closer to *Hypoxylon* and *Rosellinia* than to *Xylaria*, in spite of the morphological similarity to that genus.

Camillea has long been thought to be related to applanate species of *Hypoxylon* (DENNIS, 1957; ROGERS, 1979) and ROGERS (1979) supported that theory in finding that some species of *Camillea* share peculiar ascospore surface ornamentation with some species of *Hypoxylon*. We found that ascospores of both *Camillea bacillum* (Fig. 1) and *T. chordalis* (Fig. 2) are smooth, a common feature in the Xylariaceae (ROGERS; 1979). The *Geniculosporium* CHESTERS & GREENHALGH anamorph of *C. bacillum* does help to confirm the relationship to

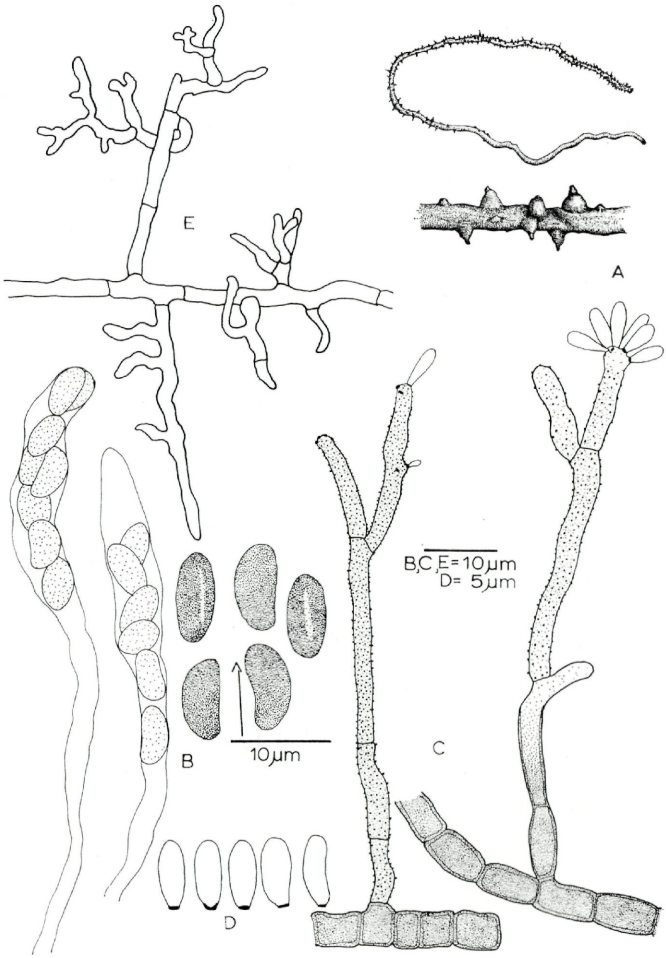


Fig. 3. *Thamnomyces chordalis*. A. Habit sketch of stroma and ascomata, not drawn to scale. — B. Asci and ascospores. — C. Conidiophores. — D. Conidia. — E. Branched hyphae found on oatmeal agar

Hypoxylon since *Geniculosporium* was previously known only in *Hypoxylon* and *Rosellinia* (ROGERS, 1979).

Descriptions of the Species

Following are redescriptions of *Thamnomyces chordalis* and *Camillea bacillum* drawn from the cited collections. Ascospores of both species were isolated with the aid of a micromanipulator. The surface of air dried, gold coated ascospores were studied with a JEOL JSM 35C scanning electron microscope.

1. *Thamnomyces chordalis* FRIES, Linnaea 5: 534. 1830. — Figs. 2, 3
= *T. rostratus* MONTAGNE, Ann. Sci. Nat. Bot. Sér. 2, 13: 339. 1840.

Anamorph: *Nodulisporium* like.

Stromata arising from wood of recently killed trees in fascicles. Individual ascostroma black, filamentous, unbranched, up to 15 cm long × 0.5—1.5 mm diam. and circular in cross section with ascomata arising along the length of the ascostroma. Stroma consisting of two intergrading regions, a central core, ca. 100 µm wide of white to tan hyphae running the entire length of the stroma. Toward the exterior of the stroma the cells becoming increasingly agglutinated and black; at the exterior of the stroma the hyphal aspect no longer apparent, cells completely encrusted in hard, black, resinous material, sticky when moist, which can be chipped away. Ascomata first appeared a hemispherical protuberances on surface of ascostroma, at maturity assuming a flask-shapped, rostrate form. Mature ascomata ca. 1000 µm high, including a 400—500 µm long papilla, × 900 µm wide basally. Ascomatal wall of two regions: outer region wide and continuous with outer region of stromal wall; inner region a discrete, very thin wall composed of unpigmented or lightly pigmented, flattened, pseudoparenchymatous cells, 10—15 × 8—10 µm, with walls <1 µm thick. Papilla cylindrical, pierced by a canal, periphyses not seen.

Asci cylindrical to clavate, sporogenus portion 40—50 µm long × 6.5—10.0 µm, stalk >100 µm long, 8-spored; apex simple, rounded, I — (with or without pretreatment with 3% KOH); forming on the entire inner surface of the ascomatal wall; deliquescing as ascospores begin to turn brown. Ascospores reform (6.6—)8.5—10.5(—11.4) × 3.8—4.8(—5.4) µm, unicellular, dark brown, with a germ slit ca. 5 µm long on the convex side of each ascospore, smooth. Paraphyses present between asci, septate branching 4.5 µm wide. Characteristics in culture Colonies on oatmeal agar (DIFCO) in 10 days at 20C, 12h darkness/12 h near ultraviolet light, 9 cm diam.; mycelium dense, felty, grey, hyphae turing green in 4% KOH, many erect hyphae having irregularly branched ends. Conidiophores arising profusely from surface of agar in areas of little aerial mycelium and from aerial

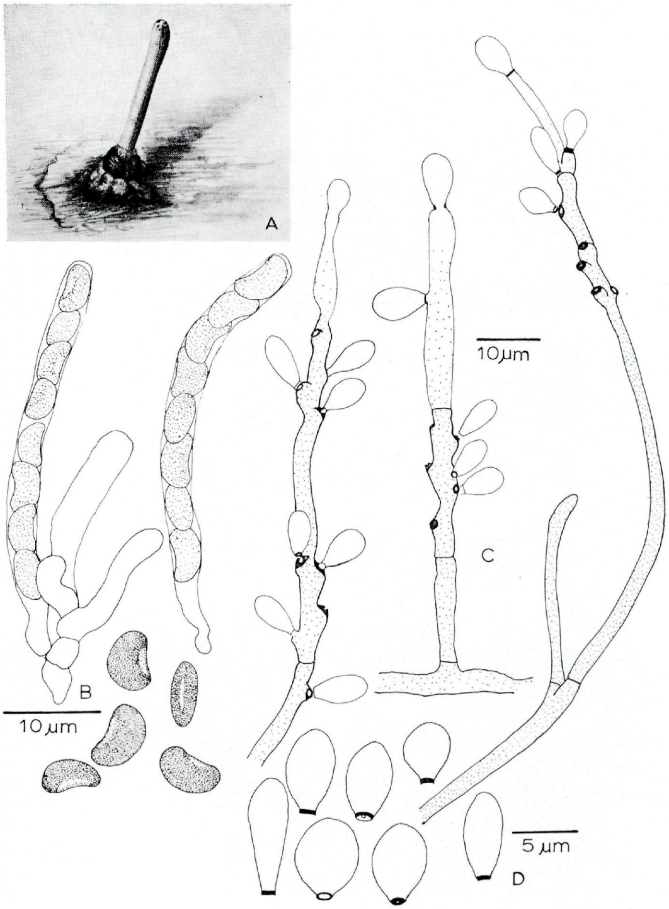


Fig. 4. *Camillea bacillum*. A. Habit sketch of stroma, approximately ×3. — B. Asci and ascospores. — C. Conidiophores. — D. Conidia

mycelium in other areas of the colony. Conidiophores pale violet in 4% KOH, arising from 3.4 µm wide hyphae, erect, 70—80 µm long × 2.3 µm basally, spinulose, septate, unbranched, or infrequently branched, each branch a sympodially elongating, 12—30 µm long conidiogenous cell bearing inconspicuous lateral and/or terminal, irregularly spaced slightly proturberant, cicaterized abscission scars.

Conidia oblong (4.7—) 5.7—7.4 (—8.0) × (1.6—) 1.9—2.6 (—2.7) µm, unicellular, with a cicatrized, basal abscission scar, hyaline; forming in basipetal succession; borne in dry, easily dispersed heads.

Specimens examined. — Brazil: Amazonas, Estacao Experimental de Silvicultural Tropical on the Manaus-Caracaraí Rd, at a point 45 km from the intersection of the Manaus-Itacoatiara Rd., on dead log, K. P. Dumont, E. M. M. Freire, D. R. Hosford, G. J. Samuels, W. C. Steward, W. R. Buck, 6 Nov 1977 (Dumond-BR 156: INPA, NY); Territorio de Roraima, along the Manaus-Boa Vista Rd. (BR 174) at a point ca 335 km from the intersection of the Manaus-Itacoatiara Rd., on dead log, K. P. Dumont, D. R. Hosford, G. J. Samuels, W. R. Buck, I. Araijo, M. A. Souza, J. C. Bernardi, 17 Nov 1977 (Dumont-BR 443: INPA, NY). — Ecuador: Quito, leg. Dr V. Lagerheim, 1890 (Rehm: Ascomyceten 1029, as *Thamnomyces rostratus*, ZT).

2. *Camillea bacillum* (Montagne) Montagne, Ann. Sci. Nat. Bot. Sér. 4, 3: 113. 1855. — Figs. 1, 4

= *Thamnomyces bacillum* Montagne, Ann. Sci. Nat. Bot. Sér. 2, 8: 858. 1837.

Anamorph: *Geniculosporium* sp.

Stromata arising from wood of recently killed trees, solitary, scattered, 3—6 mm long × 0.50—0.75 mm diam., black, columnar, finely, longitudinally sulcate over entire length and annellate on the lower half of the stroma; apex rounded, bearing a few inconspicuous depressions corresponding to ascomatal openings, base slightly bulbous. Stroma comprised of two intergrading regions: a central flexuous core of white to tan hyphae and a brittle outer crust lacking apparent cellular structure. Ascomata immersed just below the stromal tip in groups of 2—6. Individual ascomata up to 1.5 mm long with a very thin, discrete wall; each with an ostiolar canal.

Asci cylindrical, 34—45 (—55) × 3—5 µm, 8-spored; apex simple, rounded, I—(with or without pretreatment with 3% KOH), arising from croziers in an extensive ascogenous system that lines the ascomatal wall; ascospores uniseriate, ascal wall deliquescing soon after spores are delimited. Ascospores reniform, 6—7 × 3—4 µm, with a germ slit in the concave side of the spore, brown, smooth. Paraphyses present between asci, septate, thin-walled, ca. 2 µm wide.

Characteristics in culture: Colonies on potato dextrose agar (Difco) in one month at 20C, 12h darkness/12h near ultraviolet and cool while fluorescent light ca. 8 cm diam; mycelium dense, aerial hyphae short; hyphal tufts arranged in poorly defined radial lines; grey-green. In reverse black pigment localized under the hyphal tufts and under the margin of the colony. On malt extract agar colonies transparent with scattered hyphal tufts; poorly developed, brown synnematous structures forming in center of colony.

Conidiophores arising from hyphal tufts and synnematous structures, erect, variable in length, light brown, conidia forming along the entire length. Conidiogenous cells tretic, sympodially elongate, with irregularly spaced geniculations, each geniculation with a pronouced, cicatrized pore. Conidia subglobose to elliptic to clavate to oblong, (4.7—) 5.6—8.1 (—9.4) × 3.3—4.5 (—5.4) µm, unicellular, hyaline, smooth.

Specimens examined. — Brazil: Territorio de Roraima, Acampamento do 6° BEC-Jundia, on the Manaus-Caracarí Rd. at a point ca. 328 km from the intersection of the Manaus-Itacoatiara Rd., on wood, K. P. Dumont, D. R. Hosford, G. J. Samuels, W. R. Buck, A. Araujo, M. A. Souza, J. C. Bernardi, 17 Nov 1977 (Dumont-BR 346: NY, INPA).

Acknowledgments

The authors express appreciation to Dr. Ian C. Hallett (PDD) for his assistance with electron microscopy and to Ms. Marie E. Lanigan (PDD) for preparing the habit sketches of *Thamnomyces chordalis* and *Camillea bacillum*.

Research was supported in part by Projecto Flora Amazonica — The New York Botanical Garden (NSF, INT 77-17704) and by a grant from the American Philosophical Society to the senior author.

References

Brefeld, O. & Tavel, F. von (1891). Ascomyceten II. Chapter 10 [in] O. Brefeld, Untersuchungen aus dem Gesammtgebiete der Mykologie. Fortsetzung der Schimmel- und Hefenpilze. — 370 p, pl. 1—13. Heinrich Schoningh. Münster.

Dennis, R. W. G. (1957). Further notes on tropical American Xylariaceae. — Kew Bulletin 1957: 297—332.

— (1961). Xylarioideae and Thamnomycetoideae of Congo. — Bull. Jard. Bot. Etat Brux. 31: 109—154.

— (1970). Fungus Flora of Venezuela and adjacent countries. — Kew Bulletin Additional Series III. XXXIV+531 p, pl. 1—15, fig. 1—9. J. Cramer, Lehre.

Hawksworth, D. L. (1971). A revision of the genus *Ascotricha* Berk. — Mycol. Pap. 126: 1—28+pl. 1—5.

— (1977). *Rhopalostroma*, a new genus in the Xylariaceae s. l. — Kew Bulletin 31: 421—431.

Khan, R. S. & Cain, R. F. (1977). The occurrence of amyloid plugs in the asci of *Ascotricha erinacea*. — Mycotaxon 5: 409—414.

LLOYD, C. G. (1917). Synopsis of some genera of the large pyrenomycetes. — 16 p. published by the author, Cincinnati.

MALLOCH, D. & ROGERSON, C. T. (1977). *Pulveria*, a new genus of Xylariaceae (Ascomycetes). — Canad. J. Bot. 55: 1505—1509.

MÖLLER, Alfred (1901). Phycomyceten und Ascomyceten Untersuchungen aus Brasilien. Vol. 9 [in] SCHIMPER, A. F. W. [ed] Botanische Mittheilungen aus den Tropen. — 319 p+pl. 1—11. Verlag Gustav Fischer, Jena.

MORGAN-JONES, G. & HASHMI, M. H. (1973). The conidial state of *Xylaria johorensis*. — Canad. J. Bot. 51: 109—111.

MÜLLER, E. & ARX, J. A. von (1973). Pyrenomycetes: Meliolales, Coronophorales, Sphaeriales Chapter 6 [in] G. C. AINSWORTH, K. K. SPARROW & A. S. SUSSMAN [eds.] The Fungi An Advanced Treatise. Vol. IVA A Taxonomic Review with Keys: Ascomycetes and Fungi Imperfecti XVIII+621 p. ACADEMIC PRESS, New York & London.

ROGERS, J. D. (1979). The Xylariaceae: Systematic, biological and evolutionary aspects. — Mycologia 71: 1—42.