MYCOTAXON

AN INTERNATIONAL JOURNAL DESIGNED TO EXPEDITE PUBLICATION OF RESEARCH ON TAXONOMY & NOMENCLATURE OF FUNGI & LICHENS

Volume XI April-June 1980 No. 1

CONTENTS

[MYCOTAXON for January-March 1980 (10: 265-524) was issued February 23, 1980]

ISSN 0093-4666 *MYXNAE 11(1) 1-408 (1980)*

Library of Congress Catalogue Card Number 74-7903

Published quarterly by MYCOTAXON, Ltd., P.O. Box 264, Ithaca NY 14850
For subscription details and availability in microform, see back cover

MYCOTAXON

Vol. XI, No. 1, pp. 1-129 April-June 1980

GAEUMANNOMYCES, LINOCARPON, OPHIOBOLUS AND SEVERAL OTHER GENERA OF SCOLECOSPORED ASCOMYCETES AND PHIALOPHORA CONIDIAL STATES, WITH A NOTE ON HYPHOPODIA

J. WALKER

Biology Branch, Biological and Chemical Research Institute, N.S.W. Department of Agriculture, Private Mailbag No.10, Rydalmere, N.S.W., 2116, Australia

SUMMARY

The genera Acanthophiobolus Berlese, Acanthotheciella v. Höhn., Cylindrina Pat., Dilophia Sacc., Exilispora Tehon & Daniels, Gaeumannomyces v. Arx & Olivier, Lidophia Walker & Sutton, Linocarpon H.& P. Sydow, Microstelium Pat., Ophiobolus Riess, Ophiochaeta (Sacc.) Sacc.,Ophiosphaerella Speg.,Ophiosphaeria Kirschst., Ophiotrichia Berlese and Schizacrospermum P. Henn. are described and discussed on the basis of their type specimens. Gaeumannomyces is re-defined as a hyphopodiate genus. G. caricis n. sp. on Carex and Ophiosphaerella erikssonii n. sp. on Calamagrostis are described. New combinations are made in the genera Leptospora Rabenh., Lophodermium Chev., Ophioceras Sacc., Ophiosphaerella Speg., Phialophora Medlar, Plagiosphaera Petrak and Sphaerulina Sacc.. Several other species in the above genera and in Lasiosphaeria Ces. & de Not., Leptosphaeria Ces. & de Not., Leptosphaeriopsis Berlese, Leptosporopsis v. Höhn., Linospora Fckl., Phaeosphaeria Miyake, Rhaphidophora Ces.& de Not., Rhaphidospora Fr. & Mont., Sphaeria Haller ex Fr. and Winterella auct. are also considered. Phialophora radicicola Cain is described from its type specimen and culture, and related Phialophora spp. and conidial states of Gaeumannomyces are considered. The use of the terms hyphopodium and appressorium for some organs of attachment and penetration is discussed.

INTRODUCTION

During work on the taxonomy of the cereal take-all and related fungi (Walker, 1972, 1980), type specimens and other collections of several genera of scolecospored perithecial and pseudothecial fungi have been examined. Descriptions of some of these have been included (Walker, 1980) in a book dealing with the biology and control of take-all (Asher and Shipton, 1980) but this does not include taxo-

nomic detail, no specimens are listed and several genera unconnected with take-all are not included.

The aim of the present paper is to provide taxonomic and specimen details for the genera and species included in Walker (1980) and to give similar information and detailed descriptions for several other genera and species not dealt with there. Details are also included for Phialophora conidial states of Gaeumannomyces, and related Phialophora spp., and a short discussion on the use of the term hyphopodium for hyphal organs of attachment and penetration in these fungi is given. Genera are considered in alphabetical order, and synonyms are cross-referenced in the text. Herbarium abbreviations used are those of Holmgren and Keuken (1974, 1976, 1977, 1978). The symbol ! after a herbarium abbreviation indicates that type material from that herbarium has been studied. Publication dates for some earlier references and, in particular, for the various pages and parts in the four volume Icones Fungorum by A.N. Berlese, are taken from Stafleu and Cowan (1976). Indices under specific epithet, and host or substrate, are given at the end.

Frequent reference is made, especially under Gaeumannomyces, Ophiosphaerella, Phaeosphaeria and Phialophora to Walker (1980) where details not repeated here will be found. The various chapters in Asher and Shipton (1980) give details of the biology and pathology of Gaeumannomyces graminis and its varieties, and also an extensive bibliography on all aspects of the cereal take-all diseases and the associated fungi.

It is possible that the name Phialophora graminicola (Deacon) Walker, published formally as a new combination in the present paper, may be found already in papers by other authors dealing with cereal root fungi, especially S.D. Garrett and J.W. Deacon. Use of the name in such papers is provisional, pending its formal publication in this paper. This is mentioned in order to avoid any confusion at a later date about the publication date of this binomial.

ACANTHOPHIOBOLUS

Acanthophiobolus Berlese, separate from Atti del Congresso Bot.Int., Genova, pp.4-5, 1892 (see note below about date) Type sp. A. helminthosporus (Rehm) Berl.
≡ Ophiotrichia Berlese, Icon. fung. 1, 105, Jan.1893 (not validly published; based on Leptospora helminthospora Rehm, as Acanthostigma helminthosporum (Rehm) Sacc., see discussion under Ophiotrichia).
≡ Ophiochaeta (Sacc.) Sacc., Syll. Fung. II, Pt. 3, 352, 1895.
Lectotype sp. O. gracilis (Niessl) Sacc.
= Ophiosphaeria Kirschstein, Verh.Bot. vereins Prov. Brandenb.48 (1906), 47-48, 1907.

Type sp. O. tenella Kirschst.

Berlese (1892) erected his new genus for Leptospora helminthospora Rehm (1882), originally described on rotting cloth from Augsburg, West Germany. He also included several species placed by Saccardo (1883) in Ophiobolus subgenus Ophiochaeta. Acanthophiobolus was distinguished from Ophiobolus by superficial perithecia, ornamented especially on their upper surface with black, rigid divergent setae. This was the character that Saccardo (1883) had used for his subgenus Ophiochaeta. In contrast to this, Berlese (1892) removed the setose species from this subgenus to Acanthophiobolus and retained in subgenus Ophiochaeta those species attached to a meandering basal mycelium and he designated Ophiobolus herpotrichus as the subgeneric type. Further discussion of this and of the confusion surrounding the name Ophiochaeta is given below under that name.

A study of the types of several species has shown that they cannot be distinguished and should be placed in the one species of Acanthophiobolus. The earliest epithet found so far for this species comes from Sphaeria helicospora Berk. & Br. (1852). A description and illustration of the specimens of S. helicospora in K were given by Walker (1972) and a partial synonymy proposed. A more extensive synonymy and detailed description, with list of specimens examined is given here.

Acanthophiobolus helicosporus (Berk.& Br.) Walker, Trans. Brit. mycol. Soc. 58 (3), 445, 1972.

≡ Sphaeria helicospora Berk. & Br., Ann. Mag. Nat.Hist. ser.2, 9, 383, 1852 (type in K !)

≡ Ophiobolus helicosporus (Berk.& Br.) Sacc.,Syll.Fung. 2, 350, 1883.

= Sphaeria chaetophora Crouan, in Crouan & Crouan, Fl. Finist. 26, 1867 (type in CO !)

≡ Ophiobolus chaetophorus (Crouan) Sacc., Syll. Fung. 2, 353, 1883.

≡ Ophiochaeta chaetophora (Crouan) Sacc., Syll. Fung. 11, Part 3, 352, 1895.

≡ Ophiosphaeria chaetophora (Crouan) Kirschst.,Ann. Mycol. 34, 198, 1936.

= Lasiosphaeria gracilis Niessl, Notizen über neue und kritisch. Pyrenomyc., p.36, 1876 (type in M !)

≡ Acanthostigma gracile (Niessl) Sacc., Syll. Fung. 2, 210, 1883.

≡ Ophiochaeta gracilis (Niessl) Sacc., Syll. Fung. 11, Part 3, 352, 1895.

≡ Ophiosphaeria gracilis (Niessl) Kirschst.,Kryptogamenfl. Mark Brandenburg 7 (2), 204, 1935 (original not seen; from Müller, 1952).

≡ Ophiobolus gracilis (Niessl) Müller, Ber. schweiz bot. Ges. 62, 336, 1952.

≡ Acanthophiobolus gracilis (Niessl) v.Arx & Müller Studies in Mycology (Baarn) No.9, 83, 1975.

= Leptospora helminthospora Rehm, Hedwigia 21, 122,

1882, (type in S !)

≡ Acanthostigma helminthosporum (Rehm) Sacc., Syll. Fung. 2, 210, 1883 (Saccardo incorrectly gives 'Lasiosphaeria' helminthospora Rehm as the basionym)

≡ Acanthophiobolus helminthosporus (Rehm) Berlese, separate from Atti del Congresso Bot. Int., Genova, pp. 3-5, 1892.

≡ Ophiochaeta helminthospora (Rehm) Sacc., Syll. Fung. 11, Part 3, 352, 1895.

= Ophiosphaeria tenella Kirschst., Verh. Bot. vereins Prov. Brandenb. 48 (1906), 47-48, 1907 (type in B !)

(Comments on names: (i) Berlese (1892) included Lasiosphaeria gracilis Niessl, Sphaeria chaetophora Crouan and Rhaphidophora incompta Car. & de Not. in Acanthophiobolus but did not make new combinations in Acanthophiobolus for these epithets. (ii) Müller (1952) placed Ophiochaeta cladii Cruchet (1923) on Cladium mariscus (L.) Pohl as a synonym of Ophiobolus gracilis after study of the Cruchet collection, but did not mention the spirally arranged ascospores. Cruchet's specimen has not been studied during the present work so O. cladii is not listed formally in synonymy here, although it is probably A. helicosporus (for several collections on Cladium mariscus, see below). (iii) In the literature, the name 'Lasiosphaeria helminthospora Rehm' has also been seen but Rehm (1882) described his species as Leptospora helminthospora and I could find no evidence of publication of the Lasiosphaeria name. As Holm (1957) pointed out when discussing Leptospora, there was some confusion in the earlier literature regarding Leptospora and Lasiosphaeria. (iv) On the label of Sphaeria helicospora Berk. & Br. issued as F. europ. 141, Rabenhorst noted that he considered it a new genus, but apparently he never described it).

Ascocarps superficial, globose to subglobose to broadly conical, often with flattened base, dark brown to black, 150-300 µm diam, with rigid, dark brown to black setae, especially on their upper half; wall thin, of 3-6 layers of cells, outer layer a textura angularis of cells 10-20 µm diam with thin brown walls, cells smaller around the ostiole and tending to be arranged concentrically around it in some collections; ostiole 25-40 µm diam; setae arising from dark brown cells in ascocarp wall, 7-15 µm wide at the base and tapering to a rounded, paler apex 2-4 µm wide, septate, variable in length, many 150-250 (300) µm, amongst these several forming a shorter series 80-120 µm long, ostiole surrounded by 10-20 short, dark brown, conical setae, with obtuse or acute apex, 10-14 µm wide at base, 4-6 µm at apex, 25-35 (45) µm long, projecting inwards over the ostiole (Fig.1), setae sometimes with a short narrowed zone 10-20 µm behind apex, seta wall 2.5-3 µm thick near base. Asci long cylindrical to elongated clavate, bitunicate, 110-165 x 7-10 µm, narrower near base, asci of variable length and maturity seen in the one ascocarp, apex rounded and slightly thickened, apical apparatus not seen, base foot-like, eight-spored. Ascospores tightly coiled in a dense spiral, direction of spiral clockwise viewed from apex of ascus, hyaline to faintly yellowish in mass, 1.5-2 µm wide, as long as or slightly longer than the asci but due to dense spiralling length not determined accurately, estimated at about 160 µm in an ascus 130-140 µm long. Pseudoparaphyses abundant, hyaline, filiform, of variable diameter and often showing several slightly swollen bumps along their length, (1) 1.5-2 (2.5) µm wide, longer than the asci. Superficial mycelium sparse, surrounding and joined to base of ascocarp, of

hyaline to pale brown septate hyphae, septa not prominent or abundant, branching and fusing into a loose reticulum or thin sheet, hyphae 2.5-5 µm diam, non-hyphopodiate.

On dead leaves, leaf sheaths, stems and inflorescence stalks of various, mainly monocotyledonous, plants in damp places, especially but not exclusively Cyperaceae and Gramineae, and on cloth; probably common in temperate areas.

Illustrations: Berlese (1892, setose ascocarp, ascus, ascospores; 1890-1900, Vol.2, as Ophiochaeta helminthospora, habit, setose ascocarp, ascus, ascospores); Dennis (1968, as A. helminthospora, setose ascocarp, ascus with spores); Kirschstein (1907, as Ophiosphaeria tenella, habit, setose ascocarp, ascus, ascospores); Walker (1972, ascocarps, asci, spiralled ascospores).

Specimens examined: On Carex acutiformis Ehrh., Surlingham Broad, Norfolk, England, 15.vi.1944, E.A. Ellis, IMI 16728b; Flatford Mill, Suffolk, England, 9.v.1948, J.P.Morgan, IMI 28563a (both as 'Ophiosphaeria gracilis').

On Carex elata All., Flatford Mill, Suffolk, England, 9.v.1948, M.B. Ellis 28566a (as 'Ophiosphaeria gracilis').

On Carex paniculata L., Le Vallon, France, date not given, in CO, HOLOTYPE of Sphaeria chaetophora Crouan (slides as DAR 33711); Batheaston, England, 7.vi.1867 (or 1869?), in Herb. Berkeley in K (slide as DAR 33712); Wiltshire, England, April 1859, C.E. Broome, Rabh. F. Europ. 141, dups. in K, L and UPS (as S. helicospora).

On Carex pendula L., Moccas Park, Hereford, England, no date, M.B. Ellis, IMI 47041 (as 'Ophiosphaeria gracilis').

On Carex riparia Curt., Rathenow, Germany, 9.v.1905, W. Kirschstein, in B, LECTOTYPE of Ophiosphaeria tenella Kirschst., see below (slides as DAR 32150); Wheatfen Broad, Norfolk, England, 28.iii.1948, M.B. Ellis, IMI 27781; same, 25.v.1946, IMI 34659; same, 29.v.1950, IMI 42024; Half Moon Island, Hickling Broad, Norfolk, England, M.B.and J.P. Ellis, IMI 34857 (all IMI collections as 'Ophiosphaeria gracilis').

On Cladium mariscus (L.) Pohl, all from Wheatfen Broad, Norfolk, England; 10.v.1947, E.A. Ellis, IMI 15413 (as 'Ophiochaeta sp.'); 17.viii.1947, E.A. and M.B. Ellis and R.W.G. Dennis, IMI 17329; 8.ii. 1948, E.A. Ellis, IMI 34392; 25.v.1948, E.A. Ellis, IMI 34588; 1.viii. 1949, E.A. Ellis, IMI 36147 (all as 'Ophiosphaeria gracilis').

On Cyperaceae, undet., sheet in K with three packets (a) on Carex paniculata (see above) (b) No.197, Spye Park, 19.iv.1850, LECTOTYPE of Sphaeria helicospora Berk. & Br. (see below), with drawing of asci and spiralled ascospores (slides as DAR 33713) (c) labelled 'Sphaeria helispora B. & Br.' and stamped 'Herb. Berk. 1879' (slide as DAR 33714); Spye Park, Wiltshire, March 1863, C.E. Broome, in UPS (as 'Sphaeria helicospora B. & Br.').

On Glyceria maxima (Hartm.) Holmb., Wheatfen Broad, Norfolk, England, 13.v.1945, E.A. Ellis, IMI 17404b (slide only showing setose ascocarps and asci with spiralled ascospores); Flatford Mill, Suffolk, England, 7.v.1948, J.P. Morgan, IMI 28561 (both as 'Ophiosphaeria gracilis').

On Iris pseud'acorus L., Kootheimer Teich, Brünn, Germany, July

1874, Niessl, in M, LECTOTYPE of Lasiosphaeria gracilis Niessl, see below (slides as DAR 33702); Rastatt, Germany, 20.viii.1875,Schroeter, in M (slides as DAR 33703).

On Juncus subnodulosus Schrank, Wheatfen Broad, Norfolk, England, 26.v.1947, E.A. and M.B. Ellis, IMI 15470b.

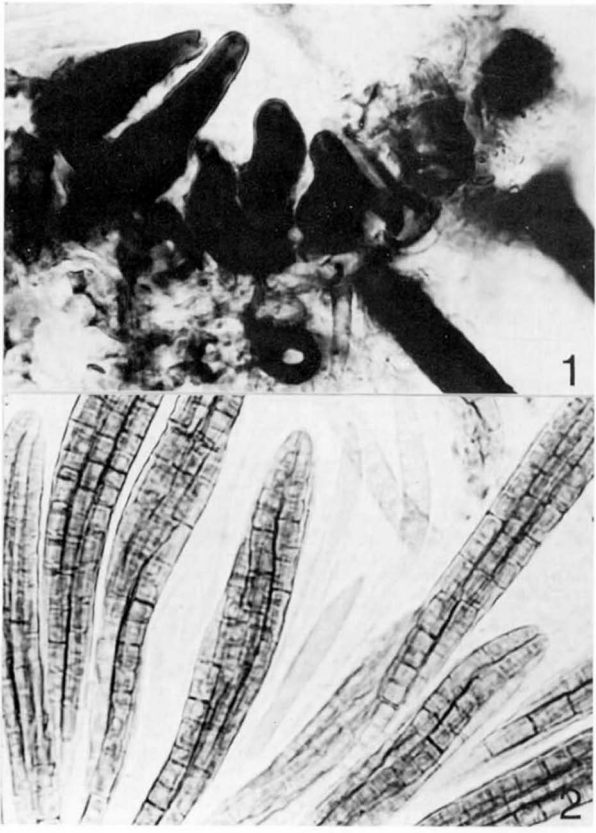
On Lepidosperma sp., Amiet's Track, near Laver's Hill, Victoria, Australia, 14.xi.1965, G. Beaton, IMI 116204 (as 'Ophiochaeta sp.'); first Australian record.

On Phragmites australis (Cav.) Trin. ex Steud. (as P. communis), Wheatfen Broad, Norfolk, England, 29.v.1950, M.B. Ellis, IMI 42032 (as 'Ophiosphaeria gracilis').

On rotted cloth, Augsburg, Germany, 14.ii.1880, M. Britzelmayr, in S, HOLOTYPE of Leptospora helminthospora Rehm (slides as DAR 33283).

Lectotypification is necessary for some of the names. In describing Sphaeria helicospora, Berkeley and Broome (1852) did not quote a definite collection, but stated 'On leaves of Cyperaceae, West of England'. From the material available in K, the small sheet numbered 197, marked 'Spye Park' and dated '19.iv.1850', showing the fungus as described above and with a drawing of an ascus with densely spirally arranged ascospores (figured in Walker, 1972) is chosen as LECTOTYPE of the name Sphaeria helicospora Berk. & Br.. It is the only collection seen which predates publication of the name and Spye Park is a country seat, 4 miles S.W. of Calne, Wiltshire, in the west of England (Bartholomew, 1943). In his original description, Kirschstein (1907) mentioned two collections of Ophiosphaeria tenella, on Glyceria spectabilis M. & K. and Carex riparia at Gross-Behnitz and Rathenow, in June 1904, and in 1905 but neither was listed as type. The collection in B labelled 'Ophiosphaeria tenella WK. Nv. sp. et. gen.' in Kirschstein's writing, on Carex riparia, Rathenow, 9.v.1905 with red sticker, is designated LECTOTYPE of the name Ophiosphaeria tenella Kirschst.. In describing Lasiosphaeria gracilis, Niessl (1876) listed two collections on Iris pseud'acorus from Brünn and Rastatt. The Brünn collection in M, labelled 'Lasiosphaeria gracilis n.s.' collected in July 1874 is chosen as LECTOTYPE.

The exact date of publication of Acanthophiobolus Berlese could not be determined from available sources. A copy of a separate from Atti del Congresso Botanico Internazionale Genova 1892 in the library of the Commonwealth Mycological Institute has pages numbered 1-10, one plate labelled 'Tab. xxii' and is dated at the end of the text 'Agosto 1892'. Acanthophiobolus is described on p.4. Saccardo (1895) in listing Acanthophiobolus as a synonym of Ophiochaeta (Sacc.) Sacc., gives its year of publication as 1892. In contrast, Clements and Shear (1931) and von Arx and Müller (1975) list it as published on p.571 of the Atti in 1893, and Lindau and Sydow (1908) cite the Berlese article on pp.567-576 of the Atti in 1893. It is not known whether the separate of the Berlese article dated August



Figures 1 and 2. 1. Acanthophiobolus helicosporus, short ostiolar setae and bases of long wall setae, x 733, from lectotype of Lasiosphaeria gracilis in M (slide DAR 33702). 2. Leptosphaeria compressa, asci and ascospores, x 733, from holotype of Exilispora plurisepta, ILLS 8404 (slide DAR 33733).

1892 was issued prior to the publication of the Atti in 1893. If it was, then August 1892 can be accepted as the date of publication of Acanthophiobolus Berlese (Art.30). If not, the date will be that in 1893 when the Atti were issued. The fact that Saccardo (1895) gave the 1892 date indicates that some printed matter may have been available then and the 1892 date has been used here.

Several authors recognised the close relationship between the species here reduced to synonymy under A. helicospora. Kirschstein (1907) commented on the similarity of Lasiosphaeria gracilis Niessl to his Ophiosphaeria tenella and, although no new combination was made at that time, suggested that Niessl's species be placed in Ophiosphaeria. Höhnel (1907) placed O. tenella in synonymy with Crouan's Sphaeria chaetophora as Ophiochaeta chaetophora. Weese (1921) commented on the extraordinarily close relationship between Leptospora (as Lasiosphaeria) helminthospora Rehm, Lasiosphaeria gracilis Niessl and Ophiobolus chaetophorus (Crouan) Sacc. and regarded them as species of Acanthophiobolus. Kirschstein (1936) agreed that O. tenella, S. chaetophora and L. gracilis were the same and reduced all to synonymy under Ophiosphaeria chaetophora. Malbranche and Niel (1890) noted the spiral arrangement of ascospores in S. helicospora and the similarity with S. chaetophora Crouan, but also noted that Berkeley and Broome (1852) had not mentioned setae in their original description of S. helicospora. Walker (1972) examined the collections of Crouan and of Berkeley and Broome, described and illustrated the setose ascocarps and spiralled ascospores, and showed that S. helicospora provided the earliest name for this fungus.

The collections of A. helicosporus examined came mainly from England and Europe, with one from Australia. It is perhaps more widespread than these collections indicate and may be a common saprophyte on dead leaves of Cyperaceae, to a lesser extent Gramineae and other monocotyledons and occasionally on textiles of plant origin. It seems to occupy an ecological position similar to that of some species of Chaetomium, another genus with appendaged ascocarps.

ACANTHOSTIGMA

Acanthostigma gracile (Niessl) Sacc. = Acanthophiobolus helicosporus (q.v.).

ACANTHOTHECIELLA

Acanthotheciella Höhn., Sitzungsber.Akad.Wiss.Wien 120, 451, 1911

Type sp. A. barbata (Pat. & Gaill.) Höhn. (as '(Pat.) Höhn!)

≡ Ophiobolus barbatus Pat. & Gaill., Bull. Soc. Mycol. Fr. 4, 114-115, 1888 (type in FH !)

≡ Ophiochaeta barbata (Pat. & Gaill.) Sacc., Syll.Fung. 11, Part 3, 352, 1895.

A full description and illustration of this and other species of Acanthotheciella and their Ypsilonia conidial states was given by Nag Raj (1977). Study of the type and other collections of A. barbata confirm his observations. Acanthotheciella is characterised by superficial dark glabrous, tuberculate or setose perithecia, seated on a pseudoparenchymatous hypostroma with surrounding mycelium, and containing aparaphysate unitunicate asci with hyaline to faintly pigmented scolecospores. It is associated with an Ypsilonia conidial state (Nag Raj, 1977). The known species occur on dead scale insects. Saccardo (1895) and Berlese (1900) listed O. barbata amongst the species they placed in Ophiochaeta (q.v.).

Illustrations: Nag Raj (1977, ascocarps, asci, ascospores, conidial state).

Specimens examined: sur écorce, Atures, Venezuela, July 1887, Herb. N. Patouillard No. 91, FH, HOLOTYPE of O. barbatus (slide as DAR 33715; only conidia seen); Puente de Chimbo, Venezuela, August 1891, Lagerheim, Patouillard sheet 5984 in FH (slides as DAR 33716; perithecia, asci, ascospores and conidial fructifications present); ad corticem arbor. frond., S. Leopoldo, Rick, no date, Patouillard sheet 5984 in FH (slide as DAR 33717; only conidia seen, possibly an aberrant form of A.barbata, see comments by Nag Raj, 1977).

COCHLIOBOLUS

The genus Cochliobolus Drechsler (1934) is not considered in this paper. Incidental mention of the genus is made under Leptospora, Ophiobolus heterostrophus and O.zeae.

CYLINDRINA

Cylindrina Patouillard, Bull. Soc. Bot. Fr.33,155-156, 1886. Type sp. C. delavayi Pat. (type in FH !)

Originally collected on dead leaves of Liparis liliiflora Reich. in Yunnan, China, Cylindrina delavayi was described with sparse smooth black cylindrical perithecia 1-2 mm high, with a truncated cupulate apex containing a circular, sometimes widely opened, ostiole, and very long thin asci 300-350 x 6-7 µm containing filiform continuous ascospores as long as the ascus. Paraphyses were described as linear. The genus was considered close to Acrospermum Tode. Arnaud (1912) noted the similarity of the descriptions of C. delavayi and Acrospermum parasiticum Syd. in Sydow & Butler (1911) (on leaf spots of Heptapleurum venulosum (Araliaceae), India) and concluded that Acrospermum and Cylindrina were closely similar genera. Ainsworth (1971), following Arnaud (1912), listed Cylindrina Pat. as a synonym of Acrospermum. Sherwood (1977, p.142) reduced Cylindrina to synonymy under Stictis Pers.. She commented on the sparse nature of the type collection and gave a brief description.

The type specimen is minute, consisting of a fragment

of leaf with one fruiting body. This is slightly less than 1 mm high and roughly 0.8 mm diam, black, circular in cross section, hollow, with its base embedded in the leaf tissue and a circular apical pore. The fruiting body is somewhat shorter than originally described and examination indicated that its apex may have been cut off at some stage. In view of the scarcity of the material, no slides were made. I doubt that it would be possible to categorise Cylindrina Pat. from this collection and would regard the synonymies suggested by Ainsworth (1971) and Sherwood (1977) as tentative. This generic name should not be used for later collections.

Specimen examined: on leaf of Liparis liliiflora, Yunnan, China, no date on label, Abbé Delavay, Herb. Patouillard 7226, in FH, HOLOTYPE of C. delavayi (a second label printed 'Herbarium Francavillanum' on which is written 'Cylindrina delavayi Pat.' is included with the specimen).

DILOPHIA

Dilophia Sacc., Syll. Fung. 2, 357, 1883 (Sphaeriaceae), non Dilophia T. Thompson, Hooker's J.Bot.5, 19, 1853 (Cruciferae).
Type sp. D. graminis Sacc. (Type in G!).

Dilophia Sacc. is a later homonym of Dilophia Thompson. The new generic name Lidophia Walker & Sutton (1974) was proposed for it (q.v.).

EXILISPORA

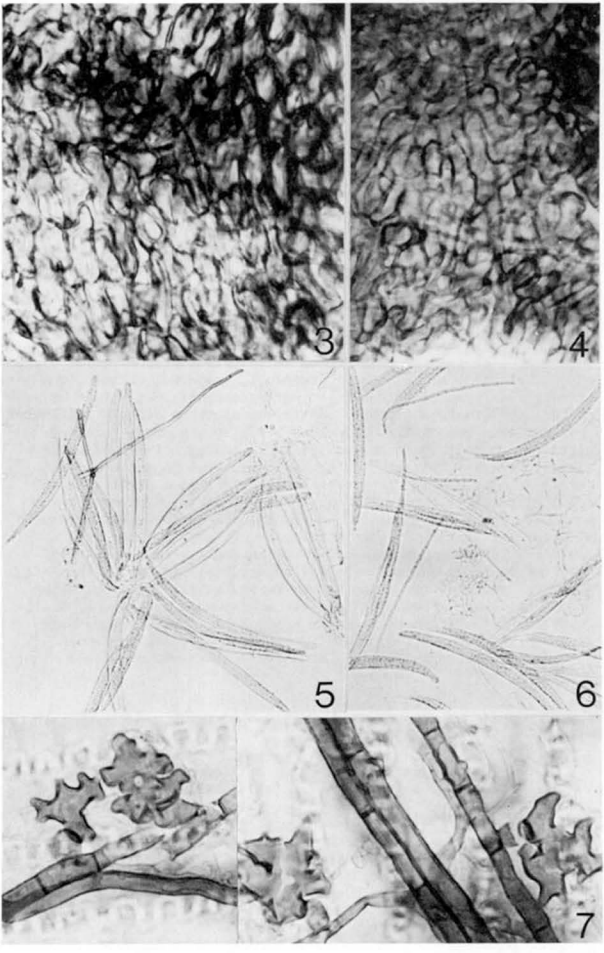
Exilispora Tehon & Daniels, Mycologia 19, 113, 1927
Type sp.E. plurisepta Tehon & Daniels (Type in ILLS !)

Petrak (1941) considered Exilispora as a synonym of Ophiobolus Riess. von Arx and Müller (1975) reduced it to synonymy with Leptosphaeria Ces. & de Not. and transferred the type (and only) species as L. plurisepta (Tehon & Daniels) von Arx & Müller. Study of the type specimen confirms its placement in Leptosphaeria, but it is considered to be not distinct from L. compressa (Rehm) Holm (see description under this name).

GAEUMANNOMYCES

Gaeumannomyces von Arx & Olivier, Trans.Brit. mycol. Soc. 35 (1), 29-33, 1952.
Type sp. G. graminis (Sacc.) von Arx & Olivier
≡ Rhaphidophora graminis Sacc., Nuovo Giorn.bot.ital.7, 307-308, 1875.

Figures 3 - 7. Gaeumannomyces. 3 and 4. G. graminis var. graminis, external wall layer of perithecium, x 733, from holotype in PAD (slide DAR 21032). 5 and 6. G. caricis, asci and ascospores, x 183, from holotype in C (DAR 32062). 7. G. caricis, associated hyphopodia, x 733, from holotype in C (slide DAR 32062)

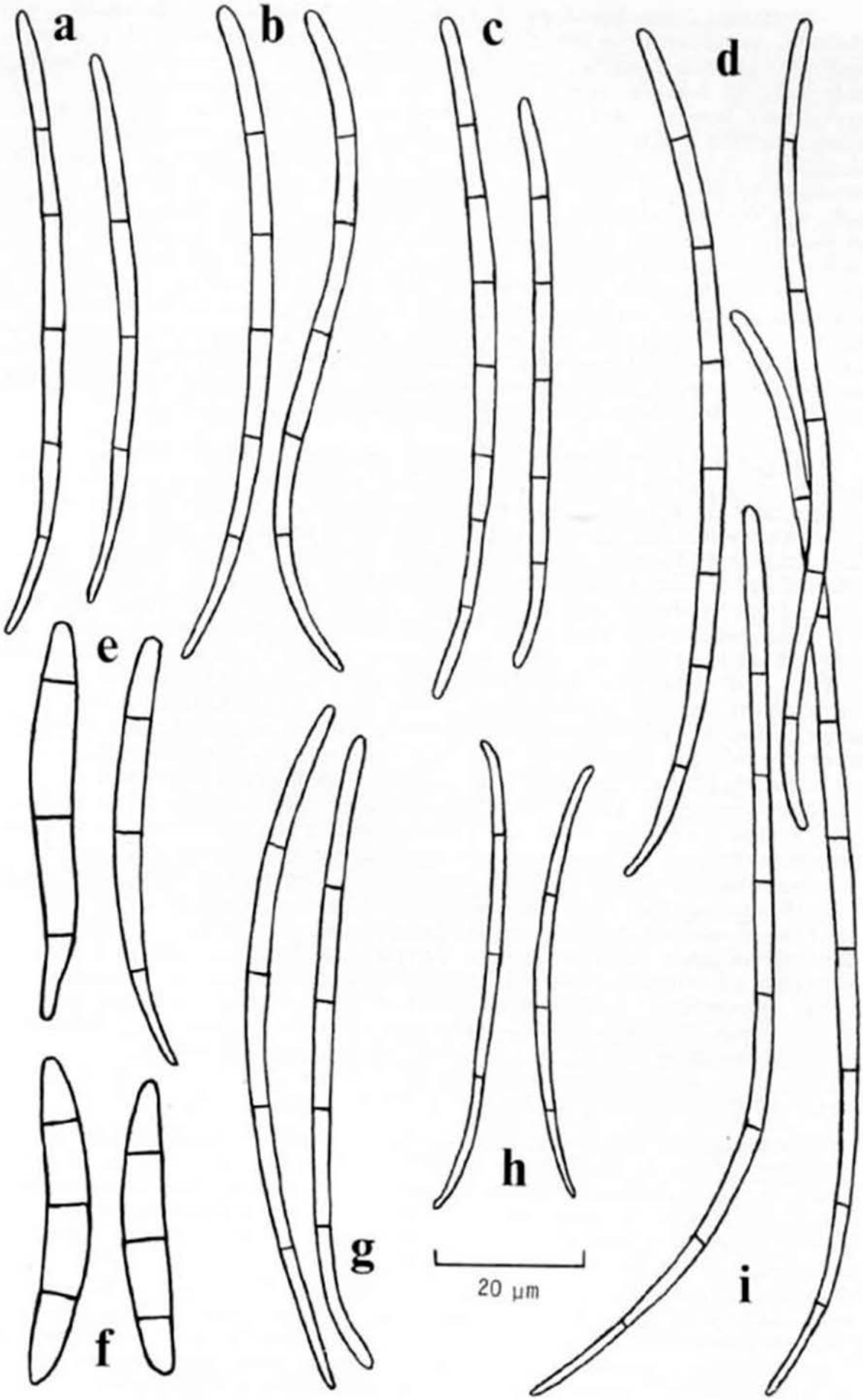

3
4
5
6
7

In describing their new genus, von Arx and Olivier (1952) did not examine the nomenclatural type, but based their description on specimens of the wheat take-all fungus, thought at the time to be Saccardo's fungus. Walker (1972) showed that they are distinct and established a new variety for the wheat take-all fungus (see below under G. graminis var. tritici). Examination of Saccardo's type and of many other collections of G. graminis and its varieties has shown that an important feature of Gaeumannomyces is production of a superficial mycelium on its hosts, with some hyphae forming strands and radiating fans, and others developing hyphopodia of various sorts. Hyphae and hyphopodia were not mentioned by von Arx and Olivier (1952) when describing Gaeumannomyces, so the generic description is amended here to include production of hyphopodia on a superficial mycelium as a generic character. The nature of the perithecial wall, of the paraphyses and of some spore characters is also clarified.

Gaeumannomyces von Arx et Olivier descr. emend.

Perithecia dispersa vel aggregata, corpus perithecii omnino immersum, globosum vel subglobosum vel late ellipticum, collo cylindrico subelongato vel elongato, erumpenti, medio vel obliquo, cum poro periphysibus punctiformi pertuso. Paries corporis cum strato externo textura epidermoidea (Figs. 3 and 4), ex pluribus stratis cellularum complanatarum compositis, olivaceus vel atro-brunneus, in sicco nigrescens. Asci numerosi, unitunicati, cylindrici vel elongati clavati, brevi stipitati, cum annulo refractivo in apice iodo non colorato, octosporis. Ascosporae (Fig. 8) in asco parallelae vel parum tortiles, filiformes vel anguste clavatae, plerumque parum arcuatae, primo continuae sed ad maturitatem septatae transversales plures, hyalinae vel dilutae ochraceae. Filamenta paraphyses simulans, septata , latissima basi, sensim decrescentia versus apices, ad maturitatem diffluentia. Mycelium superficiare ex hyphis brunneis septatis irregulariter ramosis laxe reticulatis compositum, hyphae parallelae plures plerumque in filis et interdum mycelium flabelliforme formantes, hyphae aliae cum hyphopodiis (Figs. 9 and 10) irregulariter dispositis, interdum vagina mycelialis fuliginea formantes hospiti insidens. Status conidialis (ubi cognitus) Phialophora.

Figure 8. Gaeumannomyces spp., pairs of ascospores. a. G. graminis var. graminis, from holotype in PAD (slide DAR 21032); b. G.graminis var. graminis, from lectotype of Ophiobolus oryzinus in PAD (slide DAR 21033); c. G. graminis var. tritici, from holotype, DAR 17916; d. G. graminis var. avenae, from neotype in K (slide DAR 32104); e. G. cylindrosporus, from holotype, IMI 192606 (dupl.DAR 31926); f. G. cylindrosporus, DAR 31925; g. G. tax. sp. 1 on Cyperaceae, DAR 32061; h. G.tax. sp. 3 on Cyperaceae, DAR 34174; i. G. caricis, from holotype in C (slide DAR 32062).


a
b
c
d
e
f
g
h
i
20 µm

Perithecia scattered or clustered, body completely immersed, globose, subglobose to broadly elliptical, with a cylindrical erumpent neck of variable length, placed centrally or obliquely on the body. Body wall in surface view a textura epidermoidea (Figs. 3 and 4), in section of several layers of flattened cells, olivaceous to dark brown, appearing black when dry. Asci numerous, unitunicate, cylindrical to elongated clavate, shortly stalked, with an apical refringent ring not coloured by iodine, eight-spored. Ascospores (Fig. 8) parallel or slightly curved, at first continuous but with several transverse septa at maturity, hyaline to faintly yellowish. Filaments resembling paraphyses between asci, septate, widest at the base and gradually narrowing towards the apex, dissolving at maturity. Superficial mycelium composed of brown septate irregularly branched hyphae forming a loose net-work, some parallel hyphae forming strands and sometimes radiating fans of mycelium, others with irregularly placed hyphopodia (Figs. 9 and 10), the mycelium sometimes forming a dark sheath on the host plant. Conidial state (where known) Phialophora.

All names in Gaeumannomyces are dealt with below. The accepted species are parasites on roots, crowns and lower stems and leaf sheaths of Gramineae and Cyperaceae. All produce superficial hyphopodiate mycelium, either on naturally infected stem and leaf sheath tissue and/or on inoculated cereal coleoptiles (Walker, 1980). Hyphopodia sometimes develop on roots and occasionally in agar culture (a discussion on the term 'hyphopodium' is given at the end of this paper). The aggregation of hyphae into strands, infection cushions (plate mycelium) and other organs of spread on, and infection of, the host is discussed in detail by several contributors to Asher and Shipton (1980). Ascospores in the known species are often tinted pale yellowish brown in mass and appear hyaline to faintly tinted singly. The tapering septate paraphysis-like filaments are readily seen in immature perithecia and have been figured for G. graminis var. graminis (as O. oryzinus) by Saccas and Fernier (1954) and for G. graminis var. tritici (as O. graminis) by Russell (1934) and Shoemaker (1974). In his study of perithecial development, Jones (1926) described and figured their formation by the 'mutual separation of vacuolated parenchyma to form the paraphysis-like filaments'. These so-called paraphyses in Gaeumannomyces thus represent the remains of the originally pseudoparenchymatous internal tissue of the perithecium, persisting as filamentous chains of cells during development of the asci, and later disintegrating (Jones, 1926).

Petrak (1952) reduced Gaeumannomyces to synonymy under Linocarpon H. & P. Sydow (1917). This is not in accord with the characters shown by the generic types. Gaeumannomyces produces a superficial mycelium with hyphopodia, non-stromatic perithecia are embedded in host tissue with an erumpent neck of variable length and position, and the known species are parasites of roots, crowns and lower stem and leaf sheaths of Gramineae and Cyperaceae. Linocarpon has no superficial mycelium, and perithecia are embedded in host tissue, covered by a dark clypeus and surrounded by variable development of stromatic tissue. The known

species are saprophytes on plants in various families, especially Palmae. The type species of Linocarpon, L. pandani, and Petrak's (1952) Linocarpon names are dealt with under Linocarpon.

Holm (1948) considered the wheat take-all fungus as close to Plagiosphaera Petrak (1941). von Arx and Olivier (1952), in describing Gaeumannomyces, discussed Plagiosphaera and regarded it as distinct from, though closely related to, their new genus. Barr (1978) placed the two genera in different families of the Diaporthales and present work supports their separation (see below under Plagiosphaera).

Gaeumannomyces graminis (Sacc.) von Arx & Olivier var. graminis, Trans.Brit.mycol.Soc.35 (1),29-33, 1952
- ≡ Rhaphidophora graminis Sacc., Nuovo Giorn.bot.ital. 7, 307-308, 1875 (type in PAD !)
- ≡ Ophiobolus graminis (Sacc.) Sacc. in Roum.& Sacc., Rev. mycol. 3, 45, 1881.
- ≡ Ophiochaeta graminis (Sacc.) K. Hara, Byôchû-gai Zasshi (J.Plant Prot.) Tokyo, 3(5), 342-345, 1916 (original not seen : from Tanaka, 1917)
- = Ophiobolus oryzinus Sacc., Nuovo Giorn.bot.ital., N.S. 23 (1), 203, 1916 (type in PAD !)
  - ≡ Linocarpon oryzinum (Sacc.) Petrak, Sydowia 6, 387, 1952.
  - ≡ Gaeumannomyces oryzinus (Sacc.) Schrantz (as 'oryzinum'), Bull.Soc.mycol.Fr.76(4), 337, 1961 (illegitimate, Art.33, Stafleu et al, 1972)
  - = Linospora pulchella Speg.,Anal.Mus.Nac.Hist. Nat. Buenos Aires 23, 71-72, 1912, illus. (type in LPS !)

This, the type variety of G. graminis, is a widespread, generally benign, parasite of several genera of Gramineae, although more pathogenic isolates are known (Walker,1972, 1973, 1975, 1980). Detailed descriptions, illustrations, hosts and geographic distribution are given in these references. It produces both simple and lobed hyphopodia (Fig.10) and has ascospores (70) 80-105 (110) x 2-3 (4) µm (Fig.8). Its use as a possible cross-protection agent against G. graminis var. tritici is discussed by Wong (1980).

Walker (1972) examined the types of Rhaphidophora graminis Sacc. and Ophiobolus oryzinus Sacc. and showed they were the same. Linospora pulchella Speg. also belongs here. In the type specimen, abundant perithecia are present in culm and leaf sheath tissue, associated with a superficial brown mycelium producing both pale simple and brown lobed hyphopodia. The unitunicate asci with an apical refractive ring contain ascospores typical of those of G. graminis var. graminis. From the description, Ophioceras sorghi Saccas (q.v.) may also be G. graminis var. graminis.

Details and comments are given below for several

collections examined. Others are listed by Walker (1972). Unless otherwise mentioned, all collections showed perithecia, asci, ascospores and associated superficial mycelium with pale simple and brown lobed hyphopodia. Several of the specimens are the basis for earlier literature reports of this fungus under one or other of its synonyms and, where relevant, references to the literature are included after the specimen details.

Illustrations: See Walker (1980) where some illustrations are given, and references to many in the literature are included.

Specimens examined: on Aristida sp., Tamworth, N.S.W., Australia, 1976, P.T.W. Wong ADI, DAR 33669.

on Avena sativa L., Rydalmere, N.S.W., Australia, 23.xii.1969, A.M. Smith, DAR 19212; same, 25.ii.1970, DAR 19602; same, 26.xi.1970, DAR 20645 (all artificial inoculations with culture ex DAR 19211 on Pennisetum).

on Axonopus compressus (Schw.) Beauv. (turf, mainly this species), sports stadium, Hong Kong, no date, H.C. Tang, IMI 71816, as Ophiobolus sp. (slide as DAR 33292).

on Axonopus sp. (carpet grass), Gosford, N.S.W., Australia, 8.v.1970, J. Gellatley, DAR 19982 (hyphopodiate mycelium only).

on Bromus unioloides H.B.K., Rydalmere, N.S.W., Australia, 12.vii.1972, P.T.W. Wong G1, DAR 23147 (see Wong, 1975); Walcha, N.S.W., Australia, 1977, P.T.W. Wong WAL9, DAR 33670.

on Chloris gayana Kunth., Grafton, N.S.W., Australia, 15.vi.1965, G. Wilson, DAR 14392 (hyphopodiate mycelium only).

on Cynodon dactylon (L.) Pers., Rydalmere, N.S.W., Australia, 17.i.1964, A.M. Smith, DAR 12417 (artificial inoculation with culture ex Pennisetum); Selva di Montella, N. of Treviso, Italy, 31.viii.1971, J. Walker, DAR 26005 (mycelium and lobed hyphopodia only).

on Cynodon or Agropyron, Selva, Treviso, Italy, Oct. (? 1874, P.A. Saccardo publ.1875), in PAD, HOLOTYPE of Rhaphidophora graminis Sacc. (slides as DAR 21032) (see Walker, 1972).

on Glycine max (L.) Merrill (as G. soja) isolated from pod, Indiana, U.S.A., 1974, K.W. Roy, culture producing abundant brown lobed hyphopodia, DAR 28746; same locality, colour slides of perithecia, asci and ascospores, ex K.W. Roy & D. Huber, DAR 30620. Unfortunately the perithecial material of this isolate was discarded and subsequent attempts to produce them with this culture have been unsuccessful (D. Huber, in litt.). Roy et al (1976) reported that the soybean isolates were highly pathogenic to wheat. One wonders whether the report of this fungus from soybean pods and leaves is the result of an adventitious infection from ascospores, which may have little significance as a disease of soybean.

on Microlaena stipoides R. Br., Newport, N.S.W., Australia, 1973, P.T.W. Wong G4, DAR 24168 (see Wong, 1975).

on Molinia japonica Hack., Gifu Prefecture, Japan, Feb. 1916, K. Hara, TNS - F210066 (slide as DAR 31879; formerly as Ophiobolus graminis Sacc. and Linocarpon cariceti; listed by Kobayashi (1970) as L.cariceti, specimen numbered in error as 210065).

on Oryza sativa L., all as Ophiobolus oryzinus Sacc. : Triangle, Rhodesia, 5.iii.1970, A Rothwell, IMI 147590; Peradeniya, Sri Lanka, 24.iii.1964, D.V.W. Abeygunawardena, IMI 104965; Lowland Farm, Shendam, Northern Nigeria, 3.xi.1959, Agricultural Officer, IMI 79545; Morogora area, Tanzania, July 1960, D.A. Burdekin, IMI 81744; Sembehun, Sierra Leone, Nov. 1940, F.C. Deighton, IMI 418; Mavea-Tebere, Kenya, July 1956, R.M. Nattrass, IMI 63390; Mount Maquiling, near Los Banos, Laguna Province, Philippine Islands, Oct. 1914, C.F. Baker, F.malay. 265, duplicates in BPI, DAOM, DAR 21861, K; Los Banos, Philippine Islands, Oct. 1914, C.F. Baker 3805, in PAD, LECTOTYPE of O.oryzinus Sacc. (Walker, 1972) (slides as DAR 21033); in rice crop, Calamba, Los Banos, Philippine Islands, 24.viii.1971, J. Walker, DAR 22145; from lodging plants in crop, Clare, North Queensland, Australia, 18.vii.1977, W. Pont, ex BRIP, DAR 29844; Ahuyna, Arkansas, U.S.A., 8.x.1928, E.G. Zieller, ex BPI as Ophiobolus sp. (slides as DAR 33689).

on Paspalidium sp., Walcha, N.S.W., Australia, 1976, P.T.W. Wong W2P, DAR 33671.

on Pennisetum clandestinum Hochst. ex Chiov., Tamworth, N.S.W., Australia, 28.iv.1964, A.M. Smith as Ophiobolus sp., DAR 12974; Grafton Experiment Farm, N.S.W., Australia, 28.iv.1964, A.M. Smith as O. oryzinus suspected, DAR 12981 (in both cases perithecia developed in the laboratory on field material originally showing only hypho-podiate mycelium); Bonshaw, N.S.W., Australia, 16.ii.1965, A.M.Smith, DAR 14006.

on Phalaris sp. (possibly), Entre Rios, Parana, Argentina, Sept. 1909, C. Spegazzini, LPS 2352, HOLOTYPE of Linospora pulchella Speg. (slide as DAR 25232) (Spegazzini, 1912).

on Stipa aristiglumis F. Muell., Warialda, N.S.W., Australia, Oct. 1973, P.T.W. Wong H4, DAR 25006.

on Triticum aestivum L., Rydalmere, N.S.W., Australia, 29.i.1974, P.T.W. Wong, DAR 24167 (Wong G5, see Wong, 1975) and DAR 25007 (artificial inoculations with culture ex DAR 25006 on Stipa).

on Zizania aquatica L., in greenhouse, Arlington, Virginia,U.S.A., 20.xi.1933, E.C. Tullis, as Ophiobolus oryzinus, ex BPI (slides as DAR 33691; abundant hyphopodiate mycelium and perithecia, asci and asco-spores, some germinating in perithecia to give strongly curved phialospores).

Gaeumannomyces graminis var. avenae (E.M.Turner) Dennis, British Cup Fungi, 202, 1960
≡ Ophiobolus graminis var. avenae E.M.Turner, Trans. Brit.mycol.Soc.24 (3-4), 279, 1940 (original collection lost, NEOTYPE in K !, see below).

This variety causes take-all of oats in Great Britain and other countries, and is widespread on many grasses, often causing severe disease in turf (Nilsson and Drew Smith, 1980). Detailed descriptions, illustrations, hosts and geographic distribution are given elsewhere (Turner, 1940; Walker, 1973, 1980). Within G. graminis, var. avenae is distinguished by its long ascospores, (85) 100-130 (140) x 2-3.5 (4) µm (Fig.8), and by producing simple hyphopodia only (Fig.10).

The isolates used by Turner (1940) were from Wales but later British workers found G. graminis var. avenae in England, Ireland and Scotland (Davies, 1950; Dennis, 1944; Garrett and Dennis 1943; specimens in K). In describing the new variety, Turner (1940) provided a latin diagnosis but did not specify a type collection. Her work was done at Rothamsted Experimental Station, and she mentioned in her paper that Miss E.M. Wakefield, Royal Botanic Gardens, Kew gave advice on the systematic status of the fungus. Enquiries made at both institutions failed to find her collections (J.M. Hirst, in litt.), they were not amongst the specimens of G. graminis var. avenae lent from Kew and none were located in IMI. In the absence of any of the original material and on the advice of Dr. R.W.G. Dennis, the collection from Applecross, West Ross, Scotland, 29.ix.1946, coll. R.W.G. Dennis is selected as NEOTYPE of G. graminis var. avenae.

Illustrations: See Walker (1980) where some illustrations are given, and references to many in the literature are included.

Specimens examined: unless otherwise stated, all specimens contained perithecia, asci and ascospores, and mycelium with simple hyphopodia. Other collections were listed by Walker (1972).

on Agrostis palustris Huds., Hartfield golf course, Perth, Western Australia, July 1972, G.C. MacNish, DAR 22111.

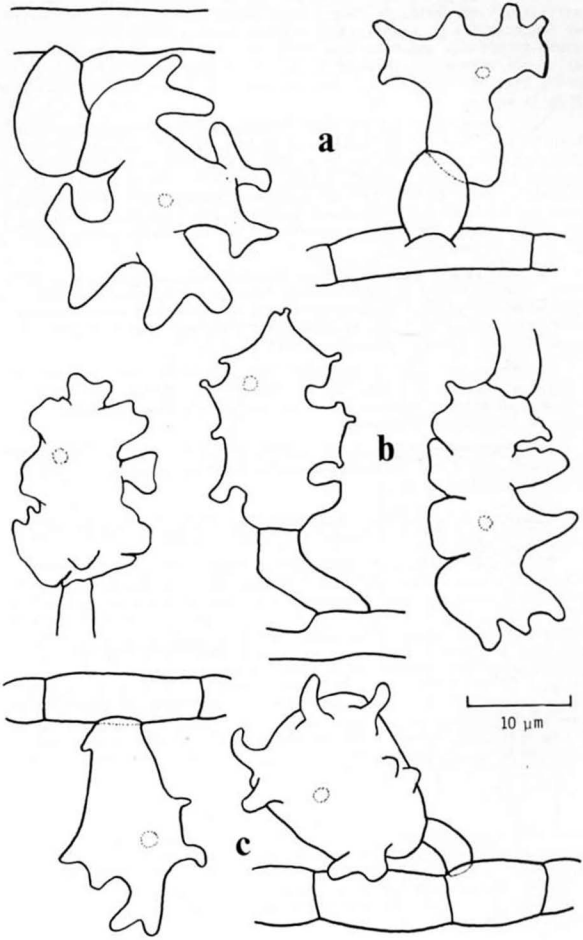
on Agrostis stolonifera L. (possibly), Victoria, Australia, 19.vi.1906, J. Harris, VPRI 276/06 (duplicates and slides filed as DAR 21034 and DAR 33272).

on Agrostis tenuis Sibth., golf course, Busselton, Western Australia, Oct. 1976, J. Yeates, DAR 31906; golf course, Bunbury, Western Australia, Oct. 1976, J. Yeates, DAR 31907; golf course, Denmark, Western Australia, July 1976, J. Yeates, DAR 31908; in lawn, Nedlands, Western Australia, Oct. 1976, J. Yeates, DAR 31909; Junee, N.S.W., Australia, 18.xi.1973, T. Siviour, DAR 25322.

on Agrostis sp., golf course, Bowral, N.S.W., Australia, April 1971, B. Stines, DAR 33697.

on Avena sativa L., Applecross, West Ross, Scotland, 29.ix.1946, R.W.G.Dennis,K, NEOTYPE of G. graminis var. avenae (slides as DAR 32104); Muckross Demesne, Killarney, Scotland, 29.viii.1946, R.W.G. Dennis, K (slides as DAR 32105); Braes of Ullapool, West Ross, Scotland, Aug. 1945, R.W.G. Dennis, K (slides as DAR 32106); Mumbles, Thornbury, Gloucestershire, England, 11.xi.1948, R.W.G. Dennis, K (slides as DAR 32101); Rademon, County Down, Northern Ireland, 16.iv.1948, R.W.G. Dennis, K (slides as DAR 32102); Wickepin, Western

Figure 9. Gaeumannomyces spp. on Cyperaceae, associated lobed hyphopodia. a. G. caricis, from holotype in C (slide DAR 32062); b. G. tax. sp. 1, DAR 32061; c. G. tax. sp. 3, DAR 34174.


a
b
c
10 µm

Australia, Nov. 1975, J. Yeates, DAR 31905; Warragul, Victoria, Australia, 9.xii.1910, J. Shugg, VPRI 958/10 (listed as first record for Victoria, as O. graminis; no perithecia seen, only mycelium, simple hyphopodia and infection cushions present; definite identification not possible); Rydalmere, N.S.W., Australia, 19.ix.1966, A.M. Smith, DAR 15857 (artificial inoculation with culture ex DAR 21022 on Agrostis sp.).

on Deschampsia bottnica (Wahl.) Hartm., Kulan, Lövånger parish, Västerbotten, Sweden, 10.ix.1945, L. Holm n.85, UPS (slides as DAR 33268; duplicate in DAOM, slide as DAR 33304; issued as Linocarpon cariceti (Berk. & Br.) Petr., F.Exs. Suecici No. 2172, Lundell and Nannfeldt, 1953; in both UPS and DAOM duplicates, asci still largely immature, but immature ascospores released under pressure commonly 110-115 µm long; very little superficial mycelium with a few simple hyphopodia present).

on Deschampsia danthonioides (Trin.) Munro ex Berth., near Kendrick, Idaho, U.S.A, 20.vii.1948, R. Sprague and Raeder, WSP 3976 (slides as DAR 33718; ascospores to 130 µm, abundant runner hyphae, simple hyphopodia and infection cushions (Walker, 1980) present. The number '16489' is also stamped on this packet).

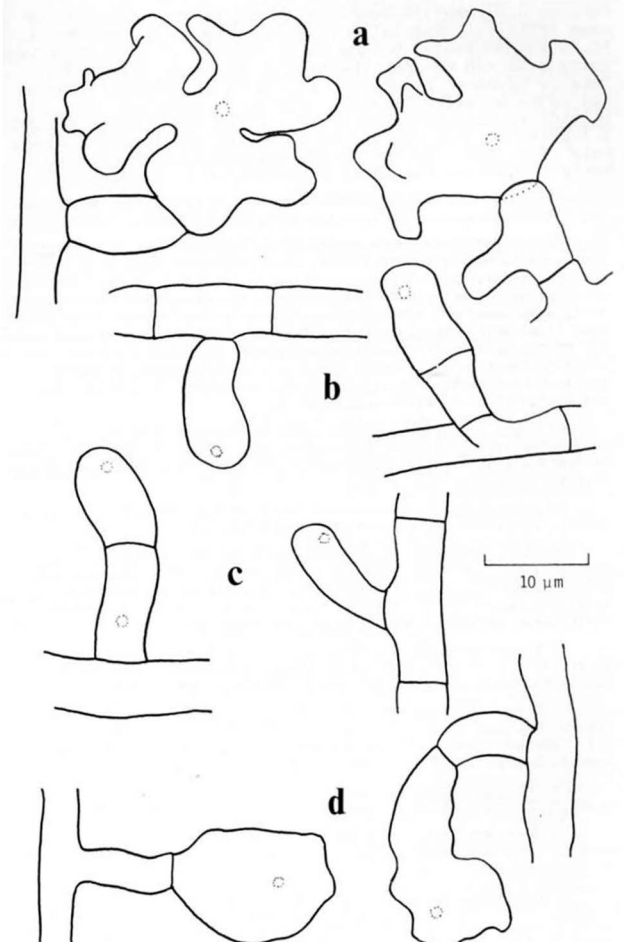
on Holcus sp., Applecross, West Ross, Scotland, 29.ix.1946, R.W. G. Dennis, K (slides as DAR 32103; growing in infected oat crop; asci and ascospores largely immature, ascospores released under pressure 102-115 µm long).

on Triticum aestivum L., Rydalmere, N.S.W., Australia, 19.ix.1966, A.M. Smith, DAR 25398 (artificial inoculation with culture ex DAR 21022 on Agrostis sp.).

Gaeumannomyces graminis var. tritici Walker, Trans. Brit. mycol. Soc. 58 (3): 439 (427-457), 1972.

The wheat take-all fungus has been fully described elsewhere (see descriptions, illustrations, references to literature, hosts and geographical distribution in Walker, 1972, 1973, 1975, 1980). It has a wide host range in the Gramineae and, under the name 'Ophiobolus graminis', has been the subject of intensive study for over 100 years (bibliographies given by Butler, 1961; Nilsson, 1969; Walker, 1975; Asher and Shipton, 1980). The name 'Ophiobolus graminis' properly applies to the fungus considered here as Gaeumannomyces graminis var. graminis but in most of the earlier literature it was used for the wheat take-all fungus G. graminis var. tritici (and sometimes also

Figure 10. Gaeumannomyces spp. on Gramineae, hyphopodia. a. G. graminis var. graminis, lobed hyphopodia, from holotype in PAD (slide DAR 21032); b. G. graminis var. tritici, from holotype, DAR 17916; c. G. graminis var. avenae, from neotype in K (slide DAR 32104); d. G. cylindrosporus, on wheat coleoptile from living culture DAR 25012.


a
b
c
d
10 µm

for the oat take-all fungus G. graminis var. avenae). In some articles, especially those dealing with grass hosts, it is not possible to know which variety of G.graminis was being referred to when the name O. graminis was used. Details of names misapplied to the wheat take-all fungus are given by Walker (1980). Within G. graminis, var. tritici is distinguished by ascospores (60) 70-105 (110) x 2.5-3 (4) µm (Fig. 8) and by producing simple hyphopodia only (Fig. 10). Walker (1980) discusses intravarietal variation within the three varieties of G. graminis.

Illustrations: See Walker (1980) where some illustrations are given, and references to many in the literature are included.

Specimens examined: a large number of collections have been seen and some were listed by Walker (1972). The list given here is a selection, containing specimens of some significance for the take-all literature, or for host and geographic ranges. Only specimens with perithecia, asci, ascospores and simple hyphopodia are listed. Some other specimens filed as 'Ophiobolus graminis'in herbaria do not show perithecia, but mycelium, infection cushions and simple hyphopodia. These, and other collections where other fungi such as Wojnowicia graminis (McAlp.) Sacc. & D. Sacc., Cochliobolus spp. etc. were found, are dealt with in a separate section below.

on Avena byzantina C. Koch, Bathurst Experiment Farm, N.S.W. Australia, Nov. 1913, W.A. Birmingham, DAR 56 and 57 (asci 100-110 µm, ascospores shorter; slightly immature but more typical of var.tritici than var. avenae).

on Avena fatua L., Mukenbudin, Western Australia, Nov. 1975, J. Yeates, DAR 31904 (ascospores 70-106 x 2.5-4 µm).

on Avena sativa L., Coonalpyn, South Australia, Nov.1917, A.J. Spafford, ADW 391 as O. graminis (slide as DAR 33719; ascospores 85-100 (102) x 2.5-3 µm); Rydalmere, N.S.W., Australia, 6.v.1971, R. Bowditch, DAR 21027 (artificial inoculation with culture from DAR 17916 (type culture of var. tritici) on Triticum).

on Bromus sterilis L., Nuskerry East, Victoria, Australia, 21.xi.1903, T. Peters, VPRI as O. graminis (slides as DAR 33274); possibly portion of same, VPRI 65/04 (slide as DAR 33273).

on Bromus vulgaris (Hook.) Shear, foot of Hurricane Ridge Trail, Olympic National Park, Washington, U.S.A., 23.vii.1955, R. Sprague and P. Halisky, WSP 37470 as O. graminis (slide as DAR 33720; ascospores 80-100 (107) x 2.5-3 µm; see Sprague and Halisky, 1955).

on Hordeum vulgare L., Shizuoka Prefecture, Japan, 19.v.1914, T. Okada, TNS - F210068 as O. graminis (slide as DAR 31880).

on Oryza sativa L., Rydalmere, N.S.W., Australia, 6.v.1971, R. Bowditch, DAR 21025 (artificial inoculation with culture ex DAR 17916 on Triticum).

on Triticum aestivum L., Shizuoka Prefecture, Japan, 11.vii.1928, K. Hara, TNS - F210065 as O. graminis (slide as DAR 31878); same, Nov. 1925, K. Hara, TNS - F210099 as Ophiochaeta graminis (slide as DAR 31885; the host is given as Oryza sativa but the specimen is clearly wheat); Kenya, no date, H.C. Thorpe, IMI 121750 as O. graminis; Ferrara, Italy, 1896, Prof. Aducco, IMI 16858a as O. graminis

(Briosi & Cavara, I funghi parassiti delle piante coltivate od utili No. 306; pycnidia of Wojnowicia graminis (McAlp.) Sacc. & D. Sacc. also present, in external appearance very similar to Gaeumannomyces perithecia); duplicate of Briosi and Cavara F. paras. No. 306, BPI (slide as DAR 33694; no perithecia found); Raleigh, North Carolina, U.S.A., Dec.1923, F.A. Wolf, BPI as O. graminis, U.S.D.A. Path. Myc. Coll. 4465 (slide as DAR 33695); same, dup. in UPS; Geneva, New York, U.S.A., 5.vii.1921, R.J. Haskell and R.S. Kirby, BPI as Ophiobolus sp. (slide as DAR 33690; see Kirby, 1925); Italy, 1913, Cattino, PAD as O. graminis (slide as DAR 33721); many Australian collections on wheat in DAR.

Gaeumannomyces caricis sp.nov.

Perithecia in vaginis foliorum, corpus immersum fuscum vel nigrum, globosum vel subglobosum 300-400 µm diam, collum obliquum erumpens 150-180 µm longum, 80 µm latum, usque ad canalis cum periphysibus hyalinis ascendentibus vestitus; paries perithecii 30-40 µm crassus, ex 6-8 stratis cellularum complanatarum 8-10 x 2-5 µm constatus, strata interiora pallida brunnea, strata externa fusca textura angularis vel textura epidermoidea, ad hyphas brunneas septatas in cavitate vaginae foliae conjuncta. Asci (Fig. 6) unitunicati, elongati clavati, ad apicem rotundati cum annulo refractivo, basin versus attenuati, brevi (10-30 µm) stipitati, 140-180 x 10-14 µm, octospori. Ascosporae (Figs. 6 and 8) uniseriatae, parallelae vel parum tortiles, filiformes vel anguste clavatae cum apice rotundato, basin versus attenuatae, rectae vel plerumque arcuatae, hyalinae vel dilutae ochraceae (praecipue in massa), 7-8 septatae, (80) 120-150 (155) x 2-3 µm, contenta subtiliter granulata. Filamenta paraphyses simulans praesentia, non visa facile in peritheciis maturis. Mycelium superficiare in vaginis ex hyphis brunneis septatis irregulariter ramosis 3-6 µm latis laxe reticulatis compositis, cum hyphopodiis (Figs. 7 and 9) brunneis lobatis, plerumque profunde lobatis, variabilis, 18-27 x 15-20 µm vel usque ad 25 µm diam, cum puncto pellucido ad locum hospitis penetrati, lignitubera abundantes.

HOLOTYPUS: in vaginis foliorum Caricis paniculatae, Trelde Sande, Denmark, 5.vii.1937, Poul Larsen, in C

ISOTYPUS: Laminae vitreae, DAR 32062

Collectio altera: in Caricis acutiformis, Flatford Mill, Suffolk, England, 9.v.1948, E.A. Ellis, IMI 28589, cum nomine 'Ophiobolus eucryptus'.

Perithecia embedded in leaf sheaths, with dark brown to black globose to subglobose body 300-400 µm diam and erumpent eccentric neck 150-180 µm long and up to 80 µm wide, joined to brown, septate mycelium in the leaf sheath cavity. Perithecial wall 30-40 µm thick of 6-8 layers of laterally compressed cells, 8-10 x 2-5 µm, inner layers paler, outer layers dark brown and forming a tissue which in surface view is a textura angularis or tending to textura epidermoidea. Neck canal lined with hyaline upwardly-pointing periphyses. Asci (Fig. 6) elongated clavate, with a rounded apex and narrowing gradually to the base, 140-180 x 10-14 µm, unitunicate with a small but definite refractive apical ring 2 µm diam, containing eight ascospores, lower 10-30 (40) µm of ascus free of spores. Ascospores (Figs.6 and 8) uniseriate, lying straight or very slightly twisted in the ascus, faintly tinted yellowish in mass, hyaline to faintly tinted singly,

filiform with rounded apex and narrower rounded base, widest slightly above the middle, straight or more commonly slightly curved, sometimes more strongly curved towards the base, usually 7-8 septate, (80) 120-150 (155) x 2-3 µm, contents granular, often appearing finely banded under phase contrast. Paraphyses present, not readily seen in mature perithecia. Superficial mycelium on leaf sheaths of brown, branched, septate hyphae 3-6 µm wide bearing brown lobed hyphopodia on short side branches up to 10-20 µm long. Hyphopodia (Figs. 7 and 9) brown, lobed, often deeply lobed, very variable in shape and degree of lobing, 18-27 x 15-20 µm or up to 25 µm diam when isodiametric, with clear dot denoting place of host penetration. Abundant lignitubers in host tissue associated with infection hyphae.

G. caricis was referred to previously as Gaeumannomyces sp. by Munk in Larsen (1952) and by Munk (1953a) but later (Munk, 1953b) he accepted Petrak's (1952) conclusion that Gaeumannomyces should be in Linocarpon and redescribed and figured the fungus under the name Linocarpon eucryptum (Berk. & Br.) Petrak (Munk, 1957). Detailed reasons for rejecting the epithet 'eucryptum' have been given previously (Walker, 1972) and generic differences between Gaeumannomyces and Linocarpon are described above and under Linocarpon (q.v.)

Pure culture work is needed to prove the connection between the perithecia of G. caricis and the closely associated hyphopodiate mycelium. Although known only from two collections at present, it is possibly more widespread (especially in Great Britain and Europe) and is described here to bring to the notice of mycologists and pathologists the presence of species of Gaeumannomyces on Cyperaceae. Other collections on Cyperaceae differing from G. caricis are mentioned below under 'Gaeumannomyces spp. on Cyperaceae'. Walker (1980) has discussed the possible relationship between these fungi and graminicolous Gaeumannomyces spp. The need to avoid confusion with the hyphopodiate mycelium of Clasterosporium spp. on Cyperaceae has been pointed out elsewhere (Walker, 1972, 1980).

Gaeumannomyces cylindrosporus Hornby, Slope, Gutteridge & Sivanesan, Trans.Brit. mycol.Soc.69 (1): 21-25, 1977 (type in IMI !)

Full descriptions and illustrations are given by Hornby et al. (1977) and Walker (1980). G. cylindrosporus is known only from a number of collections developed at Rothamsted on rotted cereal roots inoculated previously with isolates of Phialophora graminicola (Deacon) Walker (q.v.) which is probably its conidial state. Hornby et al. (1977) did not obtain germination of conidia produced in cultures derived from ascospores of G. cylindrosporus, but study of one of the original isolates they list (DAR 25011) has shown that they germinate (Fig.11). The strongly curved lunate to semicircular non-germinating phialospores seen in G. graminis have not been seen in this species. Although described originally as mostly cylindrical, most ascospores are fusoid, widest in the middle, narrower at

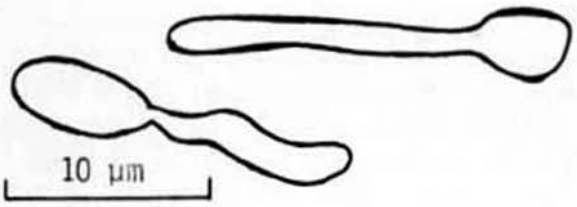


Figure 11. Gaeumannomyces cylindrosporus, germinating conidia, from culture DAR 25011.

the base than at the apex, and usually slightly curved. They are hyaline to faintly tinted yellowish in colour. Hyphopodia have been produced by cultures inoculated onto wheat coleoptiles (Hornby et al.,1977; Walker, 1980).

G. cylindrosporus is distinguished from G.graminis and its varieties by shorter, wider, fusoid ascospores (Fig. 8), (35) 40-70 (75) x 3-5 (6) µm with 3-5 (8) transverse septa, slightly lobed hyphopodia (Fig.10), production of only one type of phialospore, and much slower growth in culture (4-6 mm/24 hrs at 20-25°C compared to 6-12 mm/24 hrs for G. graminis varieties; see Table 1 under Phialophora). Conidia germinate (Fig. 11).

When borrowed originally, the type material lodged as IMI 192606 was found to be very sparse, consisting of only six or seven perithecia on two small fragments of root. In the one slide made from this material, abundant mature ascospores were seen, but no asci, and the perithecia seemed to be overmature. Dr. Hornby has now supplemented the IMI specimen with further material of the same collection and a duplicate has also been lodged as DAR 31926.

Specimens examined: All from roots of Triticum aestivum, inoculated with various isolates of Phialophora graminicola, Rothamsted, England; single ascospore isolate 99, 21.x.1974, D. Hornby, DAR 25011; single ascospore isolate 100, 21.x.1974, D. Hornby, DAR 25012; bulk ascospore isolate NA15, D. Hornby, DAR 25013; P. graminicola isolate 74/2/2-1, March 1975, D.B. Slope, IMI 192606, HOLOTYPE of G. cylindrosporus (slides as DAR 32148, dups. as DAR 25258 and DAR 31926); P.graminicola isolate 76/244-3, 4.vii.1976, D. Hornby, DAR 31925 (ascospores in this collection mainly 35-50 µm long, and practically all with only 3 septa. It does not seem to be immature as most asci have disappeared. In other collections showing longer spores with 5 or more septa, shorter 3-septate spores were seen in the same perithecium).

Gaeumannomyces leptosporus Iqbal, Trans.Brit. mycol.Soc.58 (2): 346-348, 1972 (type in K !).

This is not a Gaeumannomyces as defined here, and is transferred below to the genus Ophioceras Sacc.

Gaeumannomyces oryzinus (Sacc.) Schrantz (as 'oryzinum'), Bull. Soc. mycol. Fr. 76(4), 337, 1961.

This binomial was not validly published (Stafleu et al., 1972, Art.33) as publication details for the basionym Ophiobolus oryzinus Sacc. were not given. The accepted name is G. graminis (Sacc.) von Arx & Olivier var. graminis (q.v.).

Gaeumannomyces spp. on Cyperaceae

Under this heading are included collections on Carex producing Gaeumannomyces perithecia and an associated mycelium with both simple and lobed hyphopodia (Fig.9) and occasionally sclerotia, but with ascospores much smaller than those described above for G. caricis. Collections studied are few but fall into two overlapping groups on ascospore size. This may represent the limits of variation of one species or two closely related but distinct species. The two groups are referred to as taxonomic sp.1 and 3 (tax. sp. 2 (Walker, 1972) is G. caricis).

(i) Gaeumannomyces tax. sp. 1 (Walker, 1972): characterised by ascospores (60) 70-100 (120) x 2-3 µm (Fig.8), this fungus is very similar to G. graminis var. graminis (Fig.9). Whether it is the same, or a closely related species on a different host family requires further work (Walker, 1980). One collection (IMI28563b) also has small dark brown to black, globose to subglobose sclerotia, 80-120 µm diam embedded in the spongy leaf sheath tissue in association with perithecia. Two other collections with sclerotia and hyphopodiate mycelium but no perithecia have been seen and may belong here.

(ii) Gaeumannomyces tax. sp. 3: characterised by ascospores (50) 55-75 (80) x 2-3 (4) µm (Fig.8). Two collections in K labelled 'Sphaeria eucrypta' described by Walker (1972) and one slide collection labelled 'Leptosphaeria paludosa Feltg.' in FH are placed here tentatively. Feltgen (1901) described L. paludosa from leaves of Carex vesicaria L. in Luxembourg. The slide in FH, which may have been prepared from the original collection, has become granular and cloudy, obscuring some details, but shows a fungus as follows:

Perithecia with brown walls, 300-400 µm diam, short probably central neck to 120 µm long. Asci unitunicate, with an apical ring not readily distinguished, 95-115 x 9-11 µm. Ascospores eight, pale yellowish in mass, elongated fusiform, usually slightly curved, apex rounded, base thinner and narrowly rounded, (60) 65-75 (80) x 2.5 µm, with three distinct septa. Inter-ascal filaments resembling paraphyses, hyaline, septate with septa approximately 15 µm apart, 7-8 µm wide near base and tapering to the top. A small fragment of the host tissue bore a few brown, septate hyphae but no hyphopodia.

Saccardo and Saccardo (1905) transferred L. paludosa to Ophiobolus and listed the hosts as Carex vesicaria and Phalaris arundinacea L. Their description is similar to that given above, with perithecia 500-600 µm diam, asci 90-100 x 8-10 µm, and ascospores 60-75 x 3-4 µm with 7-10-12 septa. They also comment 'ad Ophiobolum graminis nutat'. L. paludosa could easily be a short-spored Gaeumannomyces on Cyperaceae but study of the type is needed to see if a hyphopodiate mycelium is present. The epithet 'paludosa Feltg.' may eventually provide a name in Gaeumannomyces for some of these short-spored collections.

The unsuitability of the epithet 'eucrypta Berk.& Br.'

for use in Gaeumannomyces has already been discussed (Walker, 1972). Collections in K under this name either have no host or locality information, or are on Iris foetidissima L.. Duplicates on Iris are present in L and PAD and the January 1859 collection on Iris foetidissima was issued as Rabenh. Fung. Europ. 49 under the name 'Sphaeria eucrypta Berk. & Br.'. These Iris collections do not seem to be Gaeumannomyces and are dealt with under 'Plagiosphaera sp.'.

Further collections, cultural studies to prove the connection between perithecia and the associated hyphopodiate mycelium, host range studies and comparisons with the graminicolous species are needed to elucidate the taxonomy and pathology of this little known group of Gaeumannomyces spp. on Cyperaceae.

Specimens examined: Gaeumannomyces tax. sp. 1 (see also collections on Carex sp., C. acutiformis, C. pseudocyperus L. and C. riparia listed in Walker, 1972); on C. acutiformis, Flatford Mill, Suffolk, England, 9.v.1948, J.P. Morgan, IMI 28563b (ascospores 90-115 (120) x 2.5-3 µm; found on specimen of Acanthophiobolus helicosporus in Ophiosphaeria gracilis folder, IMI 28563a); on C. riparia, Krotheimer Teich, Brünn, Germany, July, no year given, G. Niessl, in M (as 'Leptospora' or 'Leptosphaeria' with note 'sehr lange Sporen'; slides as DAR 33701). Gaeumannomyces tax. sp. 3; on host undet., probably Cyperaceae, no date or locality, labelled 'Sphaeria eucrypta, C.E.B.' {C.E.Broome}, with M.C. Cooke's herbarium stamp, in K; on host undet., probably Cyperaceae, Batheaston, April 1859, labelled 'Sphaeria eucrypta B.& B.', in K; on host undet., slide specimen A3785 Feltgen, labelled 'Ophiobolus eucryptus (ubr. Leptosph. paludosa Feltg.)', in FH. Sclerotia and mycelium with lobed hyphopodia (but no Gaeumannomyces perithecia) seen in two collections: on Carex elata, Flatford Mill, Suffok, England, 9.v.1948, M.B. Ellis, IMI 28566b (found on specimen of Acanthophiobolus helicosporus in Ophiosphaeria gracilis folder, IMI 28566a); on Carex sp. aff. C. bichenoviana Boott, Armidale, N.S.W., Australia, 17.ix.1968, P. Duff, DAR 21030a.

Collections and records which cannot be placed accurately in any variety of G. graminis

Whilst there are many records in the literature of 'Ophiobolus graminis' on a wide range of hosts, the exact identity of the fungus present is not clear in some cases. Several of the records on maize (Zea mays L.) (Petrak, 1952 as Linocarpon cariceti; Saccas, 1951) and sorghum and Johnson grass (Sorghum spp.) (Foëx and Rosella, 1934; Foëx, 1935; Saccas, 1954; Tarr, 1962) are of this kind. No specimens on Zea or Sorghum have been seen during the present work. The report by Tullis (1951) that G. graminis var. graminis (as Ophiobolus oryzinus) can overwinter on leaf sheaths of Typha latifolia L. has not been confirmed from specimens and a number of earlier grass host records in the literature are also uncertain.

In several herbaria, there are many specimens of root and crown diseases of cereals and grasses filed as 'Ophiobolus graminis' and/or with the annotation 'take-all' or

some similar term. Some do not show fruiting bodies, but have a brown superficial mycelium, with simple hyphopodia, and infection cushions, developed on lower portions of culms and leaf sheaths, and often abundant lignitubers in host cells. From notes filed with specimens, it is seen that collectors regarded the disease present as take-all and the fungus as 'Ophiobolus graminis' and this was obviously correct in many cases. Now, however, such specimens do not show characters which allow their accurate placement in one of the varieties of G. graminis. In particular, it is not possible to distinguish var. avenae and var. tritici on material such as this. In other cases, often on old, weathered or last season's culms, perithecia typical of Gaeumannomyces are present, but no superficial mycelial structures are observed and a heavy growth of saprophytic moulds is often present. No definite determination can be made of such collections and var. graminis and var. tritici could not be distinguished on them. Finally there are those collections identified as Ophiobolus graminis (and often reported as such in the literature) on which no evidence of Gaeumannomyces could be found .

Some of these specimens are the basis for cereal and grass host records and geographic distributions published in the take-all literature (Nilsson, 1969 gives a comprehensive host list compiled from the literature; Nilsson and Drew Smith, 1980 discuss take-all on grasses). As an accurate knowledge of host ranges and distributions is important, a selection of some specimens which cannot be fully identified is given below, with brief notes on them. Unless otherwise stated, all were filed originally as 'Ophiobolus graminis'and all showed only mycelium, with runner hyphae, simple hyphopodia and infection cushions (the presence of varieties of G. graminis on several of these hosts is known from other collections bearing perithecia).

on Agropyron scabrum (R.Br.) Beauv., Mordialloc, Victoria, Australia, 1.i.1904, C.F.J.M., VPRI 11/04, brown mycelium only, no evidence for Gaeumannomyces; G. graminis var tritici occurs on this host (Walker, 1972).

on Bromus vulgaris (Hook.) Shear, Stilaguanish River, Washington, U.S.A., 11.vi.1959, R. Sprague, WSP 46380 (slide as DAR 33722; G. g. var. tritici is known on this host e.g. WSP 37470).

on Deschampsia danthonioides, Mill Lake, Olympic National Park, Washington, U.S.A., 23.vii.1955, R. Sprague, WSP 37471 (slide as DAR 33723; Sprague and Halisky, 1955 as Ophiobolus graminis; G.g. var. avenae is known on this host (WSP 3976) and on other Deschampsia spp., see specimen list for G. g. var. avenae).

on Festuca subulata Trin., foot of Hurricane Ridge Trail,Olympic National Park, Washington, U.S.A., 23.vii.1955, R.Sprague and P.Halisky, WSP 37469 (Sprague and Halisky, 1955, as O. graminis; very little mycelium present, no hyphopodia found. G. graminis var. tritici was collected at the same time on Bromus vulgaris, WSP 37470.

on Glyceria maxima (as Poa aquatica), Malmedy, France, no date,

Reliquiae Libertianae, Roum. Fung. Sel. Gallici Exsicc. 1591, DAOM (as Ophiobolus (Rhapidospora) graminis; slides as DAR 33299; perithecia, asci and ascospores similar to those of a Lejosphaerella sp. present, with pycnidia containing short cylindrical brown aseptate conidia; no Gaeumannomyces seen).

on Hordeum vulgare L., Tootoomi, Shizouka Prefecture, Japan, 1925, K. Hara, TNS - F210096 (as Ophiochaeta graminis) (slide as DAR 31883; brown runner hyphae, infection cushions and simple hyphopodia present, possibly either G. graminis var. tritici or var. avenae).

on Oryza sativa L., old stalks with saprophytes, Samaru, Zaria Province, Northern Nigeria, 26.vi.1961, E. Harris (618a and b), IMI 88650a (as O. graminis; perithecia with ascospores 70-100 µm, no hyphopodiate mycelium, probably G. graminis var. graminis, which is recorded from Northern Nigeria, see specimens listed and Harris et al., 1962 as O. oryzinus); Shizuoka City, Shizuoka Prefecture, Japan, Nov. 1925, K. Hara, TNS - F210098 (as Ophiochaeta graminis) (slide as DAR 31884; no sign of Gaeumannomyces seen, several fungi on leaf sheaths (a) Cochliobolus sp. (b) Pyrenochaeta oryzae Shirai ex Miyake (c) Sphaeropsidales undetermined (d) small sclerotia in leaf sheath tissue similar to those of Magnaporthe salvinii (Catt.) Krause & Webster; this collection was listed as Linocarpon cariceti by Kobayashi (1970).

on Panicum curtisii Chapm., Louisiana, U.S.A., no date or collector, ex Herb. Ellis 5021, PAD (as O. graminis; slides as DAR 33724; various fungi on leaf sheaths and stem; no evidence of Gaeumannomyces).

on Paspalidium geminatum (Forsk.) Stapf, Haifa Lake, West Pakistan, 10.xi.1966, S.R. Bagruar, IMI 134097a; perithecia with ascospore 70-100 µm long present; possibly G. graminis var. graminis but in the absence of hyphopodia cannot be distinguished from var. tritici.

on Pennisetum americanum (L.) K. Schum. (as P. typhoides), on old stalks from last year's plants, Samaru, Zaria Province, Northern Nigeria, 19.vii.1961, E. Harris, IMI 88659b (as Ophiobolus graminis); perithecia with ascospores 70-100 µm, no hyphopodiate mycelium, probably G. graminis var. graminis; Harris et al. (1962) reported var. graminis (as O. oryzinus) on seedlings of this host in Northern Nigeria and commented that it may survive on old millet stems.

on Phalaris aquatica L. (as P. tuberosa), south-eastern South Australia, Nov.1932, no collector given, ADW 1968; no perithecia, superficial mycelium or hyphopodia found, no evidence for presence of Gaeumannomyces.

on Phalaris minor Retz., Merredin Experiment Farm, Western Australia, Nov. 1932, no collector given, ADW 1967; very little mycelium, with a few infection cushions and simple hyphopodia, possibly a variety of G. graminis.

on Poa pratensis L., near Kendrick, Idaho, U.S.A., 20.vii.1948, R. Sprague and Raeder, WSP 3978 (slide as DAR 33725; no evidence of G. graminis was found. The lower leaf sheaths were discoloured and rotting, with several moulds and an amorphous black substance present. A note reads 'Apparently resistant as compared to other grasses in area'. G. graminis var. avenae was found at the same time on Deschampsia danthonioides, WSP 3976); start of Hurricane Ridge Trail, Olympic National Park, Washington, U.S.A., 23.vii.1955, R. Sprague,

WSP 37472, (slide as DAR 33726; Sprague and Halisky, 1955 as O. graminis; small plants with stems brown near ground level and abundant algal cells forming a dark sheath at and just above the crown node. No evidence of G. graminis seen on this specimen. G. graminis var. tritici was found at the same time on Bromus vulgaris, WSP 37470); Clearwater River, Idaho, U.S.A., 1.viii.1948, R. Sprague and G. Fischer, WSP 3998 (slides as DAR 29776; no mycelium or other evidence for Gaeumannomyces found. Ascocarps of Phaeosphaeria herpotrichoides (de Not.) Holm in leaf sheaths and pycnidia of Dinemasporium graminum Lév. on sheaths).

on Trisetum cernuum Trin., Mill Lake, Olympic National Park, Washington, U.S.A., 23.vii.1955, R. Sprague, WSP 37474 (slide as DAR 33727; Sprague and Halisky, 1955 as O. graminis; runner hyphae, infection cushions, simple hyphopodia and lignitubers present, perhaps either G. graminis var. avenae or var. tritici).

on Triticum aestivum L., many wheat take-all specimens in herbaria do not show perithecia. This is to be expected as many specimens collected during the growing season are not at the stage where perithecia have developed. Some collectors developed perithecia on such specimens by alternate wetting and drying in the laboratory of crowns and attached culms and leaf sheaths soon after collection and material prepared in this way is very valuable for reference and authentication of the record at a later date. A selection from collections without perithecia is given with brief comments:

on Triticum aestivum, property of Mr. Skewes, Goolwa, South Australia, Nov. 1932, no collector given, ADW 1970 (abundant mycelial sheath, runner hyphae, infection cushions and simple hyphopodia, probably var. tritici); Bruce Rock, Western Australia, Jan. 1933, no collector given, ADW 1974 (abundant runner hyphae, infection cushions and simple hyphopodia, probably var. tritici); Lameroo, South Australia, 20.xi.1912, T.G.B. Osborne, ADW 390 (as Linocarpon cariceti in Hansford's writing; abundant mycelium with infection cushions and simple hyphopodia, probably var. tritici); Langhorne's Creek, South Australia, Oct. 1932, no collector given, ADW 1972 (specimen fragmentary, no evidence for Gaeumannomyces present); Horsham, Victoria, 3.x.1901, Mr. Smith, VPRI 1701 + 1 (as Ophiobolus herpotrichus Sacc.; slide as DAR 33275a; a little brown mycelium and a few very immature fruiting bodies in leaf sheaths, possibly Gaeumannomyces); Shizuoka Prefecture, Japan, 5.xii.1920, K. Hara, TNS - F210094 (as Ophiochaeta graminis; slide as DAR 31881; rectangular brown stem flecks containing brown clusters of fungal cells, a few empty fruiting bodies with outer wall layer a textura angularis present, no evidence for Gaeumannomyces); Suruga, Shizuoka Prefecture, Japan, June 1925, K. Hara, TNS - F210095 (as Ophiochaeta graminis; slides as DAR 31882; similar to TNS - F210094, no sign of Gaeumannomyces); Junction City, Oregon, U.S.A., 22.vi.1921, no collector given, WSP 4826 (slides as DAR 33728; abundant dark mycelial sheath, runner hyphae, infection cushions and simple hyphopodia, probably var. tritici); Vancouver Experiment Station, Washington, U.S.A., 26.vi.1959, R. Sprague, WSP 46801 (slide as DAR 33729; dark mycelial sheath, runner hyphae, infection cushions and simple hyphopodia present, probably var. tritici); Hungary, 1899, Linhart, PAD (as O. graminis; slide as DAR 33730; mycelium and simple hyphopodia, probably var. tritici).

on Vulpia bromoides (L.) Gray (as Festuca), Pinnaroo, South

Australia, 8.xi.1923, G. Samuel, ADW 388, (as Linocarpon cariceti in Hansford's writing), a little mycelium, a few infection cushions and simple hyphopodia, could be either var. tritici or var. avenae; var. tritici recorded on Vulpia myuros (L.) Gmel. in South Australia, ADW 389, see Walker, 1972.

on Gramineae undet., no locality, Herb. Libert 70, PAD (as Ophiobolus graminis; slides as DAR 33731; no perithecia or mycelium seen; pseudothecia of Paraphaeosphaeria michotii (Westend.) O. Eriks., Mycosphaerella sp. and Pleospora sp. seen; collection listed by Roumeguère and Saccardo (1881) as O. graminis and portion examined by Fitzpatrick et al., 1922, who also found no perithecia; see Walker, 1972); on grass culm, University of Pennsylvania, 2.iv.1911, no collectors name, PAD (as O. graminis; slides as DAR 33732; only pseudothecia of Ophiosphaerella herpotricha seen).

LASIOSPHAERIA

Lasiosphaeria gracilis Niessl = Acanthophiobolus helicosporus (q.v.).

'Lasiosphaeria' helminthospora Rehm - for discussion of this name, see under Acanthophiobolus helicosporus.

Lasiosphaeria raciborskii (Penz. & Sacc.) Carroll & Munk - see under Ophiochaeta raciborskii.

LEPTOSPHAERIA

Leptosphaeria Cesati & de Notaris, Comment.Soc.Critt.Ital. 1, 234, 1863 (from Holm, 1957)
Type sp. L. doliolum (Pers.ex Fr.) Ces. & de Not. (for typification, see Holm, 1957).

Many species of Leptosphaeria are described in Müller (1950) and Holm (1957). The concept of the genus followed is that of Holm (1957) as set out in the keys of Luttrell (1973) and von Arx and Müller (1975). Some names encountered during current investigations are discussed here.

Leptosphaeria compressa (Rehm) Holm, Symb.bot.Upsal.14 (3), 29-30, 1957
= Exilispora plurisepta Tehon & Daniels, Mycologia 19, 113, 1927 (type in ILLS !)

Petrak (1941) considered Exilispora Tehon & Daniels (1927) as not distinct from Ophiobolus, but von Arx and Müller (1975) reduced it to synonymy with Leptosphaeria. Present work supports the latter view and indicates that the type (and only) species, E. plurisepta, is not distinct from L. compressa, as defined by Holm (1957). The type of L. compressa has not been examined, but a duplicate of one of the exsiccati listed by Holm (1957; Petrak Myc.gen.463) has been seen. The following description is based on the type of E. plurisepta:

Pseudothecia on dead stems, abundant, in lines between the vascular strands, at first covered by host tissue, later erumpent,

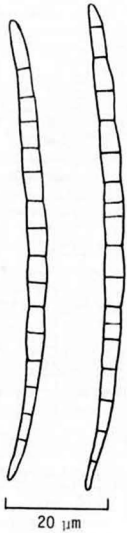


Figure 12. Leptosphaeria compressa, ascospores, from holotype of Exilispora plurisepta, ILLS 8404 (slide DAR 33733).

seated in the stem on internal woody tissue, often two or more laterally compressed, subglobose to somewhat flattened, black, 200-400 µm diam, 200-300 µm high, with a short broad slightly protruding papillate neck, some ascocarps with a slightly thickened pressure ridge just below the neck (as described by Walker and Smith (1972) for L. narmari and L. korrae); wall 25-30 µm thick at sides, to 40-50 µm at base and near neck junction, of several layers of brown cells, 3-4 outer layers dark brown to black and almost opaque, 4-6 inner layers lighter in colour, cells oval to angular, 8-12 x 4-7 µm, in outer layers with much thickened walls, radially flattened especially in inner layers; ostiolar canal 20-25 µm diam, periphyses not seen. Asci (fig.2) numerous, arising from a basal hymenial layer, subcylindrical, apex rounded, widest in upper half and tapering gradually to the narrow, short base, bitunicate, 100-125 x 11-15 µm, several smaller immature asci also present, apical apparatus not seen (not studied), eight-spored. Ascospores (Figs.2 and 12) subcylindrical to elongated fusiform, ends obtuse, widest about 1/3 of length below apex, 75-100 (110) x 3.5-4.5 µm, tapering towards the base, lying parallel or slightly twisted in the ascus, 15-18 septate (counts in spores of different ages indicates that septation develops in the order 1,3,7,15, with secondary septa developing in some of the cells formed by these primary septa), constricted at the first formed septum (usually about 0.4 of length below apex and dividing the spore into a shorter apical and longer basal segment), usually less constricted at every second septum on either side of the first. Pseudoparaphyses abundant, hyaline, septate.

Illustrations: Holm (1957, ascospores); Shoemaker (1976, ascocarp wall, ascospores); Tehon and Daniels (1927, as Exilispora plurisepta, ascocarp, ascus with ascospores, pseudoparaphyses).

Specimens examined: on Erigeron sp., McNabb, Putnam County, Illinois, U.S.A., 28.vi.1922, C.L. Porter, ILLS 8404, HOLOTYPE of E. plurisepta (slides as DAR 33733); on Artemesia austriaca Jacq., Bisamberg, near Vienna, Austria, May 1940, F. Petrak Mycotheca generalis 463, IMI 30363 (as Ophiobolus compressus; slides as DAR 33734).

This description is very similar to that given by Holm (1957) for L. compressa. Shoemaker (1976, as O. compressus) described ascospores with slightly enlarged cells immediately on either side of the first-formed septum and

his drawing (Fig.5) and photomicrograph (Fig.66) show this in spores from the specimen of Petrak's Myc. gen. 463 in DAOM. No definite cell enlargement was detected in the specimens examined here. Shoemaker (1976) did not mention the slight constriction at other septa, figured by Holm (1957) and suggested at one or two septa in his photomicrograph. This constriction at every second septum was clearly seen in the Petrak duplicate filed as IMI 30363. There is no tendency for spores to break at the first formed septum, as in the type species of Ophiobolus, O. acuminatus.

Leptosphaeria hesperia Barr (1967) - see discussion about Ophiobolus rostrupii under Leptosporopsis.

Leptosphaeria narmari Walker & Smith and L. korrae Walker & Smith, Trans.Brit.mycol.Soc.58(3): 459-466, 1972

These Australian graminicolous species are described and illustrated by Walker and Smith (1972) and aspects of their biology discussed by various contributors to Asher and Shipton (1980).

Leptosphaeria paludosa Feltgen, Vorstud.Pilz.Luxemb.Nachtr. II, 157, 1901 (original not seen, from Saccardo & Sydow, 1902; type not seen).

For comments on this species on Cyperaceae, see under Gaeumannomyces sp. tax. sp.l.

Leptosphaeria tanaceti (Fckl.) Holm - the name accepted here for Ophiobolus tanaceti (Fckl.) Sacc.; see also under Leptosporopsis.

LEPTOSPHAERIOPSIS

Leptosphaeriopsis Berlese, Icon.fung.1, 88, 1892
Type species L. ophioboloides (Sacc.) Berl. (based on Leptosphaeria ophioboloides Sacc.).

No specimens have been examined. From the descriptions and figures given by Berlese (1894, 1900), Holm (1957) and Shoemaker (1976), it appears to be a typical Ophiobolus Riess sens. str., and is considered here as Ophiobolus ophioboloides (Sacc.) Holm. Leptosphaeriopsis is listed as a synonym of Ophiobolus by Ainsworth (1971) and von Arx and Müller (1975).

LEPTOSPORA

Leptospora Rabenhorst, Hedwigia 1, 116, 1857
Type sp. L. rubella (Pers.ex Fr.) Rabenh. (type not studied).

Leptospora is a monotypic genus and the single species, L. rubella has been described fully by several authors, either under that name or as Ophiobolus rubellus (Pers. ex Fr.) Sacc. (Müller, 1952; Holm, 1957; Dennis, 1968; Shoemaker, 1976). Müller (1952) and Holm (1957) list many synonyms. L. rubella occurs commonly on dead stems of many

herbaceous plants and often produces a reddish-purple discolouration of invaded tissue. The genus is characterised by large, flask-shaped, often laterally compressed pseudothecia, usually with some attached superficial brown to reddish-brown hyphae and long cylindrical bitunicate asci with very thin (1-1.5 µm) filiform spirally arranged ascospores, and thin septate pseudoparaphyses. Most authors do not describe periphyses and Shoemaker (1976) stated that periphyses and apical hairs are absent. However, Müller (1952) figured periphysis-like structures and von Arx and Müller (1975), in their generic key, placed Leptospora in the section with no superficial hyphae and pseudothecia with an ostiolar pore lined with hyaline or brown periphysis-like bristles, often also with setae. Periphyses and setae were not seen in collections examined during the present work. No conidial states have been found for Leptospora and Luttrell (1973) used this in his generic key as one character to separate Leptospora from Cochliobolus (in which conidial states are known).

Whilst most collections of L. rubella listed in the literature are on dicotyledonous herbaceous plants, a number of collections on Gramineae have been seen which appear to belong in Leptospora. These and some other Leptospora names are listed below.

Leptospora rubella (Pers. ex Fr.) Rabenh., Herb.Myc.Ed.II n.532, 1857 (from Holm, 1957)
= Ophiobolus trichisporus Ell. & Ev., Proc.Acad.Nat.Sci. Phil. 1890, 239, 1890 (type in NY !)

Shoemaker (1976) examined portion of the type collection of O. trichisporus in DAOM and reduced the name to synonymy under L. rubella (as Ophiobolus rubellus). Portion of a collection in NY made at the same place on the same day has been examined by the present writer and a fungus agreeing with the original description of O.trichisporus was present. This supports Shoemaker's proposed synonymy. Whether the NY collection (from the Ellis herbarium) is portion of the type is not certain. It carries the number '1735' (no such number was quoted by Shoemaker) whereas the original description of O.trichisporus gives Dearness 1734 as the type collection. All other information agrees. Briefly, the NY collection is characterised as follows:

Pseudothecia dark brown to dark reddish-brown, flask-shaped to pyriform, 300-400 µm high, 200-300 µm wide with a short conical beak 70-100 µm long, 50-70 µm wide, seated in the culm tissue and erumpent through several layers of leaf sheath. Asci numerous, long cylindrical with a foot-like base, bitunicate, (135) 150-175 (180) x 4 µm, thickened to 2 µm at the apex (thickening to 6-7 µm in immature asci) which contains a net-like nassé. Ascospores spirally arranged in the ascus and probably longer than it, 1 (1.5) µm wide, indistinctly multiseptate, pale yellowish brown in mass, faintly tinted singly. Pseudoparaphyses hyaline, septate, 2-3 µm wide, longer than the asci.

Specimens examined: on Erechtites prenanthoides (A.Rich.) DC., Spruce Cove, Trinidad, California, U.S.A., Feb.1935, H.E.Parks 5312, dupl.ex

BPI 67246 as DAR 11328. On Gramineae undet., London, Ontario, Canada, 9.vi.1890, no collector's name given, n.1735, NY as Ophiobolus trichisporus Ell & Ev. (slides as DAR 34121).

Leptospora helminthospora Rehm - a synonym of Acanthophiobolus helicosporus (Berk.& Br.) Walker (q.v.).

Leptospora implexa (Ell.& Ev.) Walker comb. nov.
≡ Lophiostoma (Lophionema) implexum Ell.& Ev., J.Mycol. 4 (8), 75, 1888 (type in NY !)
≡ Ophiobolus implexus (Ell.& Ev.) Ell. & Ev., North American Pyrenomycetes, 394, 1892.

Pseudothecia (Fig.13) on dead stem tissue and on clusters of dead adventitious roots at stem nodes, dark brown to black, with embedded globose body 300-450 µm diam and erumpent thick cylindrical to slightly tapering neck to 200-300 µm long, 200 µm diam near the base and only slightly narrower at the apex, sometimes slightly flattened, ostiolar canal circular in cross section 30-50 µm wide, inner wall a woven layer of hyaline hyphae 1.5-2 µm diam, some of which project up to 20 µm into the canal, no definite layer of periphyses seen. Wall of ascocarp to 50 µm thick at the base and sides, to 70 µm at junction with neck, with a very dense outer layer 14-18 µm thick in which cellular detail could not be distinguished and an inner layer to 30-35 µm thick of brown, thin-walled radially flattened cells 6-12 x 3-6 µm. Asci (Figs.13 and 19) long cylindrical to narrowly elongated clavate, tapered to a narrow base, bitunicate, apex rounded and only very slightly thickened, 120-160 x 7-10 µm. Ascospores (Figs.13 and 19) eight per ascus, long filiform and densely spirally coiled (6-7 turns in a 140 µm long ascus), longer than the asci, 1.5 µm wide, slightly narrower towards the base, faintly yellowish in mass, hyaline to faintly tinted singly, contents densely granular, closely and regularly beaded with small clear spherical vacuoles, some faint transverse septa seen in some spores but number and spacing (about 7-10 µm apart) difficult to determine. Pseudoparaphyses abundant, longer than the asci, hyaline, filiform, 1-1.5 µm wide, with several slightly swollen bumps along their length, indistinctly septate. Superficial mycelium joined to outer wall of pseudothecia, dense, of reddish-brown to dark brown branched septate hyphae 3-4 µm diam, no hyphopodia or conidiophores seen.

Specimens examined: on dead stem Panicum maximum Jacq., Sri Lanka, no collectors name given, letter of 15.iii.1927, IMI 16847 as Ophioceras implexum (? Lophionema implexum); on dead stem and adventitious roots of Sorghum halepense (L.) Pers., Point à la Hache, Louisiana, U.S.A., 30.vi.1886, A.B. Langlois 1439, Flora Ludoviciana, HOLOTYPE of Lophiostoma (Lophionema) implexum (slides as DAR 33682), in NY.

In the original description, Ellis and Everhart (1888) listed this fungus on dead adventitious roots of Sorghum halepense and on the lower part of sheathing leaves of a possible Andropogon sp.. However, they cite only one collection (Langlois 1439) and it is this collection, on S. halepense in the Ellis collection in NY, that is the holotype. The fungus on IMI 16847 from Sri Lanka has asci to 180 µm long but otherwise agrees exactly with the type. Whilst the necks on some pseudothecia are somewhat flattened laterally, most are circular in section and the

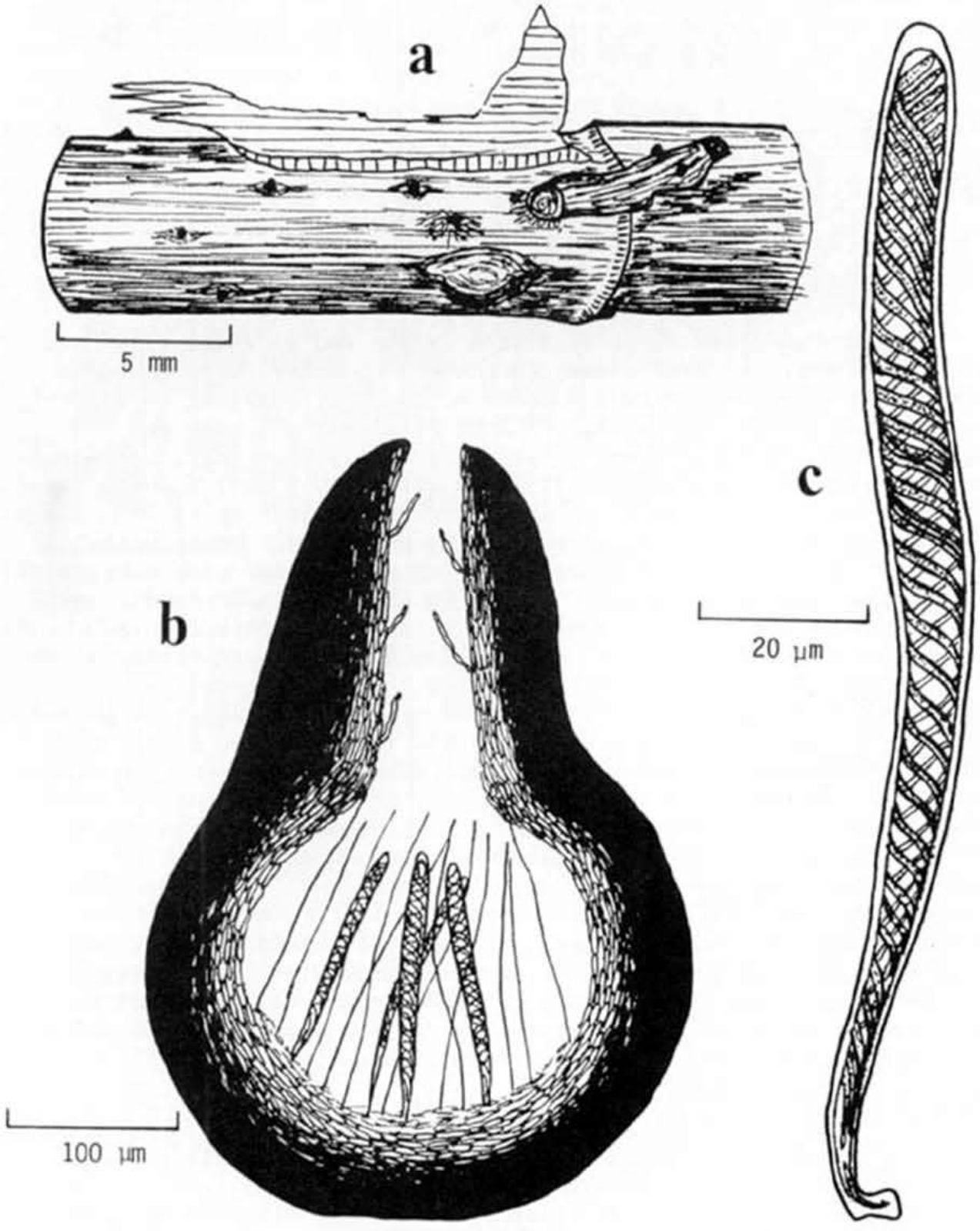


Figure 13. Leptospora implexa, from holotype in NY (slide DAR 33682). a. habit; b. section ascocarp; c. ascus with spiralled ascospores.

ostiolar canal is circular in all cases. L. implexa is not related to Lophiostoma or other genera of Lophiostomataceae (Chesters and Bell, 1970).

Other possible species of Leptospora

From their original descriptions, Ophiobolus leptosporus Saccas, O.spirosporus Ahmad and O.tortilis Sydow could be better placed in Leptospora. However, until type specimens can be examined, their exact identity remains uncertain. See under the Ophiobolus names for comments.

LEPTOSPOROPSIS

Leptosporopsis Höhnel, Akad.Wiss.Wien Sitzungsber.,Math.-Naturwiss.Kl., Abt.1, 129(3), 174, 1920.

Höhnel (1920) proposed this name for certain fungi related to Leptosphaeria with dothideaceous ascocarps and scolecospores. He did not nominate a type species and made no new combinations in Leptosporopsis but in the discussion suggested that Ophiobolus compressus Rehm, O.tanaceti (Fckl.) Sacc., O.herpotrichus (Fr.) Sacc. and O.rostrupii Ferd. & Winge should be placed in it. Petrak (1924) disagreed strongly with Höhnel's conclusions, considered that there was no basis for erection of the new genus and that 'Leptosporopsis von Leptospora Rabh. absolut nicht verschieden'. Clements and Shear (1931) listed Leptosporopsis as a synonym of Ophiobolus, and its type species as 'L.rostrupi (F. & W.) Hoehn.' (there is no evidence that Höhnel made this combination). Ainsworth (1971) quoted Clements and Shear and listed it as a synonym of Ophiobolus. It was not considered in the von Arx and Müller (1975) treatment of bitunicate Ascomycetes.

Leptosporopsis Höhnel (1920) is a nomen nudum, and not validly published (Art.41). The species suggested for it by Höhnel (1920) are disposed as follows:

Ophiobolus compressus Rehm - following Holm (1957), this is considered to be a long-spored Leptosphaeria, L. compressa (Rehm) Holm (q.v.). It is not an Ophiobolus Riess sens. str., where it is placed by some workers (Müller, 1952; Shoemaker, 1976).

Ophiobolus herpotrichus (Fr.) Sacc. - placed here as Ophiosphaerella herpotricha (Fr.) Walker (q.v.). A microscope slide labelled 'Leptosporopsis herpotrichus' was seen amongst the v. Höhnel collections in FH; see specimen list under Ophiosphaerella herpotricha.

Ophiobolus rostrupii Ferd. & Winge - a later name for the fungus considered here as Ophiobolus prunellae (Ell. & Ev.) Shoemaker (1976) based on Linospora prunellae Ell. & Ev.(as 'brunellae'). Four slides from FH marked 'A.F.Columb. Leptosporopsis brunellae' (one numbered '3786'), possibly made by Höhnel (1920), have been examined and show a fungus with the following characters:

Ascocarps broken, size not determinable. Ascocarp wall 20-35 µm thick,

of 4-5 layers of brown slightly flattened cells 7-12 (14) x 4-6 µm, cell wall in outer layers thickened to 2-2.5 µm, thinner and paler in inner layers. Ostiole central. Asci 100-125 x 12-13 µm (to 150-175 µm long in one slide), bitunicate, much thickened at tip which has a thin central canal, eight-spored. Ascospores filiform, pale yellowish in mass and singly, 112-125 (130) x 3-4 µm, 7 septate, constricted at the central septum and cell on either side slightly swollen, widest in the middle and tapering gradually to the rounded apex and more sharply to the thin base, tending to break at the central septum into two half spores. Pseudoparaphyses abundant, hyaline, filiform, septate, 1-1.5 µm wide.

With ascospores having slightly swollen cells on either side of the central septum, at which some separation into half spores is occurring, this seems to fit better into Ophiobolus than into Leptosphaeria where it was placed by Barr (1967), as L.hesperia Barr. The name Leptosporopsis rostrupi (F. & W.) Hoehn. in Clements and Shear (1931) refers to this species.

Ophiobolus tanaceti (Fckl.) Sacc. - placed by Holm (1957) as Leptosphaeria tanaceti (Fckl.) Holm. This is accepted here.

LIDOPHIA

Lidophia Walker & Sutton, Trans.Brit.mycol.Soc.62 (2),232 1974

≡ Dilophia Sacc., Syll.Fung.2, 357, 1883, non Dilophia Thompson, Hooker's J.Bot.5, 19, 1853 (Cruciferae)

Type species: L. graminis (Sacc.) Walker & Sutton (type in G !)

The new name Lidophia Walker & Sutton (1974) was proposed for the invalid later homonym Dilophia Sacc.(1883) and a full description of pseudothecia, asci and ascospores given. von Arx and Müller (1975), in their study of bitunicate Ascomycetes, commented that the Walker and Sutton description was inadequate but that the genus was close to, and probably not different from, Leptosphaeria. In collections they studied, the fungus could not be found or was insufficiently developed.

Walker and Sutton (1974) found L.graminis only in the type specimen, in close association with pycnidia of Dilophospora alopecuri (Fr.) Fr.. Pseudothecia were embedded in the slightly swollen leaf and shoot tissue of the grass host amongst the pycnidia, in a stroma composed of host and fungal tissue, whose outer layer formed a clypeus penetrated by pseudothecial and pycnidial ostioles. The bitunicate asci (100) 110-130 (135) x 7-9 µm contained eight, pale yellowish, narrowly fusiform ascospores, 60-100 x (1.5) 2 (2.5) µm, widest in the middle, tapering gradually into an elongated fine thread at each end, with about 15 septa, and slightly constricted at the central septum, where they break at maturity into two equal part spores. Hyaline pseudoparaphyses were present between the asci and longer than them. Pseudothecia were not found on leaf spots with

Dilophospora pycnidia, where stromatic development was much reduced.

These characters indicate that Lidophia is a Pleosporaceous genus, resembling Ophiobolus Riess in having spores breaking readily into half spores at the central septum, but with no swollen cells as in Ophiobolus. Several earlier authors have described and figured this ascomycete with narrowly fusiform spores associated with Dilophospora alopecuri (see details in Walker and Sutton, 1974), although it is rarely found. It may be the perfect state of Dilophospora but this remains to be proved. In contrast to the opinion of von Arx and Müller (1975), Lidophia is regarded as a distinct, if rare, genus of Pleosporaceae, close to, but distinct from, Ophiobolus Riess. With its thin (2 µm) pale yellowish elongated fusiform spores, breaking at the central septum, it seems quite distinct from Leptosphaeria as delimited by Holm (1957), Luttrell (1973) and von Arx and Müller (1975). The significance and constancy of stromatic development in Lidophia can only be determined from further collections. With the associated Dilophospora pycnidia, stroma development is variable and may be absent (Walker and Sutton, 1974). Further collections should perhaps be sought on grass shoots heavily infected with Dilophospora, where well-developed stromatic tissue is present. Specimens examined were listed by Walker and Sutton (1974).

LINOCARPON

Linocarpon H. & P. Sydow, Ann.Mycol.15, 210, 1917
Type sp. L. pandani (H.& P.Syd.) H. & P. Syd.

The genus was erected for a fungus found on dead Pandanus leaves in the Philippines. Several species have been described since, and Petrak (1952) transferred to Linocarpon a number of species formally placed in Ophiobolus and reduced Gaeumannomyces von Arx & Olivier to synonymy. Petrak's concept of Linocarpon includes several species with characters not in keeping with those shown by the type species. This is described, and various Linocarpon names are listed and their relationships discussed.

Linocarpon pandani (H. & P. Syd.) H. & P.Syd.,Ann. Mycol.15, 210, 1917
≡ Linospora pandani H.& P. Syd., Ann.Mycol.11,60,1913, (basionym, type in S !)
= Linospora pandani Rehm, Leaflets of Philippine Botany 8, 2954, 1916 (later homonym; duplicates of Rehm specimens in DAR !)

Fruiting bodies on host leaves as black, often shiny, slightly raised circular spots up to 1 mm diam, with a small central ostiolar dot; in section, lenticular, developing amongst leaf cortical cells beneath the host epidermis and above a layer of host fibre bundles (bundles to 100 µm diam, and 75-100 µm apart), composed of a lenticular perithecium (Fig.14), with overlaying clypeus and variable development of stromatic tissue laterally. Clypeus to 1 mm diam, composed of epidermal cells packed with fungal hyphae and beneath this a layer of

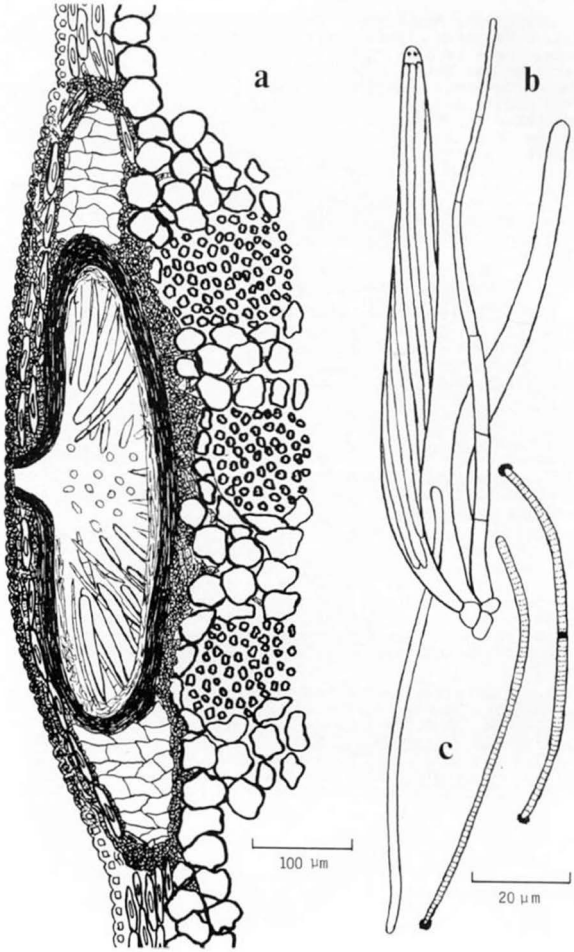
radially arranged dark brown septate hyphae 2.5-3 µm wide (Figs. 15 and 16); stromatic tissue surrounding perithecium, in young fruiting bodies composed of pale brown irregularly shaped cells 5-10 x 3-4 µm, later interspersed with vertical bands of dark brown hyphae, mixed with host tissue and bounded at sides and below by a dark layer 15-20 µm thick of compressed hyphae (Figs. 14,17 and 18). Perithecia one per stroma, lenticular, to 600-650 µm diam and 200-300 µm thick when mature, several 150 x 40-50 µm and immature, with dark brown to black wall 15-25 µm thick at sides, of 4-6 layers of radially flattened dark brown cells, fusing with the clypeus above and with the stromatic tissue and invaded discoloured layers of host cells below, ostiole central 20-30 µm diam, piercing the clypeus, periphyses not seen. Asci (Fig. 14) in a basal layer, long cylindrical, with a tapering base, 100-130 x 5-8 µm, unitunicate, apex rounded, thickened to 2 µm, with small apical ring, eight-spored. Ascospores (Fig.14) filiform, pale yellowish in mass, hyaline to faintly tinted singly, (65) 70-100 x 1.5-2 µm, very slightly wider centrally, ends rounded, parallel or slightly spiralled, containing numerous refringent septum-like bands 2 µm apart, with a small, inconspicuous gelatinous appendage at one or both ends. Paraphyses (Fig.14) seen only in immature perithecia, hyaline, 3-4 µm wide at base, tapering to apex, longer than asci, sparingly septate. Hyphae in host tissue, hyaline to pale brown, branched, septate, 1.5-2.5 µm diam, no superficial mycelium developed.

Illustrations: Schrantz (1961, section ascocarp, ascus tip structure, ascospores).

Specimens examined: on Pandanus laevis Lour., Davao, Mindanao, Philippine Islands, March 1904, E.B. Copeland 592,S, HOLOTYPE of Linospora pandani Syd. (slides as DAR 31927); on Pandanus sabotan Blanco, Mount Maquiling, Los Banos, Philippines, April 1914, C.F. Baker Fungi Malayana 152a (as Linospora pandani Rehm), DAR 25194; on Pandanus utilissimus Elm., Mt. Banahao, Philippine Islands, Dec.1913, C.F. Baker 2247, S, (slides as DAR 31928); same, C.F. Baker Fungi Malayana 545, DAR 31929; same, C.F. Baker Fungi Malayana 152 (as Linospora pandani Rehm), DAR 25193.

H. & P. Sydow (1917) erected their new genus Linocarpon for the previously described Linospora pandani H.& P.Sydow (1913), listed in synonymy. The specimen on Pandanus laevis (E.B. Copeland 592) cited in their 1913 paper is the type of Linospora pandani and thus of the genus Linocarpon; the collection cited in their 1917 paper, on P. utilissimus (C.F. Baker 2247), is merely another collection. Rehm (1916) independently described this species as Linospora pandani Rehm from Philippine collections but his name is a later homonym of L. pandani H. & P. Sydow.

Figure 14. Linocarpon pandani, from type in S (slide DAR 31927), a. section ascocarp showing some marginal stromatic tissue and epidermal clypeus; b. young asci and paraphysis; c. ascospores (two on right from DAR 31928)


a
b
c
100 µm
20 µm

Stromatic development varies between collections. In all, a definite clypeus is always present but, in the holotype, there is also marked stromatic development around the perithecium. This is not so marked in Baker 2247. The fungus develops amongst the large thin-walled cells of the leaf cortex and, as it enlarges, flattens host cells above and below it. The firm layer of fibre bundles beneath the cortex (Fig.14) prevents development in that direction and growth occurs radially into the cortex as a wedge of stromatic tissue (Figs.14,17 and 18). The overlaying tissues are slightly raised, the black clypeus develops in and below the epidermis and the fungus is seen as shallow shield-shaped circular black dots on the leaf. Petrak and Deighton (1952) and Pirozynski (1972) have commented on the influence of host anatomy on perithecium shape in the closely related (perhaps identical) L.elaeidis Petrak apud Petrak & Deighton on oil palm.

With its clypeate, stromatic, embedded, centrally ostiolate perithecia, no superficial hyphopodiate mycelium and saprophytic habit, Linocarpon is quite distinct from Gaeumannomyces.

Other Linocarpon names

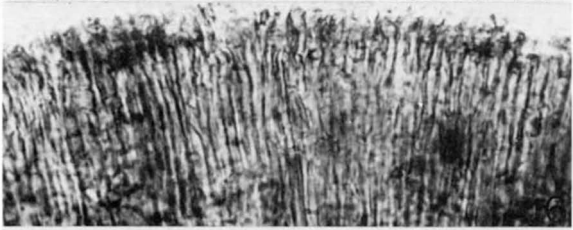
L.cajani Deighton apud Petrak & Deighton (1952), on Cajanus cajan (L.) Huth, Newton, Sierra Leone, 16.xi.1950, F.C. Deighton, IMI 46618, HOLOTYPE ! This is a good Linocarpon and is described and illustrated by Pirozynski (1972) from the type and from a collection he places here on dead, decaying rachides of oil palm (Elaeis guineensis Jacq.) from Tanzania.

L.cariceti (Berk.& Br.) Petrak (1952), basionym Sphaeria cariceti Berk.& Br. (1861). Petrak (1952) used this name for the cereal take-all fungi and reduced Gaeumannomyces von Arx & Olivier (1952) to synonymy under Linocarpon. These two genera are quite distinct (see above and descriptions of the type species given in this paper). The unsuitability of the epithet 'cariceti Berk.& Br.' for current use and its typification have been dealt with elsewhere (Walker, 1972).

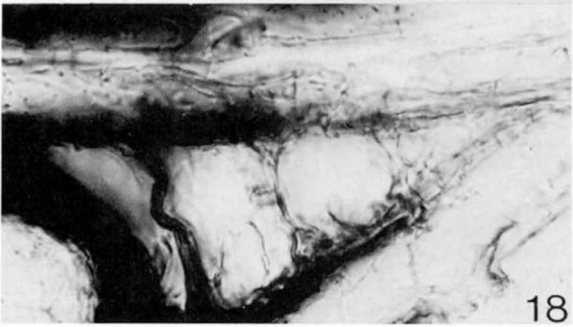
L.elaeidis Petrak apud Petrak & Deighton (1952), on Elaeis guineensis, Newton, Sierra Leone, 16.xi.1950, F.C.Deighton, IMI 46620a, HOLOTYPE ! This seems hardly distinct from the generic type, L.pandani. However, until further work is carried out on a range of palm fungi with names in Linocarpon, Ophiobolus and other genera, it is kept separate. It is fully described and illustrated by Pirozynski (1972).

Figures 15-18. Linocarpon pandani from type in S (slide DAR 31927). 15. Radial hyphae in clypeus, x 183. 16. Detail of radial structure, x 733. 17. Margin of ascocarp showing wedge pushing into host tissue, and epidermal clypeus, x 183. 18. Detail of marginal wedge, x 733.


5


6


17


18

L. eucryptum (Berk. & Br.) Petrak - see under Sphaeria eucrypta Berk. & Br.; not a Linocarpon.

L. halimum (Diehl & Mounce) Petrak (1952) - now placed as Lulworthia halima (Diehl & Mounce) Cribb & Cribb (1955); originally as Ophiobolus halimus Diehl & Mounce (q.v.).

L. livistonae (P.Henn.) Schrantz (1961) - combination not validly published (Art.33); see under Ophiobolus livistonae P. Henn. and note at end of this list.

L. manihotis (Syd. in Syd. & Butler) Petrak (1957) - see under Ophiobolus manihotis Syd. in Syd. and Butler.

L. maritimum (Sacc.) Petrak (1952) - based on Rhaphidophora maritima Sacc.; type sterile; for description and synonymy see Walker (1972); not a Linocarpon, but the exact identity of this species, described with fragmenting ascospores, is not known; see also Ophiobolus maritimus.

L. medusae (Ell. & Ev.) Petrak (1952) - now placed as Lulworthia medusae (Ell. & Ev.) Cribb & Cribb (1955); see under Ophiobolus medusae Ell. & Ev.

L. muroianum Hino & Katumoto (1966) - placed here as Plagiosphaera muroiana (Hino & Katumoto) Walker (q.v.).

L. nipae (P. Henn.) Schrantz (1961) - combination not validly published (Art.33); see under Ophiobolus nipae P. Henn. and note at end of this list.

L. oryzinum (Sacc.) Petrak (1952) - this is Gaeumannomyces graminis (Sacc.) von Arx & Olivier var. graminis (q.v.).

L. palmetto (Ell. & Ev.) Barr (1978) - described originally as Linospora palmetto Ell. & Ev. (1887) and transferred by Barr (1978) to Linocarpon after study of the type.

L. stipae Hansford (1954) - redisposed here as Ophiosphaerella stipae (Hansf.) Walker (q.v.).

L. umbelliferarum Barr (1961) - transferred by Barr (1978) as Plagiosphaera umbelliferarum (Barr) Barr (q.v.).

L. verminosum (Mont.) Schrantz (1961) - combination not validly published (Art.33); see under Ophiobolus verminosus (Mont.) Sacc.

L. versisporum (Ell. & Mart.) Petrak (1952) - based on Ophiobolus versisporus Ell. & Mart. (1885) on Sabal, this is considered by Barr (1978) as a true Linocarpon, with ascospores similar to those of L. palmetto (also on Sabal), broadest in the upper third and tapering to the base. Ellis and Martin (1885) described the ascospores of L.versisporum as 60-70 x 2-2.5 µm, somewhat larger than those

described for L. palmetto.

L. williamsii Hansford (1954) - placed here as Ophiosphaerella williamsii (Hansf.) Walker (q.v.).

In the sense of the generic type, Linocarpon is readily distinguished from genera such as Gaeumannomyces, Linospora and Plagiosphaera (see also Barr, 1978) and consists of several species found mainly on dead leaves and petioles of Palmae, with fewer records on other hosts. Of the species considered here, five are accepted in Linocarpon - L. pandani, L. cajani, L. elaeidis, L. palmetto and L. versisporum. The relationship of these to one another and to some Ophiobolus species on Palmae such as Ophiobolus oedema (Mont.) Sacc., O.licualae Syd., O. livistonae P. Henn., O. nipae P.Henn. and O.verminosus (Mont.) Sacc. requires further study. The Montagne species could well provide earlier epithets in Linocarpon for some of these palm fungi.

LINOSPORA

Linospora Fuckel, Jahrbücher des Nassauischen Vereins für Naturkunde 23-24, 123, 1870. Type sp. L.capreae (DC) Fckl.

Linospora is characterised by oblique or horizontal perithecia surrounded by a pseudostroma embedded in the substrate, and limited by a dark clypeus, a long protruding lateral beak, unitunicate asci with an apical ring, and hyaline filiform ascospores. The type species L.capreae, occurs on dead fallen leaves of Salix, and has been described frequently (von Arx and Olivier, 1952; Barr,1978; Dennis, 1968; Munk, 1957). Several Linospora names are dealt with by Barr (1978).

Six species described originally in Linospora have been examined and found to belong to other genera. They are disposed as follows:-

Linospora antarctica Speg. - redisposed as Sphaerulina antarctica (Speg.) Walker (q.v.).

Linospora magellanica Speg. - redisposed as Lophodermium magellanicum (Speg.) Walker (q.v.).

Linospora palmetto Ell. & Ev. - transferred by Barr (1978) as Linocarpon palmetto (Ell.& Ev.) Barr (q.v.).

Linospora pandani Rehm - placed here as a synonym of Linocarpon pandani (Syd.) Syd. (q.v.).

Linospora prunellae Ell.& Ev. - see discussion of Ophiobolus rostrupii under Leptosporopsis.

Linospora pulchella Speg. - reduced to synonymy under Gaeumannomyces graminis (Sacc.) von Arx & Olivier var.

graminis (q.v.).

LOPHODERMIUM

Lophodermium Chevallier, Fl.Paris 1, 435, 1826 (from Darker, 1967). Type sp. L. arundinaceum (Schrad. ex St. Amans) Chev.

Generic and specific synonyms and other nomenclatural details are given for twenty one species by Darker (1967). Several species are described by Tehon (1935, under various generic names) and Terrier (1942). Two species seen on Gramineae are considered here.

Lophodermium gramineum (Fr.) Chev.: on dead leaves of Bromus unioloides H.B.K., in sandhills, Tuggerah Lakes, N.S.W., Australia, 14.v.1969, J. Walker DAR 17198.

In this locality, the few host plants present were heavily infected. The fungus agreed with the description of L. gramineum given by Tehon (1935).

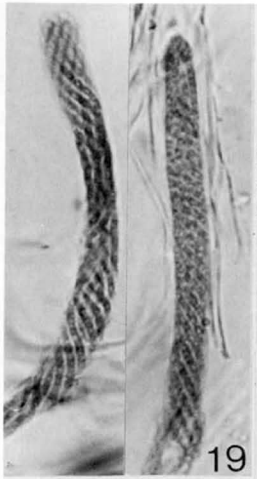
Lophodermium magellanicum (Speg.) Walker comb.nov.
≡ Linospora magellanica Speg., Bol.Acad.Nac.Cienc. Republ.Argent.Cordoba 27 (4), 378-379, 1924 (type in LPS !)

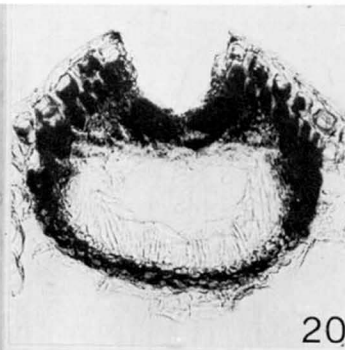
Perithecia (Figs.20-23) embedded in leaf, subepidermal, black, oval in outline, up to 400-500 µm long, 250 µm wide, opening by a longitudinal slit, wall with labia up to 40 µm thick on either side of slit, thinner at sides, 15-20 µm thick at base, dark brown to black outside, paler inside, composed of cells 7-10 µm diam forming a pseudoparenchyma, in surface view brown hyphae clearly seen at margin of perithecia, hyphae developing below and in host epidermal cells, which are packed with small dark fungal cells. Asci (Figs.21-23) developing in basal layer, cylindrical to more commonly obclavate, usually widest about one quarter the height above the base, tapering gradually to the slightly thickened rounded apex and more sharply to the flattened base, no apical apparatus seen, up to 90 x 17 µm, eight-spored. Ascospores (Figs.21-23) long cylindrical (bacillary), straight but usually sinuate or curved towards the apex which is rounded and occasionally very slightly swollen, base slightly narrower, non-septate, 35-40 x 2-2.5 µm, completely surrounded by a hyaline sheath 2-2.5 µm thick, lying at 2-3 levels in the ascus. Paraphyses thin, hyaline, probably septate, as long as or longer than the asci.

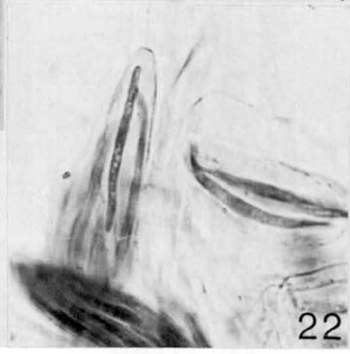
Illustrations: Spegazzini (1924, habit, section ascocarp, asci, ascospores, paraphyses).

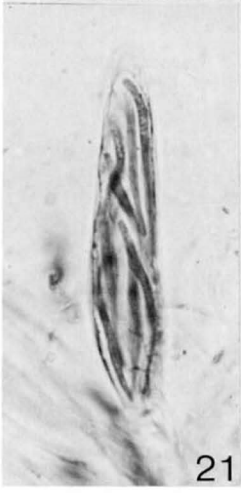
Specimen examined: on dead leaves of Festuca purpurascens Banks & Soland., Sholl Bay, Capitan Aracana Island, Chile, 13.i.1924, C. Spegazzini LPS 881, HOLOTYPE (slides as DAR 33290).

Spegazzini (1924) described the lenticular perithecia as 150-160 µm diam with a central ostiole. However, his pencil drawing on the type packet (similar to the published illustration) shows an oval fruiting body 250 x 150-160 µm like those on the specimen. Some perithecia were immature with the ostiolar slit poorly developed and these appeared

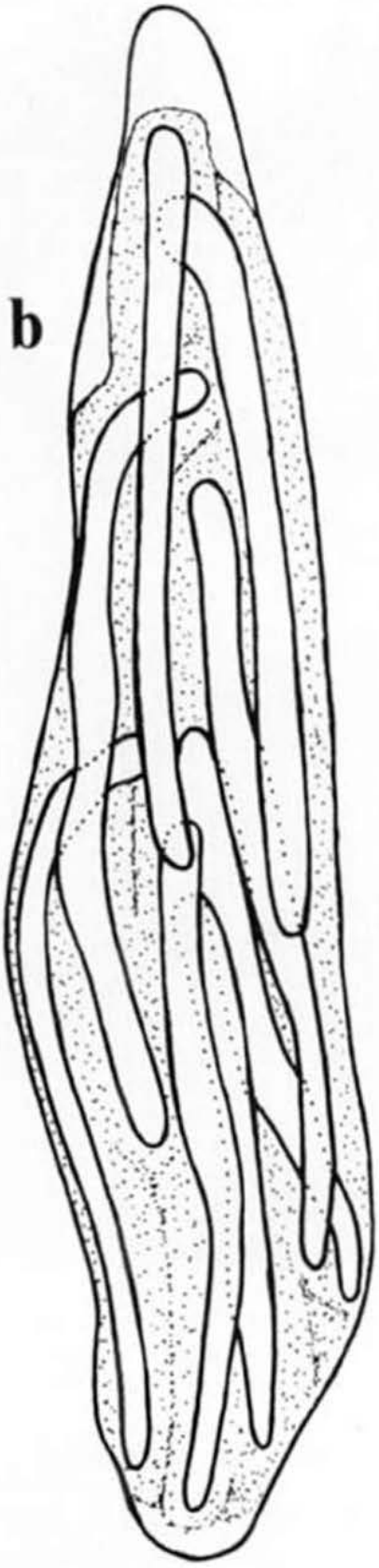








Figures 19-22. 19. Leptospora implexa, two asci with spiralled ascospores, x 733, from holotype in NY (slide DAR 33682). 20-22. Lophodermium magellanicum, from holotype, LPS 881 (slide DAR 33290). 20. Cross-section ascocarp, x 183. 21-22. Asci with ascospores, x 733.



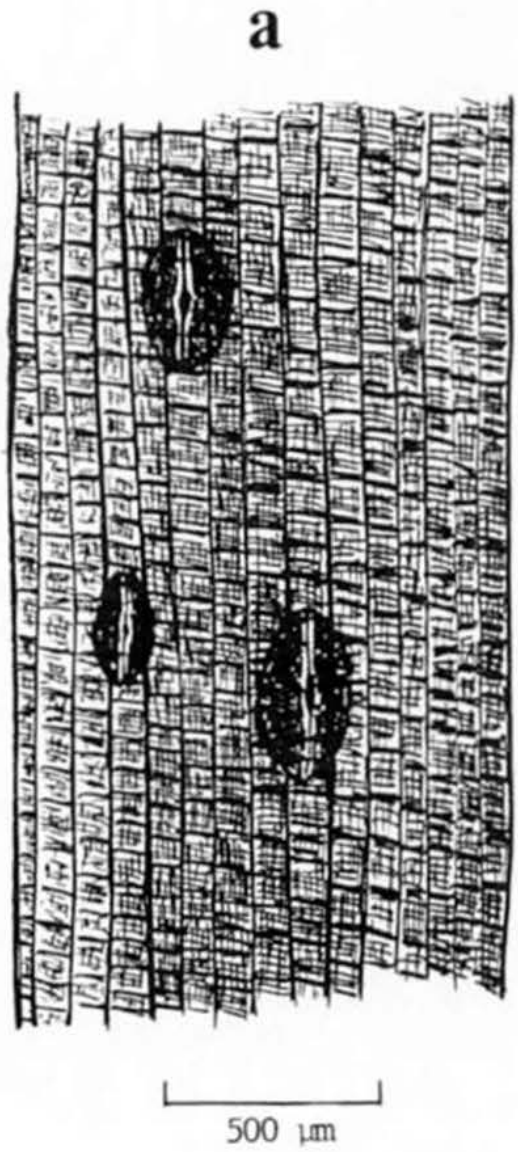


Figure 23. Lophodermium magellanicum, from holotype, LPS 881 (slide DAR 33290). a. habit; b. ascus with ascospores.

superficially to have a round central pore. Asci, ascospores and paraphyses agreed with those described and figured by Spegazzini (1924), except that he did not mention the spore sheath.

L. magellanicum is a typical Lophodermium. Of the several species described from Gramineae, it is similar to the fungus described and figured (Plate 8, Fig.4) by Terrier (1942) as L. alpinum (Rehm) Rehm, described originally as L. arundinaceum var. alpinum from a collection on Nardus stricta. Terrier (1942) thought that two distinct Lophodermium spp. were present on Rehm's type and that his description perhaps combined characters of both. Although it is very similar to the fungus Terrier described, Spegazzini's species is best kept separate until the above problem is resolved. Terrier (1942) listed another collection of L. alpinum from Switzerland on Festuca, and Savile (1959) listed Arctic collections on species of Elymus, Festuca and Pucciniella. His description of mature asci as (10) 12-16 µm wide and ascospores (1.8) 2.2-2.8 (3) µm wide is similar to those of L. magellanicum.

The detailed locality information given for this species (and for Sphaerulina antarctica (Speg.) Walker, collected at the same time) is slightly confused. On Spegazzini's original packet, the only locality given is Sholl Bay (in his handwriting) and this is repeated in Spegazzini (1924). The locality Sholl Bay, Capitan Aracana Island, Chile is typed on the outer packet. Farr (1973) gives it as Tierra del Fuego, South America and Cash (1972) as Sholl Bay, Southern Republic of Argentina. All seem to be referring to the same place.

LULWORTHIA

For a discussion of the genus, see Kohlmeyer (1972). The two species L. halima (Diehl & Mounce) Cribb & Cribb and L. medusae (Ell.& Ev.) Cribb & Cribb are mentioned briefly under their previous Linocarpon and Ophiobolus names (q.v.).

MICROSTELIUM

Microstelium Patouillard, Bull.Soc.Mycol.Fr.15, 208, 1899. Type sp. M.hyalinum Pat. (type in FH !)

This genus, described from bark encrusted with algae and mosses, was characterised by sparse, cylindrical, apically obtuse, stipitate, fleshy-coriaceous perithecia, 1 mm high, perhaps with an apical pore, very long cylindrical asci 8-10 µm wide and filiform ascospores as long as the asci, breaking into many fragments 6-8 µm long. Filiform paraphyses were also said to be present. The perithecial wall was brownish violet in colour and composed of an inner layer of very long thin brown parallel hyphae whose thickened tips turned towards the outside and formed the outer wall layer. A white superficial mycelium was

described and the genus was said to be related to Barya and Acrospermum.

The type specimen in FH is very small and appears to be a mixture of dried moss and moss rhizoids. A note in the type packet reads 'Peut-être un lichen?'. No sign of any fungal structures was seen. The so-called Microstelium perithecia seem to be the erect dried tips of young rhizoids. These are dark brown with darker blackened tips and have dried to a flinty consistency very difficult to section. No asci, ascospores or ascocarp wall structures were seen in slides prepared from this specimen. It is suggested that the genus may have been based on moss rhizoids blackened at their tips.

Illustrations: Patouillard (1899, habit, ascocarps and cells of outer wall).

Specimen examined: on bark of a living tree, near Bains-Larmes, Guadeloupe, no date or collectors name, 1070, Pat. herb.sht. 6616, FH, HOLOTYPE (two slides as DAR 33736).

OPHIOBOLUS

Ophiobolus Riess, Hedwigia 1 (6), 27-28, 1854.
Type sp. O.disseminans Riess, now O.acuminatus (Sow. ex. Fr.) Duby ap. Rabh.

The strict generic concept adopted by Holm (1957) and followed in the works of Luttrell (1973) and von Arx and Müller (1975) is accepted here. As there does not appear to be a recent description of the generic type specimen, one is given here.

Ophiobolus acuminatus (Sow.ex Fr.) Duby ap. Rabh.
= O.disseminans Riess, Hedw.1 (6), 27-28, 1854 (Rabh.Herb.Myc. I n. 1823, duplicate in M !)
A more extensive synonymy is given by Müller (1952) and Holm (1957).

Pseudothecia (Fig.25) embedded in dead stem, black, with erumpent necks, many broken off, ostiole seen from above as a minute white circular area with surrounding black wall and central pore. Pseudothecia roughly pyriform, body globose, embedded in spongy cortical stem tissue, base resting on harder woody internal tissue, joined to a loose to dense brown mycelium in stem cortex, 300-450 µm high (including neck), 250-300 µm diam, wall 25-30 µm thick, somewhat thicker near junction of neck, of several (8-12) layers of cells, outer layers very dark brown and cells with thickened walls, inner layers of thinner walled pale brown to hyaline radially flattened cells 9-12 x 6-8 µm; neck 50-100 µm long (many broken and perhaps originally longer), 50-75 µm wide, lined internally with hyaline periphyses, ostiolar canal 20-25 µm diam. Asci (Fig.26) abundant, long cylindrical with narrower short basal stalk terminating in a foot-like base, bitunicate, 130-150 x 10-12 µm, many not fully mature, apical apparatus not seen (not studied in detail), eight-spored. Ascospores (Fig.24) long cylindrical, brown in mass, pale brown singly, lying parallel or more commonly slightly spirally twisted in the ascus, 120-150 x 2-3 µm, tapering slightly near each end, ends rounded, spores breaking easily into two

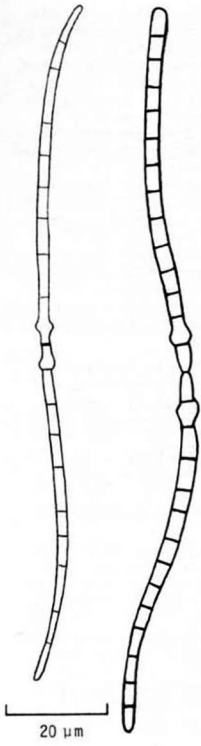


Figure 24. Ophiobolus acuminatus, ascospores. a. young spore from isotype of O.disseminans in M (slide DAR 32063); b. from specimen in K as Sphaeria penicillus (slide DAR 33308).

halves at the central septum, the second cell on either side being swollen, several (20-25) septa per spore, some septa more prominent than others. Pseudoparaphyses abundant, hyaline, septate, longer than the asci, 2-2.5 µm wide.

Illustrations: Dennis (1968, habit, ascus, ascospores); Holm (1957, ascospore); Müller (1952, section ascocarp, ascospores); Shoemaker (1976, section ascocarp, ascus, ascospores).

Specimen examined: on dry dead stem of Cirsium arvense (L.) Scop. (as Carduus arvensis), near Kassel, Germany, spring 1853 (Rabh.Herb.Myc.In. 1823) in M, ISOTYPE (slides as DAR 32063).

The above description agrees very well with that given by Müller (1952, as O.acuminatus) but measurements of asci and ascospores are somewhat smaller than those given by Holm (1957, asci 150-190 x 9-10 µm; ascospores 120-165 x 3.5-5 µm) and Shoemaker (1976, asci 150-190 x 13-17 µm; ascospores 140-180 x 3-4 µm), both as O.acuminatus. Many ascocarps on the type specimen seemed to be not fully mature.

Many scolecospored fungi have been placed in Ophiobolus by Saccardo (1883) and later workers, and Ophiobolus names in the literature now refer to a wide range of scolecospored perithecial and pseudothecial species. In current work on the take-all fungi of cereals and grasses (Walker, 1972, 1980), many Ophiobolus names have been considered and type specimens of several examined. These are listed in alphabetical order of specific epithet with comments on the disposition accepted here for each species. Full synonymy will be found either in the references listed, or under the name in this chapter where the species is treated.

Ophiobolus andropogonis Ell.& Ev., Proc. Acad.Nat.Sci.Phil.1893, 448, 1894.

Exact identity not known. The sheet in NY bears two packets and a description. The two packets are (i) on Vetiveria zizanioides (L.) Nash (formerly as Andropogon muricatus), St.Martinsville, Louisiana, 9.iii.1889, A.B.Langlois 1687, which is empty, with a note reading 'empty 3/31/67' and (ii) same host and

locality, Jan.1890, Langlois 2209 (partly) (slides as DAR 33737) which contains several grass leaf sheaths bearing pseudothecia of a species of Ophiosphaerella, similar to O. herpotricha (Fr.) Walker (q.v.). The note on the packet is headed 'Ophiobolus andropogonis E.& E.', gives details for Langlois 1687, and describes a fungus with ascocarps 400 x 300 µm, asci 100-120 x 10 µm, ascospores nearly as long as the asci and 2.5 µm wide, paraphyses present. The name 'O.andropogonis' on this note has been crossed out and 'O.medusae E.& E.' written in. This description is very similar to that of O.medusae var. minor Ell.& Ev.(1890) described from another collection (Langlois 1771) made at St. Martinsville on Vetiveria zizanioides (as Andropogon muricatus) in Feb.1889. This collection has not been located but Meyers (1957), in proposing the new name Ophiobolus salinus for O.medusae var. minor, stated that an examination of the type material showed a fungus with paraphyses, and ascospores 90-110 x 2.5 µm with no appendages. This is also similar to the description of Langlois 1687 given on the NY sheet of O.andropogonis.

When describing O.andropogonis, Ellis and Everhart (1894) stated that, in their North American Pyrenomycetes (Ellis and Everhart, 1892), they had included it under O. medusae (where they list two collections on Spartina and Vetiveria zizanioides, as Andropogon muricatus), but they now regard it as a separate species, with clavate cylindrical asci 60-80 x 8-10 µm, straight multiseptate ascospores 40-80 x 2-2.5 µm and abundant paraphyses. The only collection they quote is on V.zizanioides (as A.muricatus), Louisiana, Langlois (without number).

This published description does not agree either with the description on the note in NY (based on Langlois 1687) or with the fungus found on Langlois 2209. From the note, Langlois 1687 would seem to have been intended originally as the type collection. Until it (or a duplicate) or other Ellis and Everhart material labelled O.andropogonis can be examined, the discripancy between the available material (and herbarium note) and the published description cannot be resolved and the exact identity of O.andropogonis (and of the similar O.medusae var. minor on the same host) remains unknown. (See also under Ophiosphaerella herpotricha).

Ophiobolus arenarius Bomm., Rouss.& Sacc. in Sacc., Syll. fung.9, 935, 1901 (type in PAD, not seen)

Described from the type by Eriksson (1967) and transferred as Plejobolus arenarius (Bomm.,Rouss.& Sacc. in Sacc.) O.Erkiss., the type species of Plejobolus; also described and figured from a Scottish collection on the type host Ammophila arenaria (L.) Link by Dennis (1975). The clypeate perithecia with an eccentric neck contain bitunicate asci up to 400 x 10 µm with hyaline ascospores almost as long, 2-2.5 µm wide, breaking at maturity before discharge into part-spores 4-6 µm long.

Ophiobolus australiensis Johnson & Sparrow, Fungi in oceans and estuaries, p.419, 1961.

A nom.nov. for O.littoralis Cribb & Cribb (non O. littoralis (Crouan) Sacc.) on roots of Avicennia in Queensland.

Ophiobolus barbatus Pat. & Gail.(1888) - the type species of Acanthotheciella Höhn. (1911) (q.v.).

Ophiobolus brachysporus Fautr. & Roum. (from Saccardo, 1895) - a synonym of Plagiosphaera immersa (Trail) Petrak (q.v.).

Ophiobolus cariceti (Berk.& Br.) Sacc. (1883) - see under Sphaeria cariceti.

Ophiobolus chaetophorus (Crouan) Sacc. (1883) - a synonym of Acanthophiobolus helicosporus (Berk.& Br.) Walker (q.v.).

Ophiobolus coffeatus (Berk.in Hook.) Sacc.(1883) - see under Sphaeria coffeata.

Ophiobolus compressus Rehm (1881) - treated here,following Holm (1957), as Leptosphaeria compressa (Rehm) Holm (q.v.).

Ophiobolus culmorum (Crouan) Sacc. (1883) - see under Sphaeria culmorum Crouan.

Ophiobolus disseminans Riess (1854) - the type species of Ophiobolus Riess, now placed as a synonym of O.acuminatus (see above).

Ophiobolus eucryptus (Berk.& Br.) Sacc.(1883) - see under Sphaeria eucrypta.

Ophiobolus gracilis (Niessl) Müller (1952) - a synonym of Acanthophiobolus helicosporus (Berk.& Br.) Walker (q.v.).

Ophiobolus graminicola (Speg.) Petr.& Syd. (1936) (as 'graminicolus') - this is the type species of Ophiosphaerella Speg. (q.v.).

Ophiobolus graminis (Sacc.) Sacc. in Roum.& Sacc. (1881) - the type species of Gaeumannomyces, placed here as G. graminis (Sacc.) von Arx & Olivier var. graminis (q.v.). The various uses of this name in plant pathological literature are discussed in detail by Walker (1980).

Ophiobolus graminis var.avenae Turner (1940) - placed here as Gaeumannomyces graminis (Sacc.) von Arx & Olivier var. avenae (Turner)Dennis (q.v.).

Ophiobolus halimus Diehl & Mounce, in Mounce & Diehl (1934) - found on Zostera marina L. in Canada and now placed as Lulworthia halima (Diehl & Mounce) Cribb & Cribb (1955).

Placed in Linocarpon by Petrak (1952) but this opinion not accepted here.

Ophiobolus helicosporus (Berk.& Br.) Sacc. (1883) - placed here as Acanthophiobolus helicosporus (Berk.& Br.) Walker (q.v.).

Ophiobolus herpotrichus (Fr.) Sacc. in Roum. & Sacc. (1881) - placed here as Ophiosphaerella herpotricha (Fr.) Walker (q.v.).

Ophiobolus heterostrophus Drechs., J.agric.Res.31, 723-724, 1925, (type not studied) - transferred as Cochliobolus heterostrophus (Drechsler) Drechsler (1934), the type species of Cochliobolus. This genus and its associated conidial states have not been studied here.

Ophiobolus immersus Trail (1889) - see Plagiosphaera immersa (Trail) Petrak.

Ophiobolus implexus (Ell.& Ev.) Ell.& Ev. (1892) - not an Ophiobolus Riess sens. str.: placed here as Leptospora implexa (Ell.& Ev.) Walker (q.v.)

Ophiobolus incomptus (Car.& de Not.) Sacc. (1883) - see under Ophiochaeta incompta.

Ophiobolus junci Miller & Burton, Mycologia 34, 7, 1942 (type not seen).

From the description and figures, this species with large ascocarps 300-800 µm diam embedded in dead stems, with cylindrical apically thickened asci 138-160 x 14-16µm, septate ascospores yellowish to brown 115-138 x 4-5 µm, abundant paraphyses, could well be a species of Ophiosphaerella (q.v.).

Ophiobolus leptospermus (Speg.) Sacc. (1883) - placed here as Ophiosphaerella leptosperma (Speg.) Walker (q.v.).

Ophiobolus leptosporus Saccas, L'Agronomie Tropicale 9 (3), 281-282, 1954 (type not located).

The type specimen could not be obtained. It is not at PC and enquiries made to the Central Phytopathological Station, Boukoko, Central African Republic and to Dr. Saccas failed to locate it. The original collection was made on dead leaf sheaths of Sorghum vulgare L. at M'Baiki, Central African Republic in 1953, and the description and figures indicate a possible Pleosporaceous species, with dark brown immersed ascocarps 350-600 x 250-450 µm, erumpent neck 80-100 µm long, cylindrical asci 96-195 x 4.7-5.5 µm, thickened above, with eight cylindrical filiform pale yellowish ascospores 85-175 x 1-1.5 µm, 7-14 septate and spirally twisted 2-3 times in the ascus. Numerous paraphyses were present and the host tissues were discoloured red.

With its thin asci, and thin spiralled ascospores, O. leptosporus is probably a species of Leptospora. Its asci and ascospores are of similar length to those of L.implexa (on Sorghum halepense) but the asci of O.leptosporus are only half as wide. They are similar in width to the asci of L.rubella, but asci and ascospores of L.rubella are much longer. There is a reddish discolouration of the substrate, as occurs commonly with L.rubella, but reddish discolouration is a reaction of Sorghum spp. to a wide range of organisms and injuries. Tarr (1962) commented on the similarity of O.leptosporus to Leptospora rubella (as Ophiobolus porphyrogonus (Tode) Sacc.). O.leptosporus also resembles O.trichisporus Ell.& Ev. described from dead grass culms and here placed tentatively under Leptospora (q.v.). O.leptosporus is not an Ophiobolus sens.str. but study of the type will be necessary to place it accurately.

Ophiobolus licualae Syd., Philipp.J.Sci.9 (Sect.C. Nr.2), 165, 1914 (from Syll.fung.24, 1065-1066, 1926) (type not seen).

From the description, and from a superficial examination of five collections under this name in BPI, this species on dead palm petioles from the Philippines could well be a species of Linocarpon, possibly the same as one of the several species recorded on palms.

Ophiobolus littoralis (Crouan) Sacc. (1883) - see under Sphaeria littoralis Crouan.

Ophiobolus littoralis Cribb & Cribb, Univ.Qd.Dept.Bot. Papers 3 (12), 101-102, 1956 (type in BRIU, not seen) - a later homonym of O.littoralis (Crouan) Sacc.; renamed Ophiobolus australiensis Johnson & Sparrow (q.v.).

Ophiobolus livistonae P.Henn., Hedwigia 47, 257, 1908 (type in K seen; not examined in detail).

≡ Linocarpon livistonae (P.Henn.) Schrantz, Bull. Trimest. Soc.mycol.Fr.76 (1960), 337, 1961 (not validly published, Art.33).

The original description, and superficial examination of portion of the type collection (Copeland 524, in K) indicate that this fungus on dead Livistona (Palmae) petioles from the Philippines is a species of Linocarpon, but the Schrantz combination was not validly published. Several possible Linocarpon spp. on Palmae are listed under Linocarpon and the relationships of these require further study. Schrantz (1961) briefly described and figured a perithecium, ascus and ascospores.

Ophiobolus manihotis Syd. in Syd. & Butler (1911) - after study of portion of the type, Petrak (1957) transferred this name to Linocarpon. Petrak's (1952) wide concept of Linocarpon is not accepted here and, until O. manihotis has been studied further, the most suitable genus for it

cannot be determined.

Ophiobolus maritimus (Sacc.) Sacc. (1883) - based on Rhaphidophora maritima Sacc.; type sterile; for description and synonymy, see Walker (1972). Höhnel (1920) briefly summarised the original description and suggested that it may be an undescribed Diaporthaceous genus. There is no evidence for this or any other placement of this species.

Ophiobolus medusae Ell.& Ev., J.Mycol. 1 (12), 150, 1885 as 'medusa' (type in NY !)
≡ Linocarpon medusae (Ell.& Ev.) Petrak, Sydowia 6, 388, 1952.

This is Lulworthia medusae (Ell.& Ev.) Cribb & Cribb (1955). For a discussion of the genus Lulworthia, see Kohlmeyer (1972).

Ophiobolus medusae Ell.& Ev. var. minor Ell. & Ev., Proc. Acad. Nat. Sci. Philadelphia 1890, 239, 1890 (type not found).

For discussion of this species and specimen details, see under Ophiobolus andropogonis and Ophiosphaerella herpotricha; see also Ophiobolus salinus Meyers.

Ophiobolus medusae form bromi Brenckle, Fungi Dakotensis No. 536, 1923 (printed label on specimen).

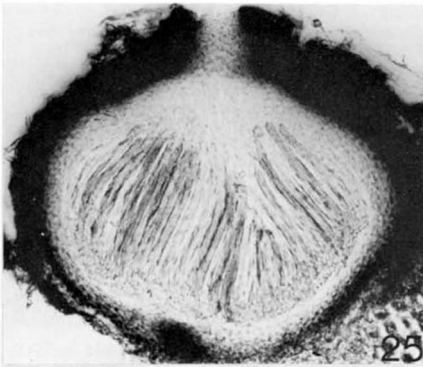
A specimen under this name in NY bears pseudothecia and pycnidia typical of Ophiosphaerella herpotricha (q.v.) where the name is listed in synonymy.

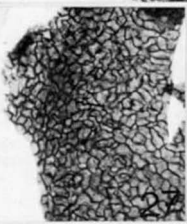
Ophiobolus moravicus Petrak (1921) - the type species of Plagiosphaera Petrak (q.v.).

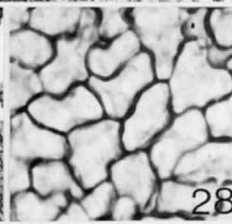
Ophiobolus nipae P. Henn., Hedwigia 47, 257, 1908 (type not seen)
≡ Linocarpon nipae (P.Henn.) Schrantz, Bull.Trimest. Soc.mycol.Fr. 76 (1960), 337, 1961 (not validly published, Art.33).

From the original description, and the illustrations of Schrantz (1961), this appears to be a Linocarpon similar to others recorded on various palms. For further discussions of these, see under Linocarpon.

Figures 25-30. 25 and 26. Ophiobolus acuminatus, section ascocarp, x 183, and ascus with young ascospores, x 733, from isotype of O. disseminans in M (slide DAR 32063). 27-30. Ophioceras leptosporum, ascocarp from dried type culture in K (slide DAR 31944). 27. Outer wall, x 183. 28. Detail of outer wall, x 733. 29. Apex of neck, x 183. 30. Detail of neck apex, x 733.

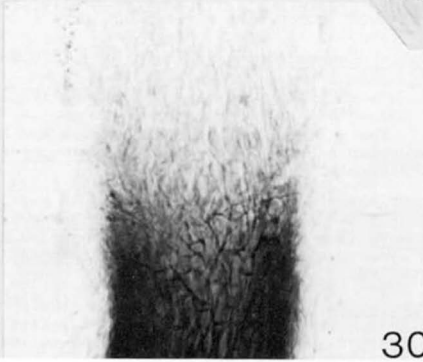

25


27


28


26


29


30

Ophiobolus oedema (Mont.) Sacc., Syll.fung.2, 351, 1883
≡ Sphaeria oedema Mont.,Ann.Sci.Nat.Bot.14,326,1840
≡ Rhaphidospora oedema (Mont.) Ces.& de Not. (from Sacc., Syll.fung.2, 351, 1883).

Described from petioles of Mauritia flexuosa L.f. (Palmae) in French Guiana, this species was said to have small black perithecia, with clavate asci 70 µm long and thin ascospores to 90 µm long. Superficial examination of what is possibly portion of the type collection in K indicates that it may be a Linocarpon. This species could well provide one of the earliest epithets for Linocarpon spp. on Palmae. These are discussed further under Linocarpon.

Ophiobolus ophioboloides (Sacc.) Holm, Svensk Bot.Tidskr. 42, 345, 1948
≡ Leptosphaeria ophioboloides Sacc., Misc.myc.No.1,23, 1884 (original not seen; from Saccardo, Syll.fung 9, 770, 1891)
≡ Leptosphaeriopsis ophioboloides (Sacc.) Berl., Icon. fung. 1, 88-89, 1892.

A true species of Ophiobolus Riess sens. str. (Holm, 1957). For references to descriptions and illustrations, see under Leptosphaeriopsis.

Ophiobolus oryzae Miyake, Bot.Mag.(Tokyo) 23 (266), 96-97, 1909 (also in J.Coll.Agric.Imp.Univ.Tokyo 2(4), 249-250, 1910) (type not seen).

Listed by Sawada (1959), and suggested by Shoemaker (1976), as a synonym of Ophiobolus herpotrichus; see discussions under Ophiosphaerella herpotricha.

Ophiobolus oryzinus Sacc. (1916) - a synonym of Gaeumannomyces graminis (Sacc.) von Arx & Olivier var.graminis (q.v.).

Ophiobolus paludosus (Feltg.) Sacc. & D.Sacc., Syll.fung. 17, 774, 1905.
≡ Leptosphaeria paludosa Feltg.,Vorst.Pilz.Luxemb. Nachtr. II, 157, 1901.

For a discussion of this species and details of specimen examined, see under Gaeumannomyces spp. on Cyperaceae.

Ophiobolus pellitus (Fckl.) Sacc. - one of the species listed by Saccardo (1883) in Ophiobolus subgenus Ophiochaeta (see under Ophiochaeta); regarded by Holm (1957) as a synonym of Nodulosphaeria erythrospora (Riess) Holm; not studied.

Ophiobolus penicillus (Schm.ex Fr.) Sacc. in Roum.& Sacc. (1881), cited in error as '(K.et S.) Sacc.', citation corrected in Syll.fung.2, 352, 1883 - see under Sphaeria penicillus.

Ophiobolus prunellae (Ell.& Ev.) Shoemaker (1976) - see discussion of Ophiobolus rostrupii under Leptosporopsis.

Ophiobolus rostrupii Ferd. & Winge (1909) - see discussion under Leptosporopsis.

Ophiobolus rubellus (Pers.ex Fr.) Sacc. in Roum. & Sacc. (1881) - see under Leptospora rubella (Pers.ex Fr.) Rabenh..

Ophiobolus salinus Meyers, Mycologia 49, 518, 1957, as 'salina'. Meyers (1957) proposed this as a new name for O. medusae var. minor Ell.& Ev., which he recognised as quite different from O.medusae. For discussion of O. medusae var. minor, see under O. andropogonis and Ophiosphaerella herpotricha.

Ophiobolus spirosporus Ahmad, Sydowia 2, 75-76, 1948 (type not examined).

Two collections on the type host identified by Ahmad were examined. These agreed with the original description and showed a fungus with embedded black subglobose ascocarps with a short erumpent neck containing abundant broad clavate asci with eight hyaline filiform ascospores arranged in a dense spiral of several turns and abundant septate pseudoparaphyses. The asci are thin-walled but seem to be bitunicate. The ascospores were described originally as continuous, but are transversely septate at about 10 µm intervals with a finely granular vacuolate contents.

This is not an Ophiobolus Riess sens.str. and is probably better placed in Cochliobolus. With its thin asci and spirally arranged ascospores, it also shows some resemblance to fungi placed here in Leptospora but differs in its wide asci (9-12 µm) and hyaline ascospores. Study of the type specimen (and also of the fungus in culture) is necessary before any formal transfer is made.

Specimens examined: on dead culms of Saccharum spontaneum L.,Lahore, West Pakistan, 26.ii.1967, S. Ahmad, Fungi of West Pakistan 19764 in BPI (slides as DAR 33696); same, Fungi of West Pakistan 19767 in BPI (slides as DAR 34128); same date and locality, IMI 127027.

Ophiobolus stictisporus (Cke.& Ell.) Sacc. (1883) - based on Sphaeria stictispora Cke.& Ell.. The type has been examined and described by Walker (1972) who considered it a member of the Ostropales related to Stictis. In the Index (Syll.fung.12, Part 1, 481, 1897), the epithet is spelt incorrectly as 'strictisporus'.

Ophiobolus stipae Doidge, Bothalia 4, 212-213, 1941 (type in BPI and IMI examined).

O. stipae was described from a collection on dying leaf sheaths of Stipa dregeana Steud. from South Africa (Doidge (1950) listed the host as S.dregeana var. elongata Stapf).

It was said to have black ascocarps 250-350 µm diam, containing cylindrical clavate asci 100-150 x 7-8 µm, rounded and thickened at the apex, with filiform ascospores 100-120 x 2-2.6 µm, yellow-brown in mass and subhyaline singly, and abundant, hyaline filiform paraphyses 1 µm wide.

The fungus as described could not be found on two portions of the type collection examined. Abundant superficial growth of Meliola panici Earle was present and several small ascocarps of a species of Phaeosphaeria with three septate pale brown ascospores were seen on the portion in BPI. From the description, O.stipae could be a species of Ophiosphaerella but until it can be found on the available type material its exact identity remains in doubt.

Specimens examined: on Stipa dregeana, Xumeni Forest, near Donnybrook, Natal, South Africa, 5.ix.1937, K.E.Morgan & E.M.Doidge 29828 and 29829, TYPE collection, dups. as IMI 35983 and in BPI (slides as DAR 34129).

Ophiobolus tanaceti (Fckl.) Sacc.(1883) - see under Leptosphaeria tanaceti.

Ophiobolus tortilis Syd.,Ann.Myc.35, 263, 1937 (type not seen).

This was described from a collection on leaves and culms of Vetiveria zizanioides (as Andropogon zizanioides) in the Philippines. The dark brown clustered ascocarps had an immersed globose body 350-450 µm diam, with a thick obtuse conical erumpent neck, asci elongated clavate, narrower towards the sessile or shortly stalked base, 150-180 x 6.5-7.5 µm, containing eight greenish-yellow filiform ascospores, twisted in the ascus and as long as it, 1.5-2 µm wide, sometimes slightly narrower at the base, and somewhat curved or sigmoid singly. Septa were not mentioned but the contents were described as finely granular with several small oil droplets. Abundant thin septate paraphyses were present. Dark brown hyphae were present at the base of the ascocarps.

It has not been possible to obtain the type specimen. It is not present amongst the Sydow collections in S or B and Dr. B. Hein (B) suggested that it may have been destroyed. From the description, O.tortilis is very similar indeed to Leptospora implexa and may not be distinct from it. However, until the type is located, its exact identity remains unknown.

Ophiobolus trichellus Bomm., Rouss.& Sacc. in Sacc., Syll. fung.9, 934, 1891 (type not seen).
≡ Ophiochaeta trichella (Bomm.,Rouss.& Sacc.in Sacc.) Sacc., Syll.fung.11, Part 3, 352, 1895 (cited by Berlese, 1899, as '(B.R. et S.) Berl.').

According to Berlese (1899), the type specimen on

leaves of Ammophila (as Psamma) arenaria, Belgium, is sterile and the exact identity of this fungus is not known. From the description, it is not an Acanthophiobolus (syn. Ophiochaeta) as considered here. See under Ophiochaeta for discussion of this generic name.

Ophiobolus trichisporus Ell.& Ev.(1890) - following Shoemaker (1976), this species is placed under Leptospora rubella (Pers.ex Fr.) Rabenh. and a description and discussion are given under that name. Saccardo (1891) listed it as O.trichosporus Ell.& Ev. and later (Saccardo, 1895) as O.trechisporus Ell.& Ev.

Ophiobolus verminosus (Mont.) Sacc., Syll.fung.2, 351,1883
- ≡ Rhaphidospora verminosa (Mont.) Mont., Syll. Gen. Sp. crypt., 252, 1856
- ≡ Sphaeria verminosa Mont. (from Montagne,1856) (type not seen).
- ≡ Linocarpon verminosum (Mont.) Schrantz, Bull.Trimest. Soc.Mycol.Fr.76 (1960), 337, 1961 (not validly published, Art.33).

From the original description (on palm petioles, Cayenne, French Guiana) and from the illustrations of a perithecium and an ascus given by Schrantz (1961), this is probably a species of Linocarpon. Petrak (1952) also considered it a typical Linocarpon but did not transfer it to this genus. For a discussion of several similar fungi on palms, see under Linocarpon.

Ophiobolus versisporus Ell.& Mart.(1885) - considered here as Linocarpon versisporum (Ell.& Mart.) Petrak (q.v.).

Ophiobolus zeae Saccas, Rev.Path.veg.Entom.agric.Fr.30 (3), 183-186, 1951 (type in PC !)

Listed as a synonym of Ophiosphaerella herpotricha (Fr.) Walker (q.v.). Tarr (1962) thought it may be a Cochliobolus and stated 'If the generic name Cochliobolus be accepted for Ophiobolus-like fungi with spirally arranged ascospores (see Drechsler, 1934) this fungus should presumably be named Cochliobolus zeae'. Ascospore twisting in Ophiosphaerella herpotricha is discussed under that name.

Ophiobolus sp. (IMI 136978a on culms of Chrysopogon) - an immature Ophiosphaerella sp. (q.v.).

Ophiobolus sp. (IMI 71816 on Axonopus) - this is Gaeumannomyces graminis (Sacc.) von Arx & Olivier var. graminis.

Ophiobolus sp. (IMI 145643b, on leaf spot of Zea mays L., Khumal, Nepal, 15.viii.1969, slides as DAR 33294) - the only fungi seen were (a) ascocarps immature, possibly Phaeosphaeria sp. (b) Pithomyces sp.aff. P.maydicus (Sacc.) Ellis but most spores with three transverse septa.

Ophiobolus sp. (Padwick, 1950, p.153) - Padwick quoted a North American report of an Ophiobolus sp. on rice. The identity of this fungus is not known. Gaeumannomyces graminis var. graminis (q.v.) is known on rice in North America.

Ophiobolus sp. (Wadsworth, 1967) - the identity of this fungus associated with root rot of Bermuda grass (Cynodon dactylon) in the spring dead spot disease in the United States is not known and no specimen could be traced.

OPHIOCERAS

Ophioceras Saccardo, Syll.fung.2, 358, 1883.
Lectotype sp. O. dolichostomum (Berk.& Curt.) Sacc., Syll.fung.2, 358, 1883 (see Höhnel, 1911 for lectotypification).
≡ Sphaeria dolichostoma Berk.& Curt., J.Linn.Soc. London 10, 388, 1869 (type not seen).

Conway and Barr (1977) described O.dolichostomum in detail from an isotype collection in NY and a 1968 collection on partially submerged wood from a stream in Florida. The genus is characterised by perithecia with a long (1-5 mm) beak, the peridium of the perithecial body being a textura angularis and of the beak a textura intricata, unitunicate asci with a chitinoid apical annulus and in some cases a subannular non-chitinoid globule, asci containing eight hyaline to faintly tinted septate scolecospores. Conway and Barr (1977) considered that these characters, and the hypersaprobic habit, indicate that Ophioceras should be excluded from Diaporthales and is placed best in the family Lasiosphaeriaceae, order Sordariales.

Other Ophioceras names

Ophioceras filiforme (P.Henn.) Höhnel (1911) - see under Schizacrospermum filiforme.

Ophioceras leptosporum (Iqbal) Walker comb. nov.
≡ Gaeumannomyces leptosporus Iqbal, Trans.Brit.mycol. Soc.58 (2), 346-348, 1972 (type in K !)

Perithecia (Figs.29-31) with globose body and long filiform neck, on stem tissue body embedded or superficial, neck erumpent, in culture some perithecia with long necks completely embedded in agar, scattered singly or clustered into groups of 10-12 or more (especially in culture), body globose, dark brown to black, 250-300 (400) µm diam, wall 15-20 µm thick, easily broken when dry, of 4-5 layers of cells, outer layer a textura angularis of brown cells 10-16 x 10-13 µm (Figs.27 and 28), inner layers of paler flattened cells, neck dark brown to black, placed centrally on the body, 1-2(2.5) mm long, 40-60 (90) µm wide near the base, for most of its length 30-50 µm wide, 20-30 µm near the paler, thinner walled tip (Figs.29 and 30), wall of neck in lower part 20-25 µm thick, outer layer of roughly parallel rows of elongated dark cells 8-18 x 2.5-5 µm (textura porrecta) or cells more irregularly arranged

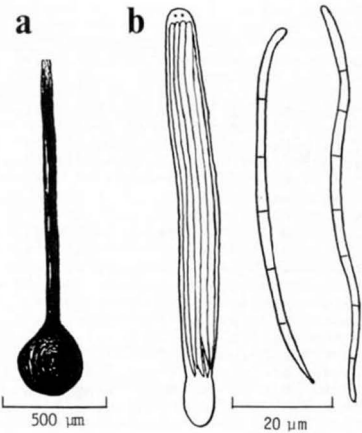


Figure 31. Ophioceras leptosporum. a. ascocarp, from holotype in K (slide DAR 33269); b. ascus and ascospores, from dried type culture in K (slide DAR 31944).

(textura angularis), except near the tip (apical 100-150 µm) where the wall is much paler and made up of thin septate pale brown to almost hyaline hyphae diagonally interwoven (textura intricata) (Figs.29 and 30); ostiolar canal 20-50 µm wide, periphyses not observed in perithecia from stem tissue, short upwardly pointing hyaline periphyses seen near to neck tip in perithecia in dried type culture. Asci (Fig. 31) cylindrical, straight or more often very slightly curved, (60) 70-95 (105) x 5-6 (7) µm, arising from a basal layer of hyaline gelatinising hyphae and eventually freed into the perithecial cavity, eight-spored, unitunicate, with a distinct refractive apical ring, seen in side view as two slightly elongated rods, 1-1.5 µm diam, 1.5-2 µm long. In a minority of asci, a small clear area 2-3 µm diam was seen between the apical ring and the tips of the ascospores. Ascospores (Fig.31) hyaline to faintly tinted singly, pale yellowish in mass, filiform, straight or more often slightly curved or sigmoid, apex rounded, often almost hemispherical, base acute, (65) 70-80 (85) x 1-1.5 µm, with 3-7 indistinct septa, contents finely granular and vacuolate, borne in a parallel fascicle in the ascus. Paraphyses not observed in either immature or mature perithecia but some hyaline non-staining material with little structure or occasionally with a few septate hyaline hyphae was seen between asci in several perithecia. Conidial state not known.

Illustrations: Iqbal (1972, ascocarps, asci, ascospores).

Specimens examined: on dead submerged stems of unidentified Umbelliferae, in river Creedy, near Cowley Bridge, Exeter, England, 6.ii.1970, S.H. Iqbal, K, HOLOTYPE (slides as DAR 33269); same locality, dried cultures with perithecia, K, dried type culture (slides as DAR 31944); same, type culture, CBS 894.70 (dried culture and slides as DAR 33738); on decaying submerged unidentified leaves, 24 km from Port Moresby, Papua New Guinea, March 1976, PNG 10147 (dried culture and slides as

DAR 34111).

O. leptosporum cannot be retained in Gaeumannomyces, whose known species are root, crown, lower stem and leaf sheath parasites of Gramineae and Cyperaceae, with a well developed superficial hyphopodiate mycelium and perithecial wall surface a textura epidermoidea. From the few collections known, O.leptosporum is a saprophyte on dead, decaying plant material in an aquatic environment. Its perithecia have an outer wall layer composed of a textura angularis and, at least near the tip, the cells of the outer layer of the neck approach a textura intricata. No superficial mycelium is associated with the perithecia in nature and, in culture, hyphae do not develop hyphopodia when inoculated onto a range of living and dead plant substrates, including cereal coleoptiles (Shaw, 1977). Tests by the present author with both the type culture and the Papua New Guinea isolate confirmed these results. Shaw (1977) described and figured ascospore germination, with formation of dark brown appressoria, 7.5-10.5 x 3.5-4.5 µm, usually terminal on the germ tube, occasionally intercalary or almost sessile on the ascospore. However, formation of appressoria is a widespread phenomenon in the fungi (Emmett and Parbery, 1975; Parbery and Emmett, 1977) and bears no obligate relationship to the formation of mycelial hyphopodia (see discussion at end).

Conway and Barr (1977) described ejection of whole asci from the perithecium of O.dolichostomum. 'The unitunicate asci become detached from the subhymenium and under moist conditions some are discharged as a unit with the ascospores from the ostiole (Fig.2). Some asci are shot several centimetres from the ascocarp as they explode from the ostiole. Most, however, are trapped at the tip of the beak as shown in Figure 2'. This figure shows a white mass of asci and ascospores at the tip of the neck, and is very similar to Plate 1E of Shaw (1977) who described how whole asci of O.leptosporum in Papua New Guinea are extruded when perithecia are placed at a lower humidity. In this species, the asci and ascospores also accumulate at the tip of the neck, in a white milky globule, changing to honey colour later (Shaw,1977). O.dolichostomum and O.leptosporum seem to be closely related fungi, although the ascospores described for O.dolichostomum are longer and distinctly wider than those of O.leptosporum.

Barr (1978) considered that G.leptosporus was probably the same as Plagiosphaera umbelliferarum (q.v.). Comparison of the type specimens indicates that they are distinct and that G.leptosporus is better placed in Ophioceras. She also mentioned that Iqbal (1972) described perithecia in culture as oblique with lateral beaks. Study of material both on the host and in culture has shown that beaks arise centrally in both cases, although in culture perithecia may lie in various positions and beaks embedded completely in the agar may be slightly twisted. Iqbal (1972) described the position when he wrote 'When the ostiole has

fully grown, it appears to arise laterally from the perithecium and the perithecia are obliquely horizontal. Nevertheless, perithecia are globose and ostioles arise from the apex'. His illustrations also show this.

Iqbal (1972) cited the holotype as specimen 2955 in the Mycological Herbarium, University of Exeter. Searches there failed to find it. Enquiries revealed that the specimen had been taken by Dr.Iqbal for further study and later forwarded to Dr. R.W.G. Dennis for permanent filing in Herb. K, where it now remains (Professor J. Webster, in litt.).

Ophioceras sorghi Saccas, L'Agronomie Tropicale 9(3), 285-286, 1954 (type not located).

The type specimen could not be obtained. It is not in PC and enquiries made to the Central Phytopathological Station, Boukoko, Central African Republic and to Dr.Saccas failed to locate it. O.sorghi was described from dead stalks of Sorghum vulgare collected at M'Baiki, Central African Republic. The description and figure show globose to subglobose black immersed ascocarps, 300-400 µm diam with an erumpent straight to sinuous neck 350-700 µm long, 100-140 µm wide, containing thin-walled cylindrical-clavate slightly curved asci, 85-110 x 12-14 µm, sessile or slightly stipitate, obtuse apex, eight-spored, and ascospores filiform, cylindrical, slightly curved, rounded apex and slightly thinner rounded base, 75-95 x 3-4 µm, 3-12 indistinct transverse septa and arranged parallel in the ascus; paraphyses not observed.

The description, measurements and figures bear a striking resemblance to the perithecia, asci and ascospores of Gaeumannomyces graminis (compare Fig.35 of Saccas, 1954 with his Fig.32 labelled 'Ophiobolus graminis' on Sorghum, and with other illustrations of G.graminis, see Walker, 1980). The long ascocarp neck is not inconsistent with this as neck length in G.graminis is very variable between collections and seems to depend on factors such as depth of ascocarps in host tissue, numbers of layers of leaf sheaths to be penetrated, and humidity (Walker, 1980). G.graminis var. graminis occurs commonly in tropical Africa (see above) and has a wide host range in the Gramineae. However, in the absence of the type specimen, of an exact knowledge of the ascus type, and of correlated mycelial characters (hyphopodia in particular), the placement of Ophioceras sorghi with G.graminis (possibly var. graminis) must remain conjectural. Tarr (1962) paraphrased the original description and commented that O.sorghi was apparently distinct from Ophioceras zeae Saccas on maize and from other species on grasses.

Ophioceras zeae Saccas, Rev.Path.veg.Entom.agric.Fr.30 (3), 186-188, 1951 (type not located).

The type specimen is not in PC and enquiries similar to those made for O.sorghi Saccas could not locate it. The

original collection is on stems and leaf sheaths of Zea mays from maize plantations near Boukoko, Central African Republic in October, 1950. The original description and figures indicate superficial, or partially embedded black, globose to subglobose ascocarps, 450-650 µm diam, with a long black neck, paler in its upper quarter, 350-900 x 90-125 µm, with cylindrical to fusiform, thick-walled shortly stalked asci, 55-65 x 7-8 µm, containing eight ascospores which are cylindrical to fusiform, at first multiguttulate and hyaline, later nonguttulate and pale yellowish, straight or more usually curved towards each end, ends rounded, always with three transverse septa, 39-50 x 2.3-2.5 µm; paraphyses not observed.

This is not an Ophioceras in the sense of the lectotype species, O.dolichostomum. With its three-septate ascospores with rounded ends and no paraphyses, it resembles some species placed in Sphaerulina Sacc. (Barr, 1972), but the large superficial ascocarps with a long neck are not characteristic of this genus. The description does not allow the nature of the asci (unitunicate or bitunicate) and other characters to be determined and, until the type specimen is found, the exact characteristics and generic placement of O.zeae remain unknown. As Tarr (1962) suggested, it seems quite distinct from O.sorghi Saccas.

OPHIOCHAETA

Ophiochaeta (Saccardo) Saccardo, Syll.fung.11, Part 3, 352, 1895.

≡ Ophiobolus Riess sensu Sacc. subgenus Ophiochaeta Sacc., Syll.fung.2, 352, 1883.

Lectotype sp. O.gracilis (Niessl) Sacc. (see below)

The literature on Ophiochaeta is confused. A chronological summary of its history is given, followed by a discussion of its typification, a list of several Ophiochaeta names and their proposed disposition.

1883 - Saccardo (1883) adopted a wide concept of the genus Ophiobolus Riess, including in it many scolecospored species now considered to belong in diverse genera. He divided the genus into two sub-genera : Eu-ophiobolus with subglabrous perithecia and Ophiochaeta with perithecia setulose, at least near the ostiole. No type species was designated for subgenus Ophiochaeta but under it he listed the following Ophiobolus spp. in this order : O.penicillus (Schmidt ex Fr.) Sacc., O.herpotrichus (Fr.) Sacc., O.pellitus (Fckl.) Sacc., O.chaetophorus (Crouan) Sacc. and O.incomptus (Car.& de Not.) Sacc..

1892 - Berlese (1892) placed setose species in his new genus Acanthophiobolus and modified the concept of the sub-genus Ophiochaeta to include species attached to a meandering basal mycelium. He designated Ophiobolus herpotrichus as the sub-generic type.

1895 - Saccardo (1895) raised his sub-genus Ophiochaeta to generic rank. Again, no type species was designated but the following species were included in this order : O.penicillus (Schmidt ex Fr.) Sacc., O.chaetophora (Crouan) Sacc., O.incompta (Car.& de Not.) Sacc., O.helminthospora (Rehm) Sacc., O.gracilis (Niessl) Sacc., O.barbata (Pat.& Gaill.) Sacc. and O.trichella (Bomm.,Rouss. & Sacc.) Sacc. (Saccardo did not include author names or references to the basionyms, but referred to Sylloge 2, p.352 where author citations were given under Ophiobolus subgenus Ophiochaeta. This does not affect the validity of his Ophiochaeta names and he definitely indicated in 1895 that the epithets listed were to be used in Ophiochaeta; see Art.33, Stafleu et al.,1972). This list contained several species not included in sub-genus Ophiochaeta 1883, but also specifically excluded Ophiobolus herpotrichus and O. pellitus which were being investigated further. Saccardo here also reduced Acanthophiobolus Berlese (1892) to synonymy under Ophiochaeta (Sacc.) Sacc..

1897 - Sydow (1897, p.482), in an index entry, stated 'Ophiochaeta Sacc. est Ophiobolus Riess'.

1899 - Berlese (1899) accepted Saccardo's (1895) concept of Ophiochaeta, including the reduction of Acanthophiobolus to synonymy (listed erroneously by Berlese as Acanthostigma but with the Acanthophiobolus reference). He gave brief descriptions of the seven species listed by Saccardo (1895) and included an eighth, Ophiochaeta raciborskii Penz. & Sacc. (1897). No generic type species was mentioned. Moreover, in contrast to his 1892 statement, he excluded Ophiobolus herpotrichus from Ophiochaeta with the words 'Peritheciis tomentosis sed non setis rigidis ornatis, Ophiochaeta adscribi non potest'.

1901 - Mussat (1901), in the Synonymia, listed Ophiobolus chaetophorus, O.incomptus and O.penicillus in Ophiochaeta, quoting the 1895 reference.

1907 - Höhnel (1907) listed the genus incorrectly as Ophiochaeta Berlese (1899) and reduced Ophiosphaeria Kirschstein (1907) to synonymy. He realised that Kirschstein's species O.tenella was identical with Ophiochaeta chaetophora (Crouan) Sacc. (see under Acanthophiobolus).

1921 - Weese (1921, p.115) regarded Sphaeria penicillus Schmidt ex Fr. (Ophiochaeta penicillus (Schmidt ex Fr.) Sacc.) as the type of the genus Ophiochaeta. (For further discussion of the epithet 'penicillus Schmidt ex Fr.', see under Sphaeria penicillus).

1931 - Clements and Shear (1931) listed Ophiochaeta herpotricha (Fr.) Sacc. as the generic type. However, there is no evidence that Saccardo ever made this combination and indeed in 1895 he specifically excluded Ophiobolus herpotrichus from Ophiochaeta, as did Berlese (1899).

1936 - Kirschstein (1936) accepted Weese's (1921) concept of Ophiochaeta based on Sphaeria penicillus and disagreed

with Höhnel's (1907) reduction of Ophiosphaeria Kirsch. to synonymy under Ophiochaeta.

1952 - Müller (1952) regarded S.penicillus as the generic type of Ophiochaeta, which he reduced to synonymy under Ophiobolus Riess. He listed it as Ophiobolus penicillus (Schmidt ex Fr.) Sacc..

1971 - Ainsworth (1971) listed Ophiochaeta (Sacc.) Sacc. = Ophiobolus, fide Müller and also listed both Acanthophiobolus Berlese and Ophiosphaeria Kirschst. as synonyms of Ophiochaeta.

1975 - von Arx and Müller (1975) regarded Lasiosphaeria gracilis Niessl as the type species of Ophiochaeta, which they listed in synonymy under Acanthophiobolus Berlese.

Saccardo's (1883) concept of the subgenus Ophiochaeta was of species with setose perithecia and he did not change that concept when he raised Ophiochaeta to generic rank in 1895. Berlese (1899) reinforced this with his statement of rejection of Ophiobolus herpotrichus from Ophiochaeta. Although Saccardo did not nominate a type species, three have been suggested by other workers.

(i) Ophiobolus herpotrichus (Fr.) Sacc. by Berlese (1892) for subgenus Ophiochaeta. This choice was later rejected (Saccardo, 1895; Berlese 1899) but was accepted by Clements and Shear (1931).

(ii) Sphaeria penicillus Schmidt ex Fr.by Weese (1921), and by Müller (1952).

(iii) Lasiosphaeria gracilis Niessl by von Arx and Müller, (1975).

Ophiobolus herpotrichus is not a suitable choice. It was rejected by Saccardo (1895) and also by Berlese (1899) who originally proposed it. It is not a setose species and is not in accord with Saccardo's concept. It is treated here under Ophiosphaerella (q.v.). Sphaeria penicillus is regarded at present as a confused name, on the basis of material studied so far and its use in the literature. It is not a suitable choice and further details are given under Sphaeria penicillus below. The third, and most recent, choice, Lasiosphaeria gracilis, is suitable. It is one of the species listed by Saccardo (1895) when he raised Ophiochaeta to generic rank and it is a setose species in accord with Saccardo's concept of Ophiochaeta. Based on L.gracilis, Ophiochaeta (Sacc.) Sacc. (1895) is a later name for fungi placed here under Acanthophiobolus Berlese (1892) (q.v.).

Several Ophiochaeta names are listed and some dispositions suggested. In earlier literature dealing with fungi with hairy ascocarps, the distinction between a sparse or dense covering of brown hyphae of indeterminate length (often associated with a brown mycelium on or in the substrate), and setae of determinate length, has not always

been recognised. Berlese (1899), Weese (1921), Drechsler (1934) and Walker (1972) discussed this in connection with Ophiochaeta and some other genera. The former condition is found in Sphaeria herpotricha Fr. and species in many genera such as Leptosphaeria, Ophiosphaerella, Ophiobolus sens. lat., Phaeosphaeria and others. The latter condition is found amongst fungi placed here in Acanthophiobolus and in some other genera.

Ophiochaeta barbata (Pat.& Gaill.) Sacc. (1895) (listed by Berlese (1899) as '(Pat.) Berl.') - see under Acanthotheciella v. Höhn.

Ophiochaeta chaetophora (Crouan) Sacc. (1895) - a synonym of Acanthophiobolus helicosporus (Berk.& Br.) Walker (q.v.).

Ophiochaeta cladii Cruchet (1923) - a probable synonym of Acanthophiobolus helicosporus; see discussion under that name.

Ophiochaeta gracilis (Niessl) Sacc. (1895) - a synonym of Acanthophiobolus helicosporus (q.v.).

Ophiochaeta graminis (Sacc.) Hara (1916, from Tanaka,1917) - this is Gaeumannomyces graminis var. graminis (q.v.).

Ophiochaeta helminthospora (Rehm) Sacc.(1895) - a synonym of Acanthophiobolus helicosporus (q.v.).

Ophiochaeta herpotricha (Fr.) Sacc. in Clements & Shear (1931) - no evidence that Saccardo made the combination attributed to him by Clements and Shear (1931) could be found. The species is placed here as Ophiosphaerella herpotricha (q.v.).

Ophiochaeta incompta (Car.& de Not.) Sacc. (1895)
≡ Rhaphiodophora incompta Car.& de Not. (1867, original not seen, from Saccardo, 1895; type not seen).

Berlese (1899) examined the type (on branch of Ribes, northern Italy) which he said was sterile, and repeated the original description. Perithecia were said to be densely hairy, carbonaceous, fragile, with a short neck, abundant asci with yellowish, filiform closely septate ascospores, and numerous filiform paraphyses. No measurements were given and the identity of this species is not known.

Ophiochaeta penicillus (Schmidt ex Fr.) Sacc. (1895) - for discussion, see under Sphaeria penicillus.

Ophiochaeta raciborskii Penz. & Sacc. (1897) - now placed as Lasiosphaeria raciborskii (Penz.& Sacc.) Carroll & Munk; for full description and discussion, see Carroll and Munk (1964).

Ophiochaeta trichella (Bomm.,Rouss& Sacc.) Sacc. (1895), type not seen (listed by Berlese, 1899 as '(Bomm.,Rouss. & Sacc.) Berl.').
≡ Ophiobolus trichellus Bomm.,Rouss.& Sacc. in Sacc. (1891).

According to Berlese (1899), the type (on Ammophila (as Psamma) arenaria leaves, Belgium) is sterile. The original description indicates small perithecia 60-100 µm diam crowned with simple acuminate brown flexuous hairs 24-33 x 4 µm and containing oblong-clavate sub-sessile asci 45-66 x 10-15 µm with eight hyaline filiform 11-15 septate ascospores 60 x 3 µm and indistinct paraphyses. The identity of this species is not known.

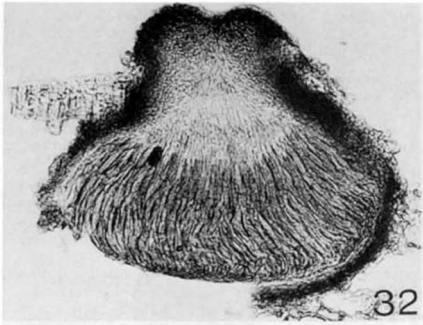
OPHIOSPHAERELLA

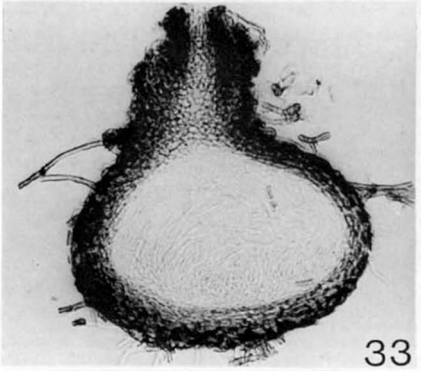
Ophiosphaerella Spegazzini, Anal.Mus.Nac.Buenos Aires 19 (Ser.3,12), 401-402, 1909.
Type sp. O. graminicola Speg.

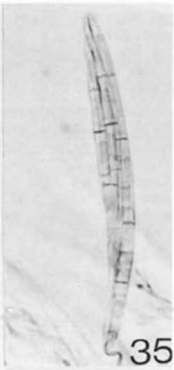
The genus Ophiosphaerella was not defined separately by Spegazzini (1909) but a description and illustration of the single new species O.graminicola were given. This provided a descriptio generico-specifica and the genus is validly published (Art.42, Stafleu et al., 1972). Petrak and Sydow (1936) examined portion of the original collection, described it in detail, transferred the type species as Ophiobolus graminicola (Speg.) Petrak & Syd. and reduced Ophiosphaerella Speg. to synonymy under Ophiobolus. This opinion was followed by Ainsworth (1971). The genus was not listed by von Arx and Müller (1975).

Examination of the holotype has confirmed that Ophiosphaerella is a Pleosporaceous genus, but it differs from Ophiobolus Riess sens.str.. It is a scolecospored fungus, closely related to, and congeneric with, Phaeosphaeria herpotricha. The genus Phaeosphaeria Miyake (1909) was described in the same year as Ophiosphaerella. Its type species, P.oryzae Miyake, has been lectotypified by Eriksson (1967) and many species studied in detail by Holm (1957), Eriksson (1967) and Hedjaroude (1969). With the exception of the scolecospored P.herpotricha, all species have either phragmospores (mainly) or dictyospores (P. vagans (Niessl) O.Erikss.), usually with either a complete

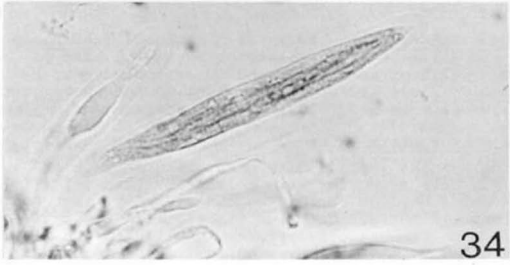
Figures 32-36. Ophiosphaerella spp. 32. O.graminicola, section ascocarp, x 183, from holotype LPS 858 (slide as DAR 34112). 33. O.herpotricha, section young ascocarp, x 183, from holotype in UPS (slide DAR 34127). 34-36. O. erikssonii from holotype, DAR 31924. 34. Young asci, x 733. 35. Ascus with ascospores, x 733. 36. Ascospore, x 733.


32


33


35


36


34

or partial gelatinous sheath and one (occasionally two) swollen cells. Whilst Holm (1957) placed P.herpotricha in Phaeosphaeria, he realised that it was not typical of this genus (L. Holm, in litt.) and Eriksson (1967) concluded that it should be in a different genus.

It is proposed that P.herpotricha be removed from Phaeosphaeria and placed in Ophiosphaerella Speg., where several other similar brown scolecospored Pleosporaceous fungi on Gramineae and Cyperaceae can be brought together. Removal of the scolecospored P.herpotricha leaves the species with sheathed phragmospores and dictyospores in Phaeosphaeria, forming a more homogenous group. The type species of Ophiosphaerella is described and several new Ophiosphaerella names considered.

Ophiosphaerella graminicola Speg., Anal.Mus.Nac.Buenos Aires 19, (Ser.3, 12), 401-402, 1909 (type in LPS !)
≡ Ophiobolus graminicola (Speg.) Petrak & Sydow, Ann. Myc. 34, 13-14, 1936 (as 'graminicolus ').

Ascocarps (Fig.32) embedded in leaf sheaths, dark brown to black, 300-350 µm diam with a centrally placed short wide neck, to 100 µm high and 100-120 µm wide; wall 20-25 µm thick at base and sides, 30-35 µm above at junction with neck (in area where penetration of leaf sheath occurs), of 6-10 layers of brown radially flattened cells, inner layers paler to hyaline, 6-10 x 3-4 µm, with unthickened or only slightly thickened walls, outer layer in surface view a textura angularis of cells 6-12 µm diam; neck canal 20-30 µm wide, with hyaline periphyses. Asci long cylindrical, narrower at foot-like base, bitunicate, 120-135 x 7-10 µm, borne in a dense basal layer, eight-spored, apical apparatus not observed. Ascospores (Fig.39) filiform, brown, 110-140 x (1.5) 2-2.5 µm, with 12-20 transverse septa arranged 7-10 µm apart, lying parallel or more commonly partly spirally twisted near their middle. Pseudoparaphyses abundant, hyaline, septate, very thin, 1-1.5 µm wide. Conidial state not known.

Illustrations: Spegazzini (1909, habit, section ascocarps, asci, ascospores).

Specimen examined: on leaf sheath of Leptochloa virgata Wight ex Steud, Tucuman, Argentina, 14.iv.1906, C. Spegazzini, LPS 858, HOLOTYPE (slides as DAR 34112).

Ophiosphaerella Speg. is distinguished from Phaeosphaeria Miyake by its scolecospores, which have no swollen cells or gelatinous sheath or appendages, and from Ophiobolus Riess by ascospores which do not have central swollen cells or separate into part spores.

Other Ophiosphaerella names

The species grouped here occur on Gramineae or Cyperaceae and have ascocarps with relatively thin walls (often 20-40 µm), composed of thin walled radially flattened cells, and long cylindrical bitunicate asci, with eight pale brown filiform multiseptate ascospores, usually in the range 100-200 x 1.5-3 µm. With the exception of Phaeosphaeria herpotricha, most are known only from the type specimen or

relatively few other collections. They may represent one variable widespread species on a large range of host genera or a complex of closely related but separate species with narrower host and geographic ranges. More collections, pure culture work, study of conidial states and intensive work on their taxonomy and pathology are needed to clarify these matters.

For the present, the species are kept separate. One, O.erikssonii, is described as new; the remainder are transfers to Ophiosphaerella. Bringing them together in the one genus indicates their similarity; keeping them separate for the present avoids possibly distinct species being buried in synonymy without sufficient work. The earliest epithet for these fungi comes from Sphaeria herpotricha Fr. and they may be regarded as members of a complex of scolecospored Pleosporaceous fungi on Gramineae and Cyperaceae, whose best known member is Ophiosphaerella herpotricha (Fr.) Walker.

Ophiosphaerella erikssonii sp.nov. (etym.erikssonii, Dr. Ove Eriksson, Umeå, studens Pleosporalium)

Pseudothecia (Fig.37) sparsa, in vaginis foliorum, corpus immersum fuscum, globosum vel subglobosum 200 µm diam, collum centrale breve erumpens; paries pseudothecii 10-20 µm crassus, facile fractus, ex 5-7 stratis cellularum fuscarum complanatarum 5-10 x 3-5 µm constatus. Asci (Figs.34 and 35) elongati clavati vel cylindrici, bitunicati, ad apicem rotundati, basin versus attenuati et unguliformes, 80-100 x 9-12 µm, octospori. Ascosporae (Figs.36 and 39) biseriatae, pallide brunneae, filiformes, in asco parallelae vel parum tortiles, cum extremis rotundatis, rectae vel plerumque arcuatae, (60) 80-95 x 2-2.5 µm, supra medium latissimae, (3) 5-7 septatae. Pseudoparaphyses numerosae, hyalinae, septatae, 1-2 µm latae. Hyphae affixae ad parietem pseudothecii sparsae, pallide brunneae, septatae, 3-4 µm latae. Conidia ignota.

HOLOTYPUS: in vaginis foliorum Calamagrostidis neglectae, ad littus, in insula petrosa, ad 1 km. S.W. phari, Vannskaren, parochia Nysatra, Vasterbotten, Suecica, 14.viii.1964. O. Eriksson 2419d, DAR 31924 (specimen et laminae vitreae).

ISOTYPUS: in UPS

Pseudothecia (Fig.37) sparse, in leaf sheaths, embedded body dark brown, globose to subglobose 200 µm diam, with a short central erumpent neck; wall of pseudothecium 10-20 µm thick, easily broken, composed of 5-7 layers of brown flattened cells 5-10 x 3-5 µm. Asci (Figs.34 and 35) elongated clavate to cylindrical, bitunicate, rounded apex, narrowed towards the foot-shaped base, 80-100 x 9-12 µm, eight-spored. Ascospores (Figs.36 and 39) biseriate, pale brown filiform, lying parallel or slightly twisted in the ascus, ends rounded, straight or more usually slightly curved, (60) 80-95 x 2-2.5 µm, widest above the middle, (3) 5-7 septate. Pseudoparaphyses numerous, hyaline, septate, 1-2 µm wide. Hyphae joined to pseudothecial wall sparse, pale brown, septate, 3-4 µm wide. Conidia unknown.

HOLOTYPE: in leaf sheaths of Calamagrostis neglecta, on the shore of a

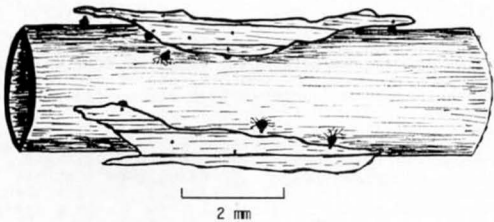


Figure 37. Ophiosphaerella erikssonii, habit, from holotype, DAR 31924.

rocky islet, 1 km. S.W. of lighthouse, Vannskaren, Nysatra parish, Vasterbotten, Sweden, 14.viii.1964, O. Eriksson 2419d, DAR 31924 (specimen and microscope slides).

ISOTYPE: in UPS

O. erikssonii is known only from the one rather sparse collection mentioned briefly by Eriksson (1967) who commented on its superficial similarity to Gaeumannomyces graminis, especially in ascospore size and shape. It is a typical Ophiosphaerella with slightly curved ascospores, shorter than those of the other species considered here. Though known only from one collection, it is described as new to bring it to the notice of mycologists and plant pathologists working with take-all and other root, crown and lower stem diseases of Gramineae.

Ophiosphaerella herpotricha (Fr.) Walker comb. nov.

≡ Sphaeria herpotricha Fr., Syst. mycol. 2, 504, 1823 (type in UPS !)

≡ Rhaphidophora herpotricha (Fr.) Tul., Sel. Fung. Carpol. 2, 255, 1863.

≡ Rhaphidospora herpotricha (Fr.) Ces.& de Not., Comment. Soc. Cryptog. Italiae, fasc. IV, 233-234, 1863 (orig. not seen; from Tulasne and Tulasne, 1863).

≡ Rhaphidospora herpotricha (Fr.) Fckl., Symb. mycol. 125, 1870, (as '(Fr.) Tul. unter Rhaphidophora').

≡ Ophiobolus herpotrichus (Fr.) Sacc. in Roum. & Sacc., Rev. mycol. 3, 45, 1881.

≡ Ophiochaeta herpotricha (Fr.) Sacc. in Clements & Shear, The Genera of Fungi, 277, 1931.

≡ Phaeosphaeria herpotricha (Fr.) Holm, Symb. bot. Upsal. 14, 119, 1957.

= Ophiobolus zeae Saccas, Rev. Pathol. veg. Entomol. agric. Fr. 30, 183-186, 1951 (type in PC !).

= Ophiobolus medusae Ell.& Ev. f.bromi Brenckle, Fungi Dakotenses 536, 1923 (in NY !)

The following description was prepared from the type specimen of Sphaeria herpotricha Fr. in UPS:

Pseudothecia (Figs.33 and 38) on pieces of grass straw with leaf sheaths attached, dark brown, body globose to subglobose 300-400 µm diam seated on the stem surface with a short conical neck to 100 µm long, 80 µm wide near base but narrower above, erumpent through the covering leaf sheaths, joined to and surrounded by an abundant dark brown mycelium. Wall (Fig.33) of body of ascocarp 25-35 µm thick, of 6-8 layers of radially flattened cells 6-12 x 4-6 µm with brown unthickened or very slightly thickened walls, outer layers dark brown, inner paler to almost hyaline, outer layer in surface view forming a textura angularis of cells 6-12 µm diam; wall of neck to 30 µm thick, ostiolar canal 20 (25) µm diam, periphyses not seen but globose hyaline cells present in canal in young ascocarps. Asci bitunicate, long, narrowly elongated clavate, apex to 3-4 µm thick, base foot-shaped, 150-190 x 7-9 µm, widest about 20-30 µm below apex. Ascospores (Fig.39) eight per ascus, long, filiform, pale brown to brown in mass, pale brown singly, lying parallel or loosely twisted for part of their length, 12-16 septate with septa 10-14 µm apart, 140-180 x 2-2.5 (3) µm, apex rounded, base rounded and narrower, widest about 20 µm below apex, straight to curved or slightly sinuous. Pseudoparaphyses abundant, hyaline, septate, 2-3 µm wide, longer than the asci. Mycelium dark brown, attached to pseudothecia and giving them a hairy appearance and running over surface of stem between leaf sheaths, little mycelium seen on outer surface of leaf sheaths, composed of dark brown branching septate hyphae 3-7 µm wide, some with nodular swellings, both smooth and rough-walled hyphae present, roughening from fine echinulations to coarse tubercules, some hyphae with intercalary hyphopodia present, abundant penetration points on stem surface associated with mycelium.

This description agrees well with the concept of O. herpotricha in the literature (Müller, 1952; Holm, 1957; Shoemaker, 1976) and with several collections examined. In the type, some pseudothecia showed asci of variable maturity and possibly most of the ascospores examined were not fully mature (they were not readily freed from asci under pressure). In IMI 98564b on Axonopus africanus, a distinct nassé apical was seen in some asci. In some collections, ascospores to 200 µm long and with up to 20 septa have been seen. Sometimes, the pseudothecial neck is longer (to 200 µm) and the amount of surrounding mycelium also varies between collections.

The ascospores of O.herpotricha are usually twisted in the ascus. The degree of twist is usually only about one complete turn in the length of the ascus, and the twisting is often only for portion of their length (often the middle) leaving the remainder of the length untwisted. The twisting is never the dense spiralling seen in Acanthophiobolus or described by Drechsler (1934) for Cochliobolus heterostrophus (Drechs.) Drechs. where several complete turns are present.

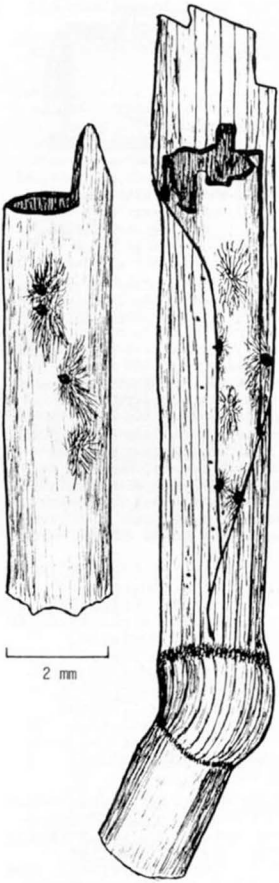


Figure 38. Ophiosphaerella herpotricha, habit, from holotype in UPS.

It is possible that several other species may belong here but study of the type collections is needed to decide this. Collections (not type) of Ophiobolus medusae Ell. & Ev. var. minor Ell.& Ev. (1890) and O. andropogonis Ell.& Ev. (1894), both described from Vetiveria zizanioides (as Andropogon muricatus), and O. oryzae Miyake (1909), have been studied and were Ophiosphaerella herpotricha. Shoemaker (1976) listed O. medusae var. minor as a synonym, but did not study the type. Sawada (1959) listed O.oryzae as a synonym of Ophiosphaerella herpotricha but it is not known whether he saw the type or not. A discussion of the confusion surrounding the names O.medusae var. minor and O. andropogonis is given under the latter name.

Saccardo (1883) described what he thought was the pycnidial state of O.herpotrichus as Hendersonia herpotricha Sacc.. The yellowish-brown cylindrical conidia measured 36 x 6 µm and had 8 septa. Webster and Hudson (1957) showed the connection in culture between O.herpotricha and a pycnidial state with 5-6 septate cylindrical conidia 69-116 x 3-4 µm with a truncate base and tapering to a thin bristle-like apex. They tentatively placed it as a species of Urohendersoniella Petrak but it is better considered as a species of Scolecosporiella Petrak (Sutton, 1977). A similar conidial state has been found on some collections in association with O.herpotricha pseudothecia. Further work on the taxonomy and

nomenclature of the pycnidial state is in progress.

Illustrations: Müller (1952, ascospore); Shoemaker (1976, ascospores and ascus).

Specimens examined: on 'Axonopus africanus' (exact identity not known; grass name not traced at Herb. NSW), near Kuida, Guinea, 12.xi.1962, F. Krantz 312, IMI 98564b as O.zeae Saccas (slides as DAR 33291). On Bromus inermis Leysser, Kulm, North Dakota, U.S.A., 15.vi.1923, J.F. Brenckle, F. Dakotenses 536, NY as O.medusae f.bromi, both pseudothecia and Scolecosporiella pycnidia present (slides as DAR 34113); Uppsala, Uppland, Sweden, 9.vii.1946, S. Lundell, dup. ex UPS as DAR 14323. On Echinochloa crus-galli (L.) Beauv. (as Panicum), U.S.A., 24.ii.1887, A.B. Langlois 1038, BPI as Ophiobolus sp. (slide as DAR 33692). On Oryza sativa, sheath rot, Fiji, 28.i.1966, K.M. Graham, DAOM 113212 formerly as Ophiobolus oryzae Miyake (slides as DAR 33305). On Vetiveria zizanioides (as Andropogon muricatus), St. Martinsville, Louisiana, U.S.A., Jan.1890, A.B. Langlois 2209 (partly), NY as Ophiobolus andropogonis Ell.& Ev., not type (slides as DAR 33737); same, 5.iv.1892, A.B. Langlois 2343, DAOM 128729, formerly as Ophiobolus medusae var. minor Ell.& Ev., not type (slides as DAR 33306). On Zea mays, near Boukoko, Oubangui-Chari, Central African Republic, 23.xi.1951, A.M. Saccas, PC, TYPE of Ophiobolus zeae Saccas (slides as DAR 33270); same, August 1958, A.M. Saccas, DAOM 59724. On undetermined Gramineae, Sweden, no date or collector, Scler.suec.exs. n. 52, UPS, HOLOTYPE of Sphaeria herpotricha Fr. (slides as DAR 34127); Krieg. F. Sax. 1574, slide A3786 in FH as Leptosporopsis herpotrichus, no collection details given.

Three collections with immature ascospores which may be O.herpotricha are: on Chloris gayana Kunth, Gainesville, Florida, U.S.A., August 1947, G.E. Ritchey, BPI as Ophiobolus (slides as DAR 33687). On Chrysopogon sp., Kharian, Pakistan, 21.vii.1964, S. Ahmad 18086, IMI 136978a as Ophiobolus sp. (slides as DAR 33293). On Oryza sativa (as Gramineae), Liberia, 1.ix.1940, S. Lennox, BPI as Ophiobolus (slides as DAR 33688).

Ophiosphaerella leptosperma (Speg.) Walker comb. nov.

≡ Rhaphidophora leptosperma Speg., Anal.Soc.Cient. Argent. 10, 18, 1880 (type in LPS !)

≡ Ophiobolus leptospermus (Speg.) Sacc., Syll.fung.2, 350, 1883.

≡ Rhaphidospora leptosperma (Speg.) Cke.,Grev.18 (85), 16, 1889 (as 'Raphidospora leptosperma Cke.').

Pseudothecia embedded in culm tissue, dark brown to black, up to 400-500 µm diam, with central erumpent neck, most broken off flush with host tissue; wall hard, 30-50 µm thick, of 10-15 (20) layers of radially flattened brown cells with unthickened walls. Asci long cylindrical to elongated clavate, 200-210 x 10-12 µm, narrower near the foot-like base, bitunicate, eight-spored. Ascospores (Fig. 39) long filiform, pale brown in mass, pale yellowish brown singly, arranged parallel or somewhat spirally twisted in the ascus, 150-200 x 2-2.5 µm, multiseptate. Paraphyses abundant, hyaline, septate, 1.5-2 µm wide. Conidia not known.

Specimen examined: on dead culms of Scirpus sp., Recoleta, Buenos

Aires, Rio de la Plata, Argentina, April or May, 1880, C. Spegazzini, LPS 2353, HOLOTYPE (slides as DAR 34115).

Many fruiting bodies are broken and empty and others are packed with hyaline hyphae. The date on the original hand-written inner packet is '5/5 1880'; on the outer packet it reads 'iv-1880'. The other information is the same except that the host was originally tentatively identified as 'in culmis ? Junci'.

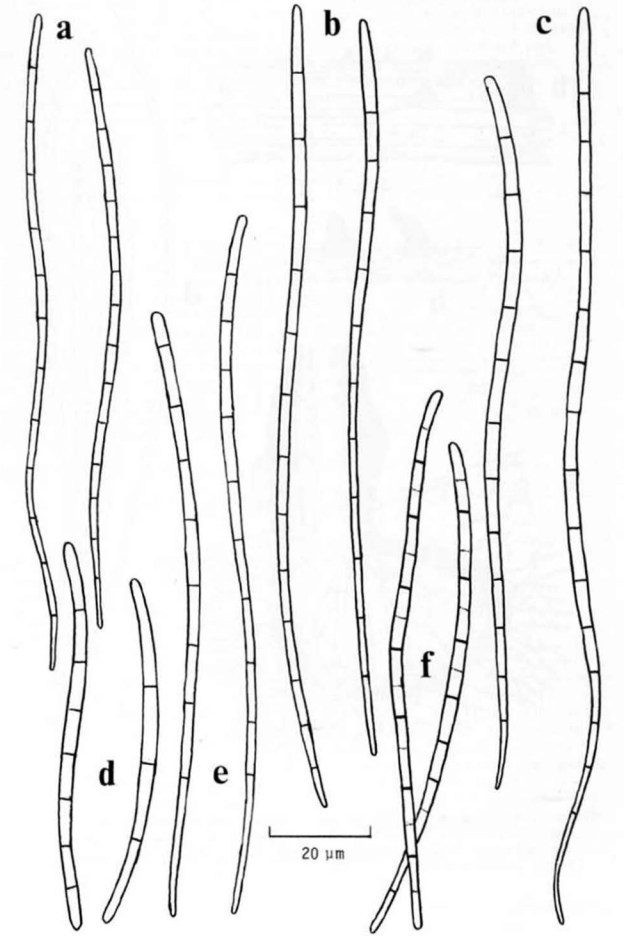
In characters of ascocarps, asci and ascospores, O. leptosperma falls within the wide range of variation found in the literature for O.herpotricha, but its pseudothecia are somewhat larger and firmer than those in many collections under that name and much less free mycelium is present. As far as can be seen, it is known only from the type specimen. Until Ophiosphaerella spp. are better known, and the relationship between those on Gramineae and Cyperaceae clarified, it is retained as a separate species.

Ophiosphaerella stipae (Hansford) Walker comb.nov.

≡ Linocarpon stipae Hansf.,Proc.Linn.Soc. N.S.W. 79, 121-122, 1954 (type in ADW !)

Pseudothecia (Fig.40) in blackened leaf sheaths associated with an abundant brown superficial mycelium, body embedded in sheath tissue, globose to subglobose, 350-500 µm diam, with central neck erumpent through several layers of leaf sheath, neck straight to slightly curved, narrowly conical, 300-350 µm long, 100-175 µm wide, with 2-3 thickened circular bulges (representing pressure ridges between successive layers of leaf sheath, see Walker and Smith, 1972); wall of body dark brown to almost black, 25-30 µm thick, of 5-10 layers of brown thin walled radially flattened cells 9-11 x 3-4 µm, outer layers joined to brown hyphae; wall of neck generally to 50 µm thick, but much thicker (from 75-125 µm) at bulges; neck canal 50-70 µm wide, densely lined with fine hyaline, slightly upwardly-pointing periphyses, up to 30 µm long, 1-1.5 µm wide and with 1-2 indistinct septa. Asci (Figs.40 and 43) bitunicate, long cylindrical or narrowly clavate, 120-180 x 10-13 µm, apex rounded 6-8 µm thick with thin internal canal, area up to 40 µm long towards bottom free of spores, base foot-like, eight-spored. Ascospores (Figs.39,40 and 44) filiform, brown in mass, pale yellowish brown singly, 90-120 (130) x 2.5-3 µm, narrowing slightly towards the base, (7) 13-15 septate, often very slightly constricted at the central (usually the eighth) septum, straight or more often slightly curved to

Figure 39. Ophiosphaerella spp., pairs of ascospores.
a. O. graminicola, from holotype, LPS 858 (slide DAR 34112);
b. O. herpotricha, from holotype, in UPS (slide DAR 34127);
c. O. leptosperma, from holotype, LPS 2353 (slide DAR 34115);
d. O. erikssonii, from holotype, DAR 31924; e. O. williamsii, from holotype, ADW 3542 (slide DAR 31931); f. O. stipae, from holotype, ADW 3488 (slide DAR 31930)


a
b
c
d
e
f
20 µm

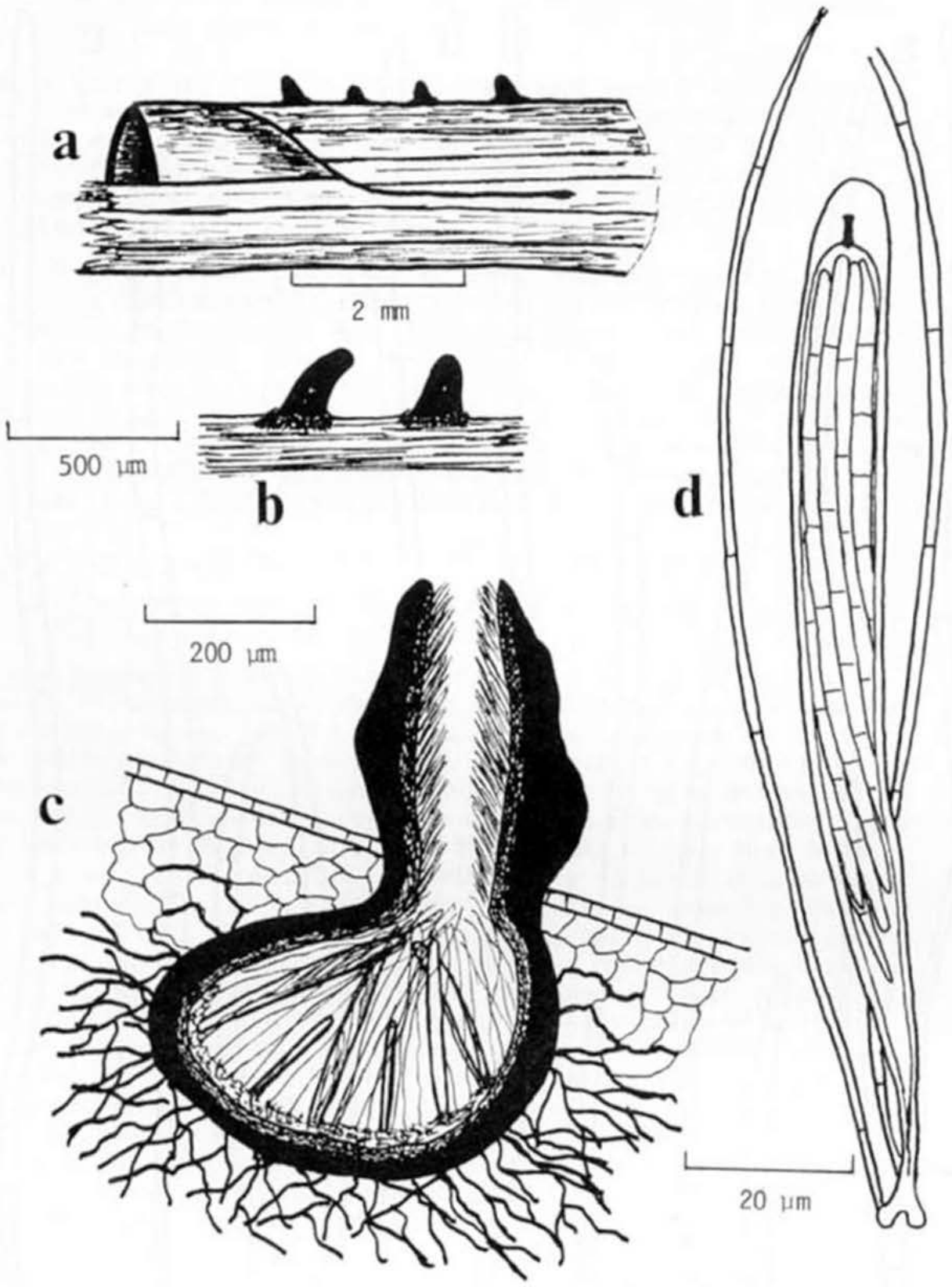


Figure 40. Ophiosphaerella stipae, from holotype, ADW 3488 (slide DAR 31930); a. habit; b. protruding necks of ascocarps; c. section ascocarp; d. ascus, ascospores and pseudoparaphyses.

sinuate, lying parallel in the ascus. Pseudoparaphyses (Fig. 40) abundant, hyaline, sparingly septate, longer than the asci, 1.5-2 µm wide. Hyphae forming an abundant mycelium on and between leaf sheaths and loosely binding them and soil particles together, attached to outside of pseudothecia and forming a dense weft around their base, individual hyphae brown, septate, 2.5-3.5 µm wide, with finely roughened walls, penetrating host cells either by slightly swollen hyphal tips or by short lateral swollen hyphopodial branches 5-8 x 5-6 µm each with a minute clear dot representing the point of host penetration. Conidia not known.

Specimen examined: on dead culm of Stipa sp., Meningie, South Australia, 24.vii.1953, L.D. Williams, ADW 3488, HOLOTYPE (slides as DAR 31930).

Hansford (1954) described this and the closely related O. williamsii (see below) in Linocarpon. Their type specimens show clearly their Pleosporaceous nature and they fit readily into Ophiosphaerella as defined here. O. stipae causes considerable blackening of infected host tissue and could be parasitic. The lateral infection branches with the minute clear penetration dot closely resemble the simple hyphopodia of Gaeumannomyces graminis and mentioned elsewhere (Walker and Smith, 1972) for Leptosphaeria korrae and L. narmari. However, the pathogenic capabilities of most species placed here in Ophiosphaerella are not known (see Walker, 1980).

Ophiosphaerella williamsii (Hansford) Walker comb.nov.

≡ Linocarpon williamsii Hansf., Proc.Linn.Soc. N.S.W. 79, 122, 1954 (type in ADW !)

Pseudothecia (Fig.41) in leaf sheaths and culms, associated with sparse brown mycelium, body embedded in sheath or in harder culm tissue, globose to subglobose to broadly conical, often with flattened base, 200-350 µm diam with central erumpent neck 100-150 µm long, 50-90 µm wide; wall of body dark brown to almost black, 25-35 µm thick, of 5-10 layers of brown thin-walled radially flattened cells 9-12 x 3-5 µm, outer layers joined to superficial brown hyphae; wall of neck 20-25 µm thick,ostiolar canal 35-40 µm diam, sparsely lined with relatively coarse, hyaline slightly upwardly pointing periphyses, to 30 µm long, 2 µm wide, distinctly 1-2 septate. Asci (Fig.42) bitunicate, long cylindrical to narrowly clavate, 140-180 x 9-12 µm, apex rounded with thin internal canal, foot shaped base, eight-spored. Ascospores (Figs.39 and 42) filiform, brown in mass, pale yellowish brown singly, 120-150 x 2 (2.5) µm, 5-12 septate, septa 12-15 µm apart, ends often non-septate in immature spores, straight or slightly curved, lying parallel or more often spirally coiled for part of their length (often in the middle half). Pseudoparaphyses abundant, hyaline, indistinctly septate, 1.5-2 (2.5) µm wide and much longer than the asci. Hyphae on inside of leaf sheaths and on surface of culm, brown, septate, branched, 2.5-4 µm wide with finely roughened walls, penetrating cell walls as described for O. stipae.

Specimen examined: on dead culm and leaf sheaths of undetermined grass, Meningie, South Australia, July 1953, L.D. Williams, ADW 3542,

HOLOTYPE (slides as DAR 31931).

O. williamsii and O. stipae are very similar. They differ in the smaller ascocarps of O. williamsii, which has longer, thinner ascospores (l : b about 60 : 1) than O.stipae (l : b about 36-40 : 1) and in the pattern of spore septation. In O. stipae it appears to be a fairly regular 1-3-7-15 development (with occasionally a few more or less giving spores with 13 or 17 septa) whereas in O. williamsii the pattern is much less clear but seems to be 1-3-5-7-9-11, with the central septum developing first and later septa developing in pairs, one on either side of the central septum and progressively further away. As noted above, the ends of immature ascospores in O.williamsii are often non-septate and this could result from such a developmental pattern. The ascospores in both species generally have fewer septa than those of O. herpotricha.

Other possible Ophiosphaerella spp.

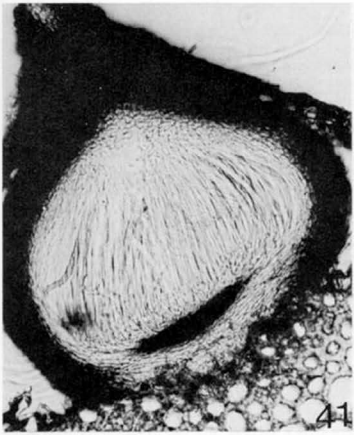
From the descriptions, it is possible that Ophiobolus junci Miller and Burton (1942) and O. stipae Doidge (1941) are species of Ophiosphaerella. Study of the type of O. junci is required; for comment on O.stipae, see under Ophiobolus. If O.stipae is found to be an Ophiosphaerella, a new name will be needed as the combination Ophiosphaerella stipae has already been used (see above).

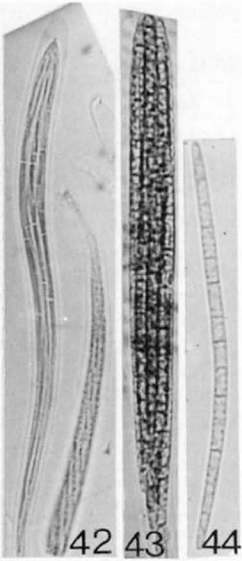
OPHIOSPHAERIA

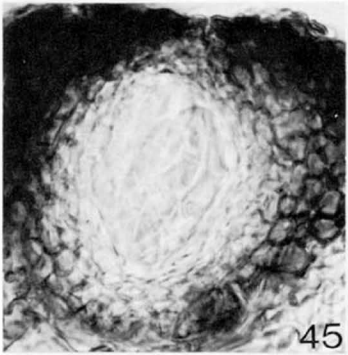
Ophiosphaeria Kirschstein, Verh.Bot.vereins Prov.Brandenburg 48 (1906), 47-48, 1907.
Type sp. O. tenella Kirschst.

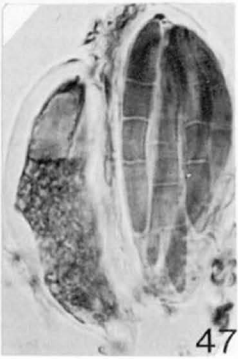
Study of the types has shown that Ophiosphaeria Kirschst. (1907) is not different from Acanthophiobolus Berlese (1892) and it is listed as a synonym of the latter genus (q.v.). Ainsworth (1971), following Höhnel (1907), considered Ophiosphaeria a synonym of Ophiochaeta (Sacc.) Sacc. Details of the status of these genera will be found under Acanthophiobolus and Ophiochaeta.

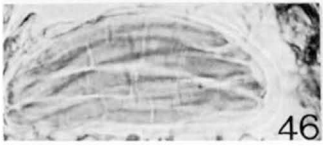
Figures 41-47. 41 and 42. Ophiosphaerella williamsii, from holotype, ADW 3542 (slide DAR 31931). 41. Section ascocarp, x 183. 42. Young asci with ascospores, x 733. 43 and 44. O. stipae, from holotype, ADW 3488 (slide DAR 31930), ascus with ascospores, and single ascospore, x 733. 45-47. Sphaerulina antarctica, from holotype, LPS 883 (slide DAR 33289). 45. Section ascocarp, slightly oblique, x 733. 46 and 47. Asci with ascospores, x 733.


41


42
43
44


45


47


46

OPHIOTRICHIA

Ophiotrichia Berlese, Icon.fung.1, 105, Jan.1893 (not validly published; based on Acanthostigma helminthosporum (Rehm) Sacc., 1883, basionym Leptospora helminthospora Rehm, 1882).

In discussing several species he excluded from Acanthostigma de Not., Berlese (1893) suggested the new generic name Ophiotrichia, based on Acanthostigma helminthosporum (Rehm) Sacc. (1883), and characterised by filiform ascospores. In Volume 2 of his Icones, dealing with scolecospored species and published in parts from 1895 to 1900 (Stafleu and Cowan, 1976), he did not take up the name but, following Saccardo (1895), included A. helminthosporum in the genus Ophiochaeta (Sacc.) Sacc. (q.v.) as O.helminthospora. Moreover, almost at the same time, he formally and fully described the new genus Acanthophiobolus Berlese (1892) with Leptospora (as 'Lasiosphaeria') helminthospora Rehm as the type species. The name Ophiotrichia was not taken up by Berlese, Saccardo or any other author. Weese (1921) listed it (as 'Ophiotricha') as a synonym of Acanthophiobolus and Kirschstein (1936) regarded it as a 'nackter name' (nomen nudum). It was not listed by Ainsworth (1971).

The name Ophiotrichia Berlese (1893) should be considered as not validly published under both Articles 34 and 41 of the International Code of Botanical Nomenclature (Stafleu et al., 1972). After its first mention, it was not accepted by the author in the same publication nor by any later author. No suitable description or diagnosis was given and no reference made to a previously published description of it as a genus or subdivision of a genus. The name is listed here as a synonym (not validly published) of Acanthophiobolus (q.v.).

PHAEOSPHAERIA

Phaeosphaeria Miyake, Bot.Mag. (Tokyo) 23 (266), 93-94, 1909 (also in J.Coll.Agric.Univ.Tokyo 2(4), 246-247, 1910).
Type sp. P.oryzae Miyake (for lectotypification, see Eriksson, 1967).

Phaeosphaeria spp. have been studied and described in detail by Holm (1957), Eriksson (1967) and Hedjaroude (1969). It is a Pleosporaceous genus of mainly graminicolous species with phragmospores or occasionally dictyospores, which have 1-2 swollen cells and a complete or partial gelatinous sheath or appendages. The only scolecospored species, P.herpotricha (Fr.) Holm, has long been regarded as an atypical Phaeosphaeria (Eriksson 1967; L. Holm, in litt.) and is removed here to Ophiosphaerella (q.v.).

PHIALOPHORA

Phialophora Medlar, Mycologia 7, 200-203, 1915.
Type sp. P.verrucosa Medlar (type not studied)

The Phialophora isolates considered here are some found in recent years associated with roots of Gramineae and include the conidial states of Gaeumannomyces spp.. Much of the literature on these fungi has centered around the name P. radicicola Cain (1952) which has been used in several different senses (Wong and Walker, 1975; Walker, 1980) and has become a source of confusion in the cereal take-all literature. It is known now that there is a complex of Phialophora-like fungi on roots of Gramineae (Scott, 1970; Walker, 1972; Deacon, 1973, 1974a,b; Sivasithamparam, 1975; Wong and Walker, 1975; Walker, 1980), including species such as P.mutabilis (Beyma) Schol-Schwarz, P.verrucosa Medlar and others (Sivasithamparam, 1975) which do not fall into the 'P.radicicola'complex. These species will not be considered here.

The isolates placed previously by various authors as P. radicicola seem to represent several closely related taxa, distinguishable only by a range of characters. A detailed knowledge of how many taxa are present, their range of variation and the reliability of differences between them can be obtained only after more intensive work on a wide range of isolates from many cereal and grass hosts in different countries. Isolates studied by the present author so far can be placed into four groups which are listed in Table 1 with the characters distinguishing them. In these groups, some characters seem to be correlated e.g. the only isolates studied which produce slightly lobed hyphopodia are also those that have the slowest growth rate (4-6 mm/24 hrs at their optimum temperature) and do not produce strongly curved non-germinating phialospores.

Undoubtedly, isolates will be found which will not fit into the four groups considered here or the groups themselves may be split up on the basis of other characters not yet considered. Hornby, Henden and den Toom (1979) isolated a Phialophora sp. from dark lesions on roots of wheat plants in a bioassay of soil at Woburn, England. This isolate was said to have germinating conidia similar to those of P.graminicola (see below) but had a faster growth rate, although not as fast as Gaeumannomyces graminis var. tritici or Phialophora sp. (lobed hyphopodia). It is felt that formal description and naming of isolates such as this would be premature and lead to an undue proliferation of names. For the present, isolates would be best referred to as Phialophora sp. with an accession number and their distinguishing characteristics listed. This would allow workers to compare isolates but no taxonomic or nomenclatural complications would have been introduced into a situation where limits of taxa are not yet known. Lodging of specimens and isolates in

herbaria and culture collections would also ensure the availability of such isolates for taxonomic work.

In this section, Phialophora radicicola (group 1) is considered on the basis of its type specimen and two living cultures said to be the original isolate. Groups 2 and 3, which have been placed by some workers as varieties of Cain's species, are described from several isolates. Isolates placed in group 4 are the conidial states of Gaeumannomyces graminis var. avenae and var. tritici. These have been described elsewhere (Walker, 1980) and details of specimens and cultures studied are given under Gaeumannomyces. They will not be considered further here.

Group 1. The only member of this group is Phialophora radicicola Cain sens. str.

Phialophora radicicola Cain, Canad.J.Bot.30, 340-342,1952) (type in TRTC !; living type culture in CBS !)

Cain (1952) described P.radicicola from a culture isolated from roots of Zea mays by W.E. McKeen at Chatham, Kent County, Ontario, Canada in the summer of 1950. At the same time, McKeen (1952) also found it in soil near Ridgetown, and studied its development on and in corn roots. As far as can be seen, there have been no subsequent records of this fungus in Canada. All material under the name P. radicicola in the University of Toronto Herbarium (TRTC) has been examined as well as a subculture from the living type culture in CBS and one from a culture of the original isolate from Professor W. E. McKeen.

The material in TRTC consists of two sheets, bearing six packets, all numbered TRTC 23660, containing dried agar cultures, thirteen microscope slides prepared from cultures and four sheets of pencil and ink drawings. One packet is marked TYPE and another Part of Type. All contain the same fungus which agrees with the description given by Cain (1952). The following description was prepared from this collection.

Dried cultures dark grey to black, some with abundant dense, fluffy greyish brown (two cultures) or pale grey (one culture) aerial mycelium, others with very sparse short aerial mycelium close to agar surface. Sclerotia numerous, black outside, black to pale grey inside, 0.75-1 mm diam, embedded in agar or produced on agar surface and then often completely or partly surrounded by dense aerial mycelium; sclerotia composed of thin walled pale brown to (more rarely) almost hyaline subglobose to oval cells 12-20 x 8-14 µm, a few as large as 28 x 16-18 µm, forming a pseudoparenchyma, outer layer with darker, thicker cell walls and dark brown septate hyphae, 2.5-3.5 µm wide growing over the surface. Hyphae very variable, from hyaline, thin, 1-3 µm wide to brown and 5-7 µm wide, septate, also moniliform hyphae of chains of brown, oval to globose cells 10-20 x 8-12 µm present, pore between adjacent cells readily seen, some similar single terminal or intercalary cells on other hyphae. Conidiophores in aerial mycelium, brown to dark brown, 2-5 µm wide, of very variable length,

some to 1 mm or more, others shorter, branched above, branches ending in a dense head whose ultimate cells are phialides. Phialides hyaline to pale brown, long cylindrical but usually slightly wider at or below the middle, straight or more commonly slightly curved, 18-20 x 2-4 µm with an apical, often slightly flared collarette. Phialospores abundant, clustered over the heads of phialides, dried masses pale brown, individually hyaline, thin, from slightly to strongly curved to semicircular, 6-8 x 1-1.5 µm.

Several of the microscope slides have partially dried out and some are contaminated with secondary moulds and a white powdery substance. In two (nos.3 and 12) a number of small 4-5 x 2-3 µm hyaline narrowly oval to X and Y shaped spores, each with a clear central vacuole, was seen. They were abundant in slide 3, in which no other spores were present, and sparse in slide 12, where abundant curved phialospores produced from heads of phialides were also present. The source of these spores is not known. They were not seen in the other eleven slides, or in several slides prepared from the dried cultures or in the living cultures examined. They differ in size and shape from the conidia produced by other graminicolous Phialophora spp. and it is suspected that they are contaminants unconnected with P. radicicola.

The type culture from CBS, studied by Deacon (1974b) and Wong and Walker (1975), does not now show several of the characteristics described by Cain (1952) and McKeen (1952) and shown by the dried type specimen in TRTC. Colonies on PDA and other media are at first white to cream, later creamy brown, thin, with little aerial mycelium, and a growth rate of 6-7 mm/24 hrs at 20°C and 10-11 mm/24 hrs at 25°C. Pronounced 'curling back' of marginal hyphae (Walker, 1980) was seen in colonies at 20°C but was not nearly so pronounced at 25°C. Phialospores as seen in the dried type specimen were formed from single or clustered phialides borne on short hyaline hyphae. No brown conidiophores or dense heads of phialides as seen in the type specimen were produced. No germinating phialospores were produced. On wheat coleoptiles, infections occurred mainly from simple, thin, hyaline hyphae but a few small simple subglobose to oval hyphopodia up to 8-10 x 5 µm or to 6 µm diam were developed (Wong and Walker, 1975; Walker, 1980). No other infection structures were seen. Abundant lignituber development occurred in coleoptile cells infected from hyphae or hyphopodia.

An isolate labelled 'P.radicicola' (33708), said to be the original isolate, was received from Professor W.E. McKeen. However, this did not agree either with the dried type material or with the living culture from CBS. It produced abundant germinating conidia, produced slightly lobed hyphopodia on wheat coleoptiles and had a growth rate of 4-6 mm/24 hrs at 25°C. No strongly curved non-germinating phialospores were produced. It is identical with P.graminicola (see below). Although this culture is said to be the original isolate, it does not agree with

the type specimen and has no type status. Whether two organisms were isolated originally, only one of which was studied by Cain (1952) as a basis for his description of P. radicicola, cannot now be determined.

Neither the type specimen nor the now degenerate type culture in CBS nor the description given by Cain (1952) and McKeen (1952) show characters necessary for accurate comparisons to be made between P.radicicola and recent Phialophora isolates from Gramineae. For the same reason the type material does not allow the various conflicting senses in which the name P.radicicola has been used in recent literature (Wong and Walker, 1975; Walker, 1975, 1980) to be satisfactorily resolved. The three main characters in question are

(i) Conidia: Deacon (1974b) and Wong and Walker (1975) have shown that Gaeumannomyces graminis and some related Phialophora spp. can produce two types of conidia

(a) germinating phialidic conidia (known only in culture) which are usually straight to slightly curved,not semicircular or strongly lunate and often in the range 5-14 x 2-4 µm and

(b) non-germinating phialospores (known in culture and in nature) which are usually strongly curved, falcate to lunate or semicircular and often in the range 3-9 x 1-1.5 µm. The species of Gaeumannomyces known in culture and the other Phialophora spp. shown in Table 1 all produce type (a) conidia but their presence in P. radicicola Cain has not been demonstrated. McKeen (1952) stated that the conidia seen in this species germinated to produce normal colonies, but this has not been substantiated with these conidia from the living culture by the present author or by others (Deacon, 1974b; Wong and Walker, 1975). No one has produced satisfactory proof of germination in the type (b) conidia of these fungi. The position regarding germinating conidia in P.radicicola Cain cannot be resolved satisfactorily from the type material or the original description.

(ii) Hyphopodia: Walker (1972) found that Gaeumannomyces graminis was a hyphopodiate fungus and subsequent work on other Gaeumannomyces spp. on Gramineae and Cyperaceae has shown that hyphopodia are a constant feature of species in the genus. In this paper, Gaeumannomyces has been re-defined as a hyphopodiate genus. Tests on several graminicolous Phialophora isolates have shown that they also produce hyphopodia (Wong and Walker, 1975) and hyphopodium production and shape has been used as a character of taxonomic value at the species level (Walker, 1980). Hyphopodia were not described for P. radicicola by Cain (1952) but McKeen (1952, p.346) described and figured on the surface of corn roots 'thick-walled brown, usually spherical, but sometimes elliptical, vesicles or chlamydospores.....and they always have a pore'. McKeen's original material is no longer available but it is possible

that he was describing hyphopodia. The living type culture, when inoculated on to wheat coleoptiles as a test for hyphopodium production (Walker, 1972, 1975, 1980) did not produce the structures described by McKeen (1952) but did produce a few small, hyaline simple hyphopodia, similar to those seen in all the other species listed in Table 1. There is no evidence from the type specimen, the living type culture or the descriptions of Cain (1952) and McKeen (1952) that lobed hyphopodia as seen in G.graminis var. graminis are produced by P.radicicola Cain. Deacon's (1974b) use of the name P.radicicola var. radicicola for British and French isolates producing lobed hyphopodia is incorrect (Art.26, Stafleu et al., 1972) and has been dealt with elsewhere (Wong and Walker, 1975; Walker, 1980).

(iii) Pathogenicity and host range: apart from McKeen's (1952) work on corn roots, there is no information on the pathogenicity of P. radicicola to cereals and grasses, or on the structures produced on and in roots of Gramineae. McKeen (1952) described and figured the spherical to elliptical bodies mentioned above on roots, and stated that 'sometimes numerous fine threads are formed in individual cells and other cells may be completely filled with enlarged fungus cells which later assume a thick, brown heavy wall (Figs.10 and 11).' His figures show root cells packed with brown fungal cells, and are very similar to Deacon's (1974b) Fig.20, showing similar structures in wheat roots produced by P.graminicola (as P.radicicola var. graminicola) and to Stetter and Leroul's (1979) Fig.4, showing similar cell clusters in barley roots produced by Microdochium bolleyi (Sprague) de Hoog & Hermanides-Nijhof (as Aureobasidium bolleyi). Deacon (1980) claims that these and similar structures in wheat roots (which he terms growth cessation structures; see Deacon, 1974b) are sufficiently constant and characteristic to provide an important means of identification of species and varieties of Gaeumannomyces and Phialophora spp. It is felt that the taxonomic reliability of these structures will need to be assessed on several hosts with a world-wide range of isolates of these and other root fungi on Gramineae before they could be used for taxonomic purposes. As far as P. radicicola Cain is concerned, the structures described originally are similar to those now known to be produced in cereal and grass roots by at least the two unrelated species listed above.

In these considerations of conidia, hyphopodia and pathogenicity, McKeen's (1952) original observations are of interest. He stated that conidia germinated, that brown vesicles with a pore were produced on roots and that host cells became packed with clusters of enlarged brown fungal cells. None of this can be reconciled with the type specimen of P.radicicola or the living type culture in CBS. However, if McKeen was using the isolate (duplicate as DAR 33708) discussed earlier and identified here as P.graminicola, his observations can be explained and agree closely with what is known for other isolates of P. graminicola

(Deacon, 1974b). It seems possible that the concept of P.radicicola could have been confused from the start, if Cain (1952) and McKeen (1952) were using two different isolates. Certainly the type specimen and type culture from CBS agree with one another and are quite distinct from the McKeen culture. Dr. McKeen (in litt.,1979) does not think that two different fungi were isolated in 1952.

It is thus recommended that the name Phialophora radicicola Cain be rejected for any isolates of Phialophora spp. other than the type specimen and type isolate because (a) it has been used in several different senses (Wong and Walker, 1975; Walker, 1980) and so has become a persistent source of error (Art.69, Stafleu et al.,1972) especially in plant pathological literature

(b) recourse to the type cannot resolve these conflicting usages

(c) the type specimen, type culture, original description (Cain, 1952) and subsequent paper dealing with the type (McKeen, 1952) show characters which are capable of different interpretations and application to several different organisms and do not show characters which would allow distinction between these various interpretations and accurate application of the name

(d) it is not possible to retypify P.radicicola (as some pathologists have suggested to me) as the holotype is still in existence (Art.7, Stafleu et al.,1972) and, in any case, selection of a neotype could not be made accurately for the reasons already given in (c).

Illustrations: Cain (1952, conidiophores, phialides, conidia, hyphae, sclerotial cells); McKeen (1952, phialides, conidia, growth in culture, and on and in corn roots); Walker (1980, simple hyphopodia).

Specimens examined: dried cultures and 13 microscope slides of cultures, isolated from roots of Zea mays, Chatham, Kent Co., Ontario, Canada, summer, 1950 (recd. Feb.1951), W.E. McKeen, TRTC 23660, HOLOTYPE packet and four duplicate packets, plus drawings (slides as DAR 33683); duplicate of type ex TRTC 23660, DAR 22004; same, living type culture ex CBS 296.53 (slides, dried cultures and subculture as DAR 23612).

Group 2. These isolates are all placed in the following species.

Phialophora graminicola (Deacon) Walker comb.nov.

≡ P. radicicola Cain var.graminicola Deacon, Trans. Brit.mycol.Soc.63(2), 322-323, 1974 (type in IMI !)

= P. radicicola sensu Scott, Trans.Brit.mycol.Soc.55 (1), 163-167, 1970, non P.radicicola Cain (1952).

P. graminicola is described fully in Walker (1980). It differs from the conidial states of Gaeumannomyces graminis varieties and from Phialophora sp. (lobed hyphopodia) (see below) in having about half the growth rate on agar and in lacking curved non-germinating phialospores (see Table 1). In cultural and morphological characters, it is

very similar to G.cylindrosporus (q.v.) and probably is its conidial state. The transfer as P.graminicola has been made here to remove it from the confusion surrounding the name P.radicicola dealt with above.

Illustrations: Deacon (1974b as P.radicicola var. graminicola, conidia, groups of pigmented cells in wheat roots); Scott (1970, as P. radicicola,conidiophores, phialides, conidia, pigmented cells in wheat root); Walker (1980, phialides, conidia, hyphopodia).

Specimens examined: on Agrostis tenuis Sibth. (bent grass), Tamworth, N.S.W., Australia, Oct.1975, P.Wong PD, DAR 26394; same, P.Wong 6H, DAR 26395. On Bromus unioloides H.B.K., Walcha, N.S.W., Australia, 1977, P. Wong TH3, DAR 33668. On Lolium perenne, Botany School Field Station, Cambridge, England, Oct.1971, J.W. Deacon P7, IMI 179703, TYPE culture (duplicate as DAR 27009). On Gramineae undet., Cambridge, England, 1966, P.R.Scott, Trans.1 (duplicate as DAR 23167); Yorkshire, England, date not given, prob. about 1971-1972, J.W. Deacon P4 (duplicate as DAR 23169). DAR 33708 ex W. McKeen (as P.radicicola Cain) also belongs here.

Group 3. Several isolates from England and Denmark are included here.

Phialophora sp. (lobed hyphopodia)

= Phialophora radicicola var.radicicola sensu Deacon (1974b) and PRR (or Prr) of subsequent British plant pathologists, not P.radicicola Cain (1952)

As mentioned earlier, Deacon (1974b) used the name P. radicicola var.radicicola for a fungus producing lobed hyphopodia found on roots of Gramineae in England and France. This is not in agreement with the type or original description of P.radicicola and the name cannot be used in this sense. Isolates of this fungus from England and Denmark have been studied and cannot be distinguised in culture or on morphology from the mycelial and conidial state of Gaeumannomyces graminis var. graminis (q.v.). They possibly represent isolates of G.graminis var.graminis for which perithecia have not yet been produced. Some pathologists have suggested that, as these isolates may be different from G.graminis var.graminis, they should be described as a new species of Phialophora. However, in studies with several isolates, nothing could be found to distinguish them consistently from G.graminis var.graminis. Isolates of G.graminis var.graminis and of Phialophora sp. (lobed hyphopodia) show some variability in cultural characteristics (especially amount of aerial mycelium and depth of colour) and conidial shape and size varies within and between isolates (Fig.48). Such variation is only to be expected in such a common widely distributed fungus. Study of more isolates and searches for the possible perfect state are required. In the meantime, the common name Phialophora sp. (lobed hyphopodia) provides a convenient label for isolates showing these characters, without any nomenclatural complications in Phialophora.

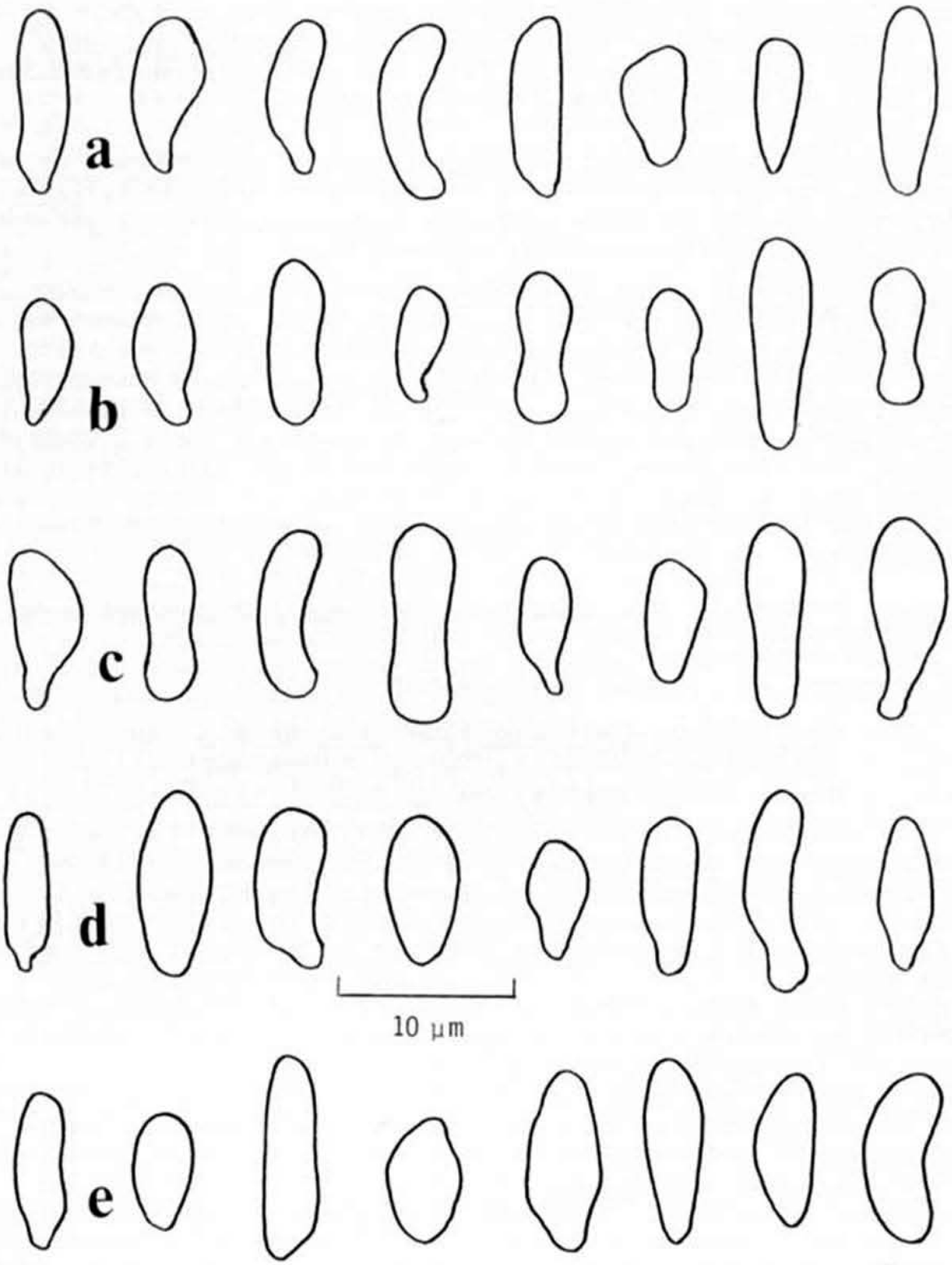


Figure 48. Germinable conidia of Gaeumannomyces graminis var. graminis (a and b) and Phialophora sp. (lobed hyphopodia) (c-e). a. DAR 30584 (N.S.W.); b. DAR 30585 (N.S.W.); c. DAR 22971 (England); d. DAR 25444 (England); e. DAR 33674 (Denmark).

Table 1: Grouping of *Phialophora* isolates from roots of Gramineae

Name	Ascospores Range in µm Length	Ascospores Range in µm Width	Hyphopodia Simple	Hyphopodia Slightly lobed	Hyphopodia Lobed	Conidia Germinating	Conidia Non-germinating	Growth rate mm/24hrs	Optimum temperature °C
Group 1									
Phialophora radicicola Cain (type)	-	-	+	-	-	-*	+	10-12	25-30
Group 2									
P. graminicola	-	-	+	+	-	+	-	4-6	20-25
Gaeumannomyces cylindrosporus	35-75	3-6	+	+	-	+	-	4-6	25
'*P.radicicola*' ex W. McKeen DAR 33708	-	-	+	+	-	+	-	4-6	25
Group 3									
P. sp. lobed hyphopodia	-	-	+	-	+	+	+	6-12	20-28
G. graminis var. *graminis*	70-110	2.5-4	+	-	+	+	+	8-12	20-30
Group 4									
G. graminis var. *avenae*	85-140	2.5-4	+	-	-	+	+	6-10	20-25
G. graminis var. *tritici*	60-110	2.5-4	+	-	-	+	+	6-10	20-25

* see discussion in text

In eastern Australia, where G.graminis var. graminis occurs commonly on a range of grasses, isolates vary greatly in their ability to produce perithecia and some have failed to do so. Whilst these isolates show a range of cultural characters and optimum temperatures for growth (see Table 1 and Walker, 1980), all resemble one another and cannot be distinguised from isolates of Phialophora sp. (lobed hyphopodia) from England and Denmark.

Illustrations: Deacon (1974b as P.radicicola var.radicicola,conidial germination, pigmented cells in wheat roots); Walker (1980, conidial germination, hyphopodia).

Specimens examined: all cultures, isolated from: Hordeum vulgare, Denmark, about 1975, S. Stetter and N. Leroul, culture sent by Dr. J. P. Skou as SpF74, DAR 33674; same, sent as SpF104, DAR 33675 (these isolates were referred to by Stetter and Leroul (1979) as 'Phialophora radicicola Cain' and illustrations of moniliform hyphae, conidiophores, phialides and curved phialospores given; the present author produced lobed hyphopodia and germinating conidia from these isolates); from Secale cereale L., Suffolk, England, August 1969, P.R. Scott, DAR 25444 (isolate P18 of Deacon, 1974b); from Zea mays, Essex, England, May 1972, J.W. Deacon G6, DAR 22971.

Grouping of isolates

The four groups of isolates and their characteristics are listed in Table 1. There is no suggestion intended that the characters listed are of equal value and, at the species level, more attention should probably be paid to morphology than to cultural growth rates and optimum temperatures. In such a widespread group of fungi, it could be expected that isolates of the same species from different geographic regions may show cultural and temperature differences. Moreover, the terms 'germinating' and 'non-germinating' for conidia arise from Wong and Walker (1975) and do not indicate other important morphological differences between the two types (see discussion in Wong and Walker, 1975 and Walker, 1980). The germinating conidia are of various shapes, but generally straight or slightly curved and usually from 1.5-4 µm wide. The non-germinating conidia are usually slightly to strongly curved or semicircular and from less than 1 to 1.5 µm wide.

PLAGIOSPHAERA

Plagiosphaera Petrak, Ann.Myc.39 (4-6), 289, 1941
Type sp. P.moravica (Petrak) Petrak, now as P.immersa (Trail) Petrak.

Petrak (1941) based his new genus on Ophiobolus moravicus Petrak (1921) found on dead stems of Urtica dioica in Austria. Later, he found that Ophiobolus immersus Trail provided an earlier epithet and made the new combination P.immersa (Trail) Petrak (1960). Dennis (1975) provided a detailed description and illustration, reduced Ophiobolus

brachysporus Fautr. & Roum. to synonymy, and commented on Trail's collections and Petrak's use of the epithet 'immersa'. A brief description prepared from the specimens examined is given.

Perithecia similar to those of Gaeumannomyces, embedded in stem tissue, with a lateral (or occasionally central) erumpent neck, and containing several unitunicate asci, 65-80 x 7-8 µm, with a small, distinct, apical ring. Ascospores parallel or loosely spirally twisted in the ascus, hyaline, slightly curved, 45-65 x 2-2.5 µm, with rounded apex, tapering to a thinner base, and with three or more indistinct septa. There is no associated superficial mycelium.

In the context of the cereal take-all fungi, Plagiosphaera is similar to Gaeumannomyces in characters of perithecia, asci, and ascospores. Holm (1948) noticed the similarity and suggested that 'Ophiobolus graminis' was closely allied to Plagiosphaera. In recent keys (e.g. Kobayashi, 1970; Bolay, 1971; Müller and von Arx, 1973), Gaeumannomyces (as Linocarpon in Kobayashi, 1970) and Plagiosphaera are placed close to one another and separated only on neck position, lateral in Plagiosphaera and central in Gaeumannomyces. However, members of both genera appear to vary in this character and presence of a superficial hyphopodiate mycelium and parasitic habit in Gaeumannomyces and its absence and saprophytic habit in Plagiosphaera seem to be more reliable differential characters.

During this work, the type specimen of Ophiobolus moravicus has not been available for study. Two other collections identified by Petrak have been examined and the fungus present agreed with the original description, and with that given by Dennis (1975).

Specimens examined: on dead stems of Aconitum napellus L. aggr., Niederösterreich, July 1939, F. Petrak, IMI 22266 (slides as DAR 34132). On dead stems of Urtica dioica L., Mähr-Weisskirchen, Austria, 1924, F. Petrak Flora Moravica 189, FH (marked co-type, but although on the type host from the type locality, this specimen is not the type collection which was made on 11.ix.1915, see Petrak, 1921; slides as DAR 34133).

Other names in Plagiosphaera

Plagiosphaera bhargavai Müller, Sydowia 12 (1958), 180-182, 1959 (type not examined).

This was described from a single collection on dead branches of Lonicera quinquelocularis Hardw. from India. It has perithecia with a lateral ostiole, embedded in a clypeate tuberous stroma, and from the description does not seem to be congeneric with the non-stromatic P.immersa. It is perhaps more closely related to Linospora Fckl.

Plagiosphaera muroiana (Hino & Katumoto) Walker comb.nov.

≡ Linocarpon muroianum Hino & Katumoto, J.Jap.Bot.41 (10), 296-297, 1966 (type in YAM !, listed by Hino & Katumoto as FAUY).

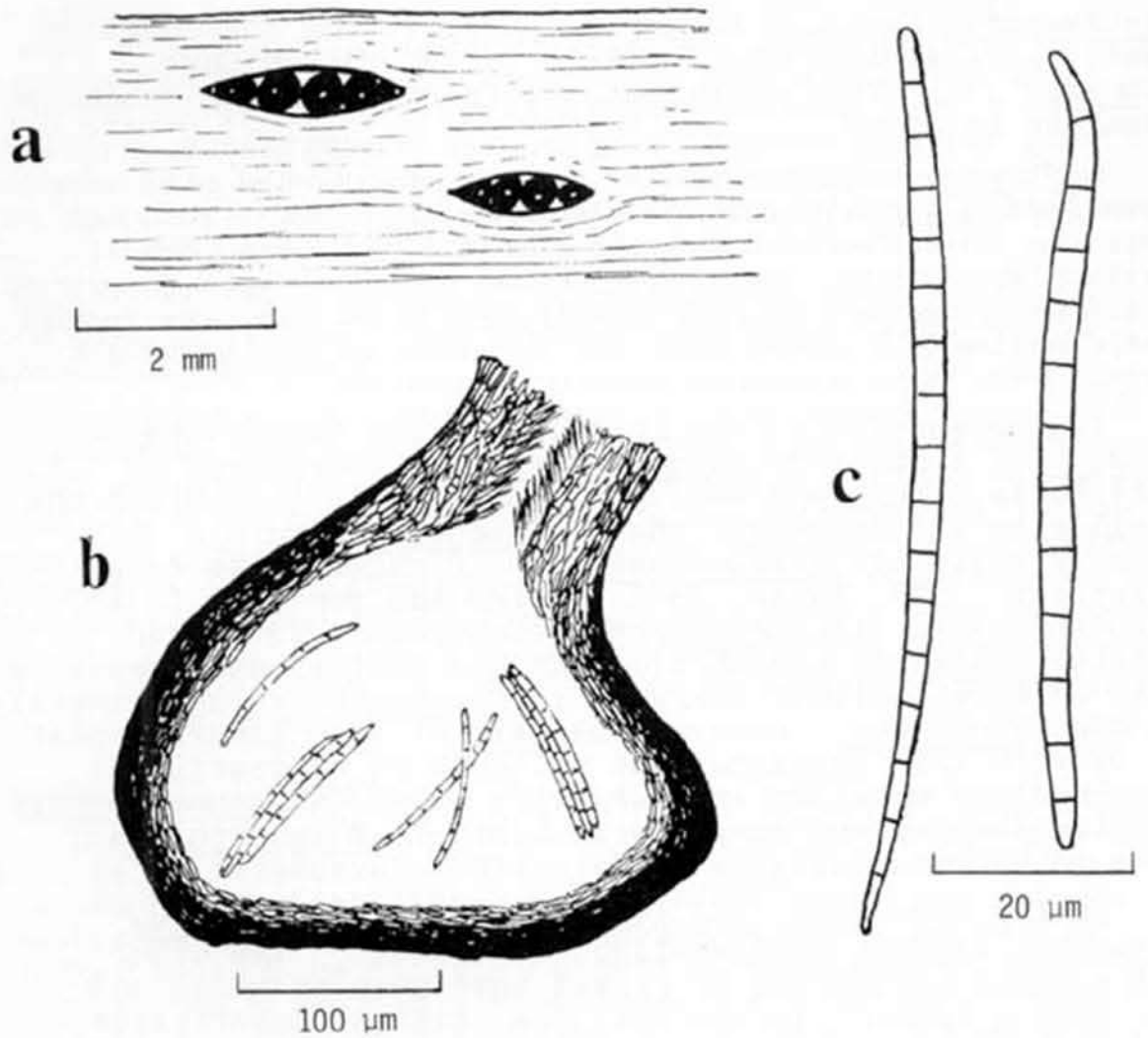


Figure 49. Plagiosphaera muroiana, from holotype in YAM (slide DAR 31877). a. habit; b. section ascocarp; c. two ascospores.

Perithecia (Fig.49) embedded in bamboo stem, with necks erumpent through stem tissue and (where present) through overlying leaf sheaths, clustered in loose groups of 3-6, often arranged in a line along the stem up to 2-2.5 mm long and less than 1 mm wide. When the firm outer layer of bamboo is removed, the black perithecia are seen to be loosely to tightly packed in the stem cortex. Body of perithecium black, 300-500 µm diam, subglobose to oval, with a central or eccentric black erumpent neck, 80-100 µm wide and up to 100 µm or more long, longer where leaf sheaths present, many broken off, internally white, lined with thin walled periphysis-like hyaline hyphae 2-2.5 µm wide, which appear to break down to form ostiolar canal. {Asci cylindrical to elongated clavate with small ring in slightly thickened, rounded apex, thinner at the base, shortly stipitate, eight-spored, 105-145 x 10.5-13.5 µm}. Ascospores (Fig.49) in a parallel bundle, not twisted, elongated fusiform, widest in the middle and tapering slightly to the rounded ends, 80-90 x 4 µm, with 10-16 septa 4-9 µm apart, septa prominent in some spores, paraphyses not seen. Stromatic tissue not observed; a few brown hyphae 3-4 µm wide attached to lower outer wall of perithecium and some similar hyaline hyphae seen in host tissue under perithecium.

Illustrations: Hino and Katumoto (1966, asci, ascospores, paraphyses); Kobayashi (1970, habit, section ascocarp, asci, ascospores).

Specimen examined: on dead culm of Sasa kurilensis Makino & Shibata, Mount Nyûtô, Akita, Japan, 4.viii.1957, H. Muroi, YAM, HOLOTYPE (slides as DAR 31877).

All perithecia examined were over-mature and asci were not observed. The description of asci given above is taken from the descriptions, drawings and photographs given by Hino and Katumoto (1966) and Kobayashi (1970). Abundant ascospores, often still arranged in bundles of eight, were present as a dry pale mass inside the perithecia.

Although Hino and Katumoto (1966) described stromata for this species, no sign of stromatic tissue was found. The perithecia were packed tightly in groups in the stem tissue with no surrounding stromatic tissue, no clypeus and no discolouration of the host tissue above or surrounding them. A few hyphae were found attached to the perithecia and in the tissue but there was no obvious development of any associated superficial mycelium on the stem or leaf sheaths. Ascospores were somewhat shorter than those described originally (87-124 x 3-3.5 µm) but agreed better with the measurements given by Kobayashi (1970; 75-100 x 4-4.5 µm). This species is more suitably placed in the non-stromatic genus Plagiosphaera than in the clypeate, partly stromatic genus Linocarpon (q.v.). It is the first Plagiosphaera recognised on a monocotyledonous plant (see below under Plagiosphaera sp. on Iris) and has larger asci and ascospores than the other species accepted here.

Plagiosphaera platensis (Speg.) Walker comb.nov.

≡ Winterella platensis Speg., Ann.Mus.Nac.Buenos Aires 19 (Ser.3,12), 403, 1909 (type in LPS !)

Perithecia embedded in stem tissue, single or several clustered together, black, body globose to subglobose or oval, 200-400 µm diam with an erumpent eccentric to lateral neck 80-100 µm wide and up to 250 µm long, many broken, often running laterally for some distance under host tissue before becoming erumpent; ostiolar canal to 30 µm wide, lined with hyaline hyphae 2-2.5 µm wide, no periphyses seen. Asci unitunicate, long cylindrical, 80-100 x 10-14 µm, with a small distinct apical ring 2 µm diam, eight-spored. Ascospores filiform, lying parallel in one bundle, faintly yellowish in mass, hyaline to faintly tinted singly, 70-75 x 2-2.5 (3) µm, several indistinct septa.

Specimen examined: on dead stem of Phytolacca (as Pircunia) dioica L., Buenos Aires, Santa Catalina, Argentina, Nov.1905, C. Spegazzini, LPS 851, HOLOTYPE (slides as DAR 34134).

In LPS, the original packet marked 'Winterella platensis Speg.n.sp.' is filed in an outer, later packet marked 'Trichospermella platensis Speg.'. As far as can be seen (Farr, 1973), Spegazzini did not publish this name. The fungus is certainly not congeneric with the type species of Trichospermella Speg. (T.pulchella Speg.)

(Walker, unpublished) but is a typical Plagiosphaera, close to P.immersa. It has slightly longer ascospores than those described for this species, but may not be specifically distinct.

Plagiosphaera quercicola Kobayashi, Mem.Nat.Sci.Mus.Tokyo 2, 88-89, 1976 (type not examined).

P. quercicola was described from wilting leaves of newly felled Quercus salicina Bl. trees in Japan. Kobayashi (1976) also mentioned a smaller spored unnamed species of Plagiosphaera causing a white circular leaf spot on Quercus glauca Thunb. in Japan. The exact generic position of these possibly parasitic species has not been studied here but they may be closer to various leaf inhabiting species of Pleuroceras Riess (see Barr, 1978) than to the saprophytic species of Plagiosphaera on dicotyledonous stems.

Plagiosphaera umbelliferarum (Barr) Barr, The Diaporthales in North America, p.123, 1978.

≡ Linocarpon umbelliferarum Barr, Canad.J.Bot.39, 320-321, 1961 (type in DAOM !)

A detailed description was given by Barr (1961). In size of perithecia, asci and ascospores, this fungus is very similar to P.immersa and may not be specifically distinct from it. Barr (1978) considered that Gaeumannomyces leptosporus Iqbal may be the same but Iqbal's species is considered here to be best placed in Ophioceras; see under Ophioceras leptosporum.

Illustrations: Barr (1961, ascocarp, ascus and detail of ascus tip, ascospores).

Specimen examined: on dead stem of Heracleum lanatum Michx.,Lac Diable, Mt. Albert, Quebec, Canada, 19.viii.1957, M.E. Barr 2198A, DAOM 74274, TYPE (slides as DAR 34116).

Plagiosphaera sp. on Iris

In discussing Sphaeria eucrypta Berk.& Br., described on Carex pendula L., Walker (1972) mentioned collections under this name in various herbaria on Iris foetidissima L. The status of the epithet 'eucrypta Berk.& Br.' and the possible identity of the fungus on available specimens of Cyperaceae is discussed under Gaeumannomyces spp. on Cyperaceae. However, the Iris collections show a different organism, which is not a Gaeumannomyces, but can be placed tentatively in Plagiosphaera.

Perithecia embedded in leaf tissue, dark brown to black, body globose to oval 250-300 µm diam, with a long erumpent neck up to 300 µm long, 50 µm wide, placed eccentrically on the body and often running horizontally in the tissue before it pierces the surface. Asci unitunicate, 70-90 x 6-9 µm, with a refringent apical ring seen as two short rods in side view, eight-spored. Ascospores hyaline to pale yellow, lying parallel in one fascicle, 50-60 x 1.5-2 (2.5) µm,

several indistinct septa. No superficial hyphae present.

In length of asci and ascospores, this is very similar to P. immersa but ascospores are somewhat narrower. Further collections on Iris are needed to clarify both the generic and specific identity of this fungus.

Specimens examined: all on Iris foetidissima; Batheaston, 7.i.1859, collector not given, K; Batheaston, Jan.1859, C.E. Broome, Rabh. F. Europ.49, two duplicates in K and one in L (all as Sphaeria eucrypta Berk.& Br.). A fragment of thick leaf marked 'Ophiobolus eucryptus (Berk.& Br.) Sacc.' with no further information, in PAD, is probably portion of this Iris collection.

Plagiosphaera sp. on Quercus glauca - see P. quercicola above.

RHAPHIDOPHORA

The generic name Rhaphidophora Ces.& de Not. (Fungi) described in 1861 is a later homonym of Rhaphidophora Hassk. (Araceae) published in 1844 (Saccardo, 1883, p.337). The former name is thus illegitimate and to be rejected for use in the fungi (Art.64). The few Rhaphidophora names in this paper are disposed as follows:

Rhaphidophora graminis Sacc.(1875) - this is Gaeumannomyces graminis (Sacc.) von Arx & Olivier var graminis (q.v.).

Rhaphidophora herpotricha (Fr.) Tul.(1863) - placed here as Ophiosphaerella herpotricha (Fr.) Walker (q.v.).

Rhaphidophora leptosperma Speg. (1880) - placed here as Ophiosphaerella leptosperma (Speg.) Walker (q.v.).

Rhaphidophora maritima Sacc.(1878) - type sterile; for discussion and synonymy, see Walker (1972); see also under Linocarpon maritimum.

RHAPHIDOSPORA

The generic name Rhaphidospora Fr.& Mont.(Fungi) published in 1849 is a later homonym of Rhaphidospora Nees (Acanthaceae) published in 1832 (Saccardo, 1883, p.337). The former name is thus illegitimate and to be rejected for use with fungi (Art.64). The Rhaphidospora names in this paper are disposed as follows:

Rhaphidospora herpotricha (Fr.) Fckl.(1870) - placed here as Ophiosphaerella herpotricha (Fr.) Walker (q.v.).

Rhaphidospora leptosperma (Speg.) Cke.(1889 as 'Raphidospora leptosperma Cke.') - placed here as Ophiosphaerella leptosperma (Speg.) Walker (q.v.).

Several of the epithets used in this paper in Acanthophiobolus, Gaeumannomyces, Ophiosphaerella and Sphaeria were listed by Cooke (1889) under Rhaphidospora (as 'Raphidospora'). They are not relisted here.

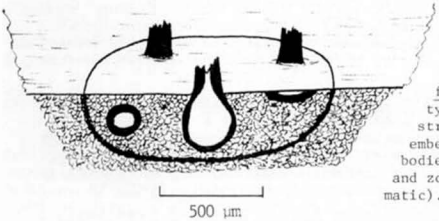


Figure 50.
Schizacrospermum filiforme, from type in FH, section stroma showing embedded fruiting bodies, broken necks and zone line (diagrammatic).

SCHIZACROSPERMUM

Schizacrospermum P.Henn., Monsunia 1, 170, 1899

Type sp. S.filiforme P.Henn & E.Nym. in P.Henn (type in FH !)

≡ Ophioceras filiforme (P.Henn.& E.Nym.) v.Höhnel, Sitzungsber.Kaiserl.Akad.Wiss., Math.-Naturwiss. Kl.,120, 432, 1911 (as 'P.Henn.) v.Höhn.').

S. filiforme was described from rotting leaf sheaths of Amomum sp. (Zingiberaceae) collected in Java. Its description may be summarised as follows:

Perithecia solitary to subcaespitose, erumpent-superficial, fleshy membranaceous but horny when dry, black, filiform, 3-5 mm long, 150-180 µm wide, with a bluntly rounded yellowish-brown apex with a pore, yellow inside. Asci clavate to fusoid, eight-spored, 100-120 x 10-13 µm. Ascospores filiform, parallel, obtuse to acute, hyaline to pale yellowish, multi-septate, 80-100 x 3-3.5 µm.

The associated discussion spoke of perithecia arising singly or in groups from a black layer in the leaf tissue. The illustrations showed a piece of leaf sheath with several long filiform necks protruding singly or in groups from it. The ascospores are figured as about 12 septate, without swollen cells and slightly but definitely constricted at each septum.

Höhnel (1911) examined portion of the type collection and found embedded globose fruiting bodies with long erumpent necks. Asci were said to be 120 x 13 µm and ascospores pale brown, filiform and septate. Höhnel concluded that Hennings had overlooked the embedded globose bodies of the perithecia and described the necks only as filiform perithecia. He placed the fungus in Ophioceras.

The portion of the type from Höhnel's herbarium in FH has been examined. It consists of one piece of leaf sheath with several globose to subglobose fruiting bodies 250-400 µm diam embedded in the tissue. They are brown, usually in groups of 3-5 and each group is

surrounded completely by a dark zone line of fungal tissue, seen on the leaf sheath surface as a dark line around the group and in the tissue as a black plate around and under the fruiting bodies (Fig.50). This zone line is a layer of host cells completely invaded by the fungus, each cell being tightly packed with a mass of dark brown irregularly shaped fungal cells up to 11 x 6 µm. The plate is very similar to that seen surrounding the ascocarps of some species of Lophodermium and termed aliform mycelium by Tehon (1935). The wall of the individual fruiting bodies is pale brown to brown, 15-20 µm thick, of several layers of cells, the outer layer a textura angularis of cells 8-14 µm diam. Most of the long necks described originally had broken off but a few necks to 100 µm long were seen. These were dark brown to black, 150 µm wide of several layers of dark brown cells 5-10 µm diam and with a central canal 40-50 µm wide. No sign of asci, ascospores, paraphyses or periphyses was seen in this collection.

As Höhnel (1911) suggested, it seems that Hennings probably described the long necks as the whole fruiting body. The fungus appears to be a stromatic ascomycete of some sort and is probably not a species of Ophioceras (q.v.). In the absence of asci and ascospores, no further comment on its possible relationships can be made.

Illustrations: Hennings (1899, Taf.V. Fig.17, habit, neck of ascocarp, ascus, ascospores, paraphyses).

Specimen examined: on dead leaf sheath of Amomum sp.,Tjibodas, Java, collection date not given on label, in Herb. F.v. Höhnel a.n. 3806 in FH, portion of TYPE (slides as DAR 34137). The date '1907-1908' on the packet is presumably when this portion was sent to Höhnel. In the original description, the specimen was collected by E. Nyman on 4.vii.1898 at Tjibodas, Java.

SPHAERIA

Sphaeria Haller ex Fries, Syst. Mycol.1, lii,1821

Type sp. S.rubra, Fragi similis Haller = S.fragiformis Pers. ex Hook. (Stafleu et al., 1972, p.256).

The name Sphaeria has been used for a wide range of perithecial and pseudothecial species. The type species is regarded as a species of Hypoxylon Bull.ex Fr.(nom.cons.) (Stafleu et al., 1972, p.256). Several Sphaeria names for scolecospored species are discussed.

Sphaeria cariceti Berk.& Br., Ann.Mag.Nat.Hist.,ser.3,7, 455, 1861 (type in K !)

Results of examination of the type and other specimens in K and detailed discussion of the epithet 'cariceti Berk. & Br.' were given by Walker (1972). The name is not available for use. The original collections do not show characters which would allow the fungus to be identified and the epithet applied accurately. As Ophiobolus cariceti (Berk.& Br.) Sacc. and Linocarpon cariceti (Berk.& Br.) Petrak, it has been applied to the wheat take-all fungus, here listed as Gaeumannomyces graminis (Sacc.) von Arx and

Olivier var. tritici Walker (q.v.); see also Walker (1980).

Sphaeria chaetophora Crouan (1867) - a synonym of Acanthophiobolus helicosporus (q.v.).

Sphaeria coffeata Berk. in Hook., Fl.N.Z. II, 205, 1855 - identity unknown, no specimen available (Walker, 1972).

Sphaeria culmorum Wallr., Fl. Cryptogam.Germ.,Pars Posterior: 770, 1833 (type not seen).

This species, described on rotting culms of Scirpus lacustris L. and 'Juncus laevis', with dark brown globose fruiting bodies in lines on blackened areas has not been studied and its identity is not known. It was mentioned by Walker (1972).

Sphaeria culmorum Cke, Grevillea 3, 68, 1874 (type not seen)

Wehmeyer (1961) discussed this species which he placed as a synonym of Pleospora phaeocomoides (Berk.& Br.) Wint. var. infectoria (Fckl.) Wehmeyer. The name is a later homonym of S. culmorum Wallr. and S.culmorum Crouan.

Sphaeria culmorum Crouan in Crouan & Crouan, Fl.Finist.26, 1867 (type in CO !) - details of this species, which cannot be identified from the type specimen, were given by Walker (1972). The name is a later homonym of S.culmorum Wallr.

Sphaeria dolichostoma Berk.& Curt. - see under Ophioceras dolichostomum (Berk.& Curt.) Sacc.

Sphaeria eucrypta Berk.& Br. - for discussion of specimens on Cyperaceae under this name, see 'Gaeumannomyces caricis and G.spp. on Cyperaceae'. For Iris specimens, see 'Plagiosphaera sp. on Iris'. See also Walker (1972) for discussion of specimens and synonymy.

Sphaeria helicospora Berk.& Br. - placed here as Acanthophiobolus helicosporus (Berk.& Br.) Walker (1972) (q.v.).

Sphaeria herpotricha Fr. - see Ophiosphaerella herpotricha (Fr.) Walker.

Sphaeria littoralis Crouan - for discussion of this species, see Walker (1972).

Sphaeria oedema Mont. - see under Ophiobolus oedema (Mont.) Sacc.

Sphaeria penicillus Schmidt ex Fr.,Syst.mycol.2,508,1823.

Fries (1823) based this species on a collection on herbaceous stems from the Lausitz region of East Germany. The covered black, smooth, glabrous perithecia were said to have a globose body, dark coloured inside, and the thick, very short papillate, cylindrical erumpent neck was said to have very short hairs at its apex.

Subsequent authors have interpreted the name in various ways and specimens bearing the name often do not show the same species. The results of investigations of S.

penicillus will be presented in a separate publication. It has no bearing on the nomenclature of the cereal take-all fungi; its relationship to Ophiobolus Riess and Nodulosphaeria Rabenh. will be dealt with elsewhere.

Sphaeria stictispora Cke.& Ell., - see under Ophiobolus stictisporus (Cke.& Ell.) Sacc.

Sphaeria verminosa Mont. - see under Ophiobolus verminosus (Mont.) Sacc.

SPHAERULINA

Sphaerulina Saccardo, Michelia 1, 399, 1878
Lectotype sp. S.myriadea (DC.ex Fr.) Sacc. (see Barr, 1972; von Arx and Müller, 1975).

The genus is discussed and several species described by Barr (1972). One species on leaves of Cyperaceae which should be included in Sphaerulina is described.

Sphaerulina antarctica (Speg.) Walker comb.nov.

≡ Linospora antarctica Speg., Bol.Acad.Nac.Cienc. Republ.Argent.Córdoba 27 (4), 377-378, 1924 (type in LPS !)

Ascocarps small, dark brown, at first embedded, later erumpent, 100-150 µm diam, wall to 30 µm thick, of several layers, outer layer of oval dark brown thin-walled cells 10-15 x 7-12 µm, inner layers paler, of subglobose cells 6-10 µm diam, centrum lined with thin layer of hyaline flattened cells, ostiole central, not well developed, 15-20 (25) µm diam. Asci 8-10 per ascocarp, broadly clavate to almost saccate, 55-77 x 22-28 µm, bitunicate, wall to 6 µm thick at the apex, apical apparatus not seen, eight-spored. Ascospores hyaline, cylindrical to narrowly clavate, slightly curved, rounded at each end, 40-60 x 5-7 µm with 3 transverse septa, lying parallel or slightly intertwined at 2-3 levels in the ascus. Paraphyses not seen. See Figs. 45 to 47.

Illustrations: Spegazzini (1924, as Linospora antarctica, habit, ascocarp, asci, ascospores.

Specimen examined: on dead leaves of Carpha schoenoides Banks & Soland. ex Hook., Sholl Bay, Capitan Aracana Island, Chile, 13.i.1923, C. Spegazzini, LPS 883, HOLOTYPE (slides as DAR 33289).

The asci and ascospores in the type are somewhat smaller than the measurements of 80-110 x 25-35 µm and 65 x 5-6 µm respectively given in the original description (Spegazzini, 1924) and in Spegazzini's notes and drawings on the type packet. Possibly the few ascocarps examined had mainly immature asci present. In all other respects, present observations on the type agree with the original description. It is a typical Sphaerulina and quite distinct from the diaporthaceous genus Linospora.

On the original packet, the name is written as Linospora subantarctica Speg. (n.sp.) but it was published as

L. antarctica (Spegazzini, 1924; Cash, 1972; Farr, 1973). The slight differences in locality information found in the literature for this species are discussed under Lophodermium magellanicum (Speg.) Walker, collected at the same time.

WINTERELLA

For Winterella platensis Speg. see Plagiosphaera platensis (Speg.) Walker.

A NOTE ON HYPHOPODIA AND APPRESSORIA

Emmett and Parbery (1975) and Parbery and Emmett (1977) have classified all fungal structures that adhere to plant surfaces and produce one or more infection threads, as appressoria. They include in this term structures named hyphopodia, stigmatopodia (or stigmopodia), stigmatocysts, node cells, infection cushions and infection plaques as well as the swollen structures often found on germ tubes generally referred to as appressoria. They considered that use of a definition based on function avoided problems associated with definitions based on morphology alone. On this basis, they gave a comprehensive review of appressoria, their morphology and function, factors influencing their formation, and the distribution of different types of appressoria in various taxonomic and ecological groups of fungi. In studies of the cereal take-all and related fungi, consideration has been given to the terms applied to the various vegetative structures they form on and in host tissue. It is concluded that use of the term appressorium in the wide sense of Emmett and Parbery (1975) and Parbery and Emmett (1977) is not always appropriate.

Walker (1972) discussed the basis of the use of the term hyphopodium for hyphal structures produced by the cereal take-all fungi. Much earlier, Mangin (1899) and Arnaud (1918) had recognised them as attachment and penetration structures and Arnaud (1918) compared them directly with the hyphopodia of the Meliolales and Asterinales and stated 'L'étude des champignons du Piétin des céréales expose d'une façon lumineuse la nature des organes perforants des Astérinées'. In many genera of Meliolales and Asterinales, hyphopodium formation occurs abundantly and regularly on epiphytic hyphae; in the cereal and grass fungi, some epiphytic hyphae (e.g. the runner hyphae and hyphal strands of G.graminis var. tritici) do not form them and hyphopodia are formed in a much less regular fashion on the associated network of branched epiphytic hyphae. The different hyphal types in these fungi are mentioned further in Walker (1980).

In Gaeumannomyces spp. and related Phialophora spp., hyphopodia have been shown to be of taxonomic value in identifying species and varieties (Walker, 1972, 1980).

Moreover, recognition of Gaeumannomyces as a hyphopodiate genus has helped clarify its separation from some other genera of Diaporthales. In the fungi as a whole, production of hyphopodia seems to be limited to genera in a relatively few orders in contrast to appressoria produced on germ tubes which, as Parbery and Emmett (1977) have shown, occur widely in all the main groups of fungi. Hyphopodia have been found in the following orders:-

Pleosporales e.g. Leptosphaeria narmari Walker & Smith (1972) and L. korrae Walker & Smith (1972), Phaeosphaeria herpotrichoides (de Not.) L.Holm (Mangin, 1899, Arnaud, 1918). In the graminicolous species, the hyphopodia are non-specialised and very similar to the simple hyphopodia and infection cushions seen in Gaeumannomyces spp.. von Arx and Müller (1975) and von Arx (1979) also tentatively placed Magnaporthe salvinii (Catt.) Krause & Webster and Buergenerula spartinae Kohlmeyer & Gessner here. The superficial hyphae of the conidial state (Nakataea sigmoidea (Cav.) Hara) of M.salvinii produce lobed hyphopodia (see Ou, 1972, pp. 235-238 and fig.iv-5). The known hyphopodiate species are mainly root, crown, stem and leaf sheath parasites of Gramineae.

Asterinales - see Theissen (1913) for Asterina, and von Arx and Müller (1975) for various genera in the families Asterinaceae, Englerulaceae and Parodiellinaceae. Hyphopodia are lateral (occasionally intercalary) and simple or lobed; all are leaf (or branch) parasites on a wide range of plants, with many species having a range restricted to a small number of hosts.

Erysiphales - see Homma (1937) and Clare (1964) where these hyphal structures are referred to as appressoria. Differences in shape, size and arrangement appear to be one of the characters of value in helping identify some conidial forms in the absence of perithecia. There seems to be no reason why the hyphal infection structures in the Erysiphales should not be referred to as hyphopodia. This would also help distinguish them from appressoria produced on germ tubes, which also have some taxonomic value (Homma, 1937; Ballantyne, 1975). All are parasites on a wide range of plants.

Meliolales - see Hansford (1961, 1963). In this order capitate and mucronate hyphopodia are distinguished. The former are very important taxonomically in their shape, size, position relative to one another and to mucronate hyphopodia, frequency and arrangement on the hyphae. The structures termed mucronate hyphopodia are not penetrating organs and their necks are usually directed up away from the host surface (Hansford, 1961). Their function is not known and Goos (1974, from Goos and Gessner, 1975) suggested that they are apparently without function. Hughes (1978) found phialoconidia produced from the open tip of mucronate hyphopodia of Asteridiella knightiae Hughes in New Zealand. This seems to be the first record of such an occurrence and may give a clue to the function of these structures. The term hyphopodium may be inappropriate for them (Goos and Gessner, 1975) but as it has been used so widely in the literature on the Meliolales, its retention is suggested at present. The Meliolales are parasites on a wide range of plants.

Diaporthales - known only in Gaeumannomyces spp. (Walker, 1972, 1980) and also in Magnaporthe salvinii (Catt.) Krause & Webster (1972) if it is placed here (see under Pleosporales and Phyllachorales). Both simple and variously lobed hyphopodia are produced by Gaeumannomyces spp. and related Phialophora spp. The hyphopodiate species are parasites of Gramineae and Cyperaceae.

Phyllachorales - lobed hyphopodia are produced by Buergenerula spartinae Kohlmeyer & Gessner (1976; Goos and Gessner, 1975 as Sphaerulina pedicellata Johnson) and by the conidial state of Magnaporthe salvinii. There is some difference of opinion concerning the placement of these species (see Pleosporales, and Barr, 1976b and von Arx, 1979 for Buergenerula). Both are parasites of Gramineae. Barr (1978) considered that Glomerella v. Schrenk & Spaulding is best placed in this order and similar simple and lobed hyphal structures have been described for some Colletotrichum conidial states (see below).

Basidiomycotina - No example of true hyphopodia in the Basidiomycetes has been found. Dodman et al. (1968a,b) have shown that some isolates of Rhizoctonia solani Kühn form lobed penetration structures on the superficial mycelium on the host and they contrast these with isolates which penetrate by forming dome-shaped infection cushions. In some respects, these structures are similar to the hyphopodia and infection cushions of Gaeumannomyces graminis varieties. Dodman et al. (1968b) were unable to obtain formation on artificial surfaces.

Coelomycetes - appressoria produced from vegetative hyphae were described and illustrated by Sutton (1968) for Colletotrichum graminicola (Ces.) Wils. and C. falcatum Wint.. These are indistinguishable from the hyphopodia produced by many fungi in the preceding orders. Sutton was able to use differences in these structures to separate isolates into three groups and he commented that appressoria produced on germ tubes did not show these differences. See also Glomerella under Phyllachorales.

Hyphomycetes - Ellis (1971, 1976) listed several genera of dematiaceous hyphomycetes with hyphopodiate mycelia. Some have perfect states in various genera of Asterinales. Some Phialophora spp. related to Gaeumannomyces also produce hyphopodia (Walker, 1980).

The majority of fungi in which hyphopodia have been found are parasites and form a more or less extensive epiphytic mycelium on their host. Apart from those whose perfect state is unknown, all are confined to six orders of Ascomycotina. In contrast, fungi which produce appressoria on their germ tubes include epiphytic and endophytic species in many orders of the fungi (Parbery and Emmett, 1977). There appears to be no correlation between ability to form germ tube appressoria and ability to form hyphopodia on vegetative hyphae. Some fungi form both, and then they may be similar (e.g. in Meliolales, see Hansford 1961) or distinct (e.g. in some Erysiphales, see Homma, 1937). In Barr's (1976a) tentative 'family tree' of the Ascomycotina, the six orders are seen to be placed in different branches, although the Erysiphales, Meliolales

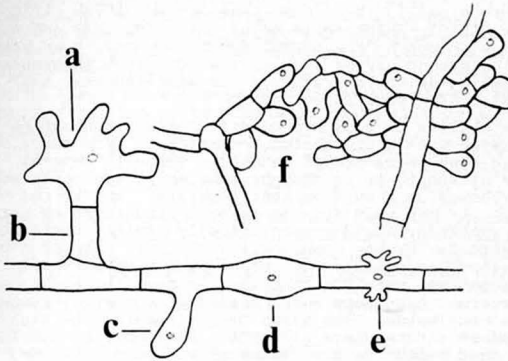


Figure 51. Diagram of hyphopodia and terms used. a. and b., stalked lobed hyphopodium with stigmatocyst (a) and stigmatopodium (b); c. sessile unlobed hyphopodium; d. unlobed intercalary hyphopodium (node cell); e. lobed intercalary hyphopodium as seen in some Erysiphales; f. developing plate mycelium (cluster of simple hyphopodia) in Gaeumannomyces graminis.

and Diaporthales are adjacent to one another. Possibly hyphopodia have developed on several occasions in these fungi, as a mechanism for penetration of surfaces by superficial hyphae. Hyphopodia seem to be essentially a surface phenomenon; in Gramineae and Cyperaceae where several layers of leaf sheaths may surround the stem, they can be found on the stem surface covered by the sheaths and also on surfaces in successive leaf sheath layers. On rare occasions they have been recorded inside plant tissue. Nilsson (1972) figured a lobed hyphopodium of Gaeumannomyces graminis var. graminis in wheat leaf sheath tissue and Deverall, Wong and McLeod (1979) mentioned lobed hyphopodia of this fungus against the endodermis of invaded wheat roots. Occurrences of this type in tissue seem to be rare and their formation on the endodermis could be regarded as a surface phenomenon in an attempt (unsuccessful) to invade the stele. The structures formed internally in invaded roots of cereals and grasses and termed 'growth cessation structures' by Deacon (1974b) are not considered to be structures equivalent to hyphopodia and other superficial organs of infection. The former seem to develop as part of a halting or slowing down of infection in invaded roots. They show some variation in size, shape and arrangement between species, but whether

these differences are constant enough to have taxonomic value requires further study (see Deacon, 1974b, 1980; Walker, 1980). Hyphopodia occur mainly on leaf and stem tissue although in the cereal fungi they have been seen on below ground organs such as the sub-crown internode (commonly) and roots (rarely). In some species, they have also been seen in culture.

As ability to form hyphopodia does not seem to be correlated with appressorium formation on germ tubes, and because hyphopodia are of taxonomic value in several groups of fungi, it is thought that the terms appressorium and hyphopodium should be kept separate. In the one species, it may seem strange to call structures on germ tubes appressoria and morphologically similar structures on vegetative hyphae hyphopodia. However, precision of expression, especially when discussing host-parasite relationships, requires that the two terms be separated. The general characters which distinguish these structures are set out below. The terms cannot possibly be rigidly defined as intermediate structures may occur but it is hoped that, with the discussion given above, they may be more logically applied.

Appressorium - a swelling, usually terminal, produced on germ tubes for attachment and penetration or terminally on a hypha within host tissue for cell wall penetration. All gradations from normal hyphae (which often penetrate host tissue) to complex structures occur (see Parbery and Emmett, 1977).

Hyphopodium - a cell or swelling produced from vegetative epiphytic hyphae for attachment and penetration. It may be terminal, lateral or intercalary (node cell), simple (Fig.51c) or lobed, hyaline or coloured, sessile or stalked (stigmatopodium or stigmopodium, with terminal stigmatocyst).

Infection cushion - a cluster of hyphae and hyphal cells under which multiple infections occur. In Gaeumannomyces graminis it represents a cluster of simple hyphopodia and, where it develops abundantly, is sometimes called plate mycelium (Fig.51f).

Node cell - an intercalary hyphopodium (Fig.51d and e).

Plate mycelium - layer of laterally fused simple hyphopodia causing multiple infections e.g. in the take-all and similar fungi on Gramineae (Fig.51f); see infection cushion.

Stigmatocyst (or stigmocyst) - the cell of a stalked hyphopodium from which the penetration peg develops (Fig.51a).

Stigmatopodium (or stigmopodium) - the stalk or short branch on which the penetration cell (stigmatocyst) is carried (Fig.51b). Defined by Arnaud (1918,p.41) as follows: 'Les cellules qui émettent des filaments

perforant la cuticle sont parfois des cellules ordinaires; le plus souvent ce rôle est dévolu à des cellules spéciales (stigmocysts différenciés) qui sont, en général, portés sur des rameaux particuliers ou stigmopodies.'

In the host tissue, invasion from hyphopodia may be limited to formation of haustoria in host cells or may be more extensive.

SYNOPSIS OF FUNGI

The list includes all generic names, and all species listed in alphabetical order of specific epithet. In the case of a species in a genus not dealt with in detail in the text, it is listed under both its generic name and specific epithet. Accepted names are underlined; synonyms and names of doubtful status are not underlined.

Acanthophiobolus, see text
Acanthostigma gracile, syn. of Acanthophiobolus helicosporus
Acanthostigma helminthosporum, syn. Acanthophiobolus helicosporus
Acanthotheciella, see text
Acrospermum, see Cylindrina and Microstelium
A. parasiticum, see Cylindrina
acuminatus, Ophiobolus, earliest name for type species of Ophiobolus
alopecuri, Dilophospora, see Lidophia
alpinum, Lophodermium
andropogonis, Ophiobolus, exact identity not known
antarctica, Linospora, see Sphaerulina antarctica
antarctica, Sphaerulina
arenarius, Ophiobolus, now Plejobolus arenarius
arenarius, Plejobolus, see under Ophiobolus arenarius
arundinaceum, Lophodermium, type species of Lophodermium
arundinaceum var.alpinum, Lophodermium, now Lophodermium alpinum
Asteridiella knightiae, see note on hyphopodia and appressoria
Asterina, see note on hyphopodia and appressoria
Aureobasidium bolleyi, see under Phialophora radicicola
australiensis, Ophiobolus

barbata, Acanthotheciella, type species
barbata, Ophiochaeta, now Acanthotheciella barbata
barbatus, Ophiobolus, now Acanthotheciella barbata
Barya, see Microstelium
bhargavai, Plagiosphaera, a doubtful Plagiosphaera
bolleyi, Aureobasidium, see under Phialophora radicicola
bolleyi, Microdochium, see under Phialophora radicicola
brachysporus, Ophiobolus, syn. of Plagiosphaera immersa
brunellae, spelling error for prunellae (q.v.)
Buergenerula spartinae, see note on hyphopodia and appressoria

cajani, Linocarpon
capreae, Linospora, type species
cariceti, Linocarpon, see also Sphaeria cariceti
cariceti, Ophiobolus, see also Sphaeria cariceti

gracile, Acanthostigma)
gracilis, Acanthophiobolus, Lasiosphaeria,) syns. of
Ophiobolus, Ophiochaeta,) Acanthophiobolus
Ophiosphaeria) helicosporus
gramineum, Lophodermium
graminicola, Colletotrichum, see note on hyphopodia and appressoria
graminicola, Ophiobolus, syn. of Ophiosphaerella graminicola
graminicola, Ophiosphaerella, type species of Ophiosphaerella
graminicola, Phialophora, see also Gaeumannomyces cylindrosporus
'graminicolus ', Ophiobolus, error for Ophiobolus graminicola
graminis, Dilophia, syn. of Lidophia graminis
graminis, Gaeumannomyces
graminis, Lidophia
graminis, Ophiobolus, syn. of Gaeumannomyces graminis var. graminis
graminis, Ophiochaeta, syn. of Gaeumannomyces graminis var. graminis
graminis, Rhaphidophora, syn. of Gaeumannomyces graminis var. graminis
graminis, Wojnowicia, see Triticum specimen under Gaeumannomyces
graminis var. tritici
graminis var. avenae, Gauemannomyces
graminis var. avenae, Ophiobolus, syn. of Gaeumannomyces graminis var.
avenae
graminis var. graminis, Gaeumannomyces
graminis var. tritici, Gaeumannomyces
graminum, Dinemasporium, see list of unplaced Gaeumannomyces specimens,
under Poa

halima, Lulworthia, see under Ophiobolus halimus
halimum, Linocarpon, see also under Ophiobolus halimus
halimus, Ophiobolus, now Lulworthia halima
helicospora, Sphaeria, syn. of Acanthophiobolus helicosporus
helicosporus, Acanthophiobolus
helicosporus, Ophiobolus, syn. of Acanthophiobolus helicosporus
helminthospora, 'Lasiosphaeria',) syns. of Acanthophiobolus
Leptospora, Ophiochaeta) helicosporus
helminthosporum, Acanthostigma, syn. of Acanthophiobolus helicosporus
helminthosporus, Acanthophiobolus, syn. of Acanthophiobolus helico-
sporus; type species of Acanthophiobolus
Hendersonia herpotricha, see under Ophiosphaerella herpotricha
herpotricha, Hendersonia, see under Ophiosphaerella herpotricha
herpotricha, Ophiochaeta, syn. of Ophiosphaerella herpotricha
herpotricha, Ophiosphaerella
herpotricha, Phaeosphaeria, Rhaphidophora,) syns. of Ophiosphaerella
Rhaphidospora, Sphaeria) herpotricha
herpotrichoides, Phaeosphaeria, see list of unplaced Gaeumannomyces
specimens under Poa
'herpotrichus, Leptosporopsis', herbarium name; see Leptosporopsis
herpotrichus, Ophiobolus, syn. of Ophiosphaerella herpotricha; see
also under Ophiochaeta and Leptosporopsis
hesperia, Leptosphaeria, see under Leptosporopsis
heterostrophus, Cochliocolus, see under Ophiobolus heterostrophus and
Ophiosphaerella herpotricha
heterostrophus, Ophiobolus
hyalinum, Microstelium
Hypoxylon, see under Sphaeria

immersa, Plagiosphaera
immersus, Ophiobolus, syn. of Plagiosphaera immersa
implexa, Leptospora, see also under Ophiobolus tortilis
implexum, 'Ophioceras', see specimens under Leptospora implexa
implexum, Lophionema, syn. of Leptospora implexa
implexum, Lophiostoma, syn. of Leptospora implexa
implexus, Ophiobolus, syn. of Leptospora implexa
incompta, Ophiochaeta, exact identity not known
incompta, Rhaphidophora, see Ophiochaeta incompta; also under Acanthophiobolus
incomptus, Ophiobolus, see under Ophiochaeta incompta

junci, Ophiobolus, see also under Ophiosphaerella

knightiae, Asteridiella, see note on hyphopodia and appressoria
korrae, Leptosphaeria, see also note on hyphopodia and appressoria

Lasiosphaeria, see text
Lejosphaerella, see list of unplaced Gaeumannomyces specimens under Glyceria
leptosperma, Ophiosphaerella
leptosperma, Rhaphidophora, syn. of Ophiosphaerella leptosperma
leptosperma, Rhaphidospora, syn. of Ophiosphaerella leptosperma
leptospermus, Ophiobolus, syn. of Ophiosphaerella leptosperma
Leptosphaeria, see text and also under Gaeumannomyces spp. on Cyperaceae, and Lidophia
Leptosphaeriopsis, see text
Leptospora, see text and also under Gaeumannomyces spp. on Cyperaceae, and Ophiobolus leptosporus
Leptosporopsis, not validly published
leptosporum, Ophioceras
leptosporus, Gaeumannomyces, syn. of Ophioceras leptosporum
leptosporus, Ophiobolus, exact identity unknown
licualae, Ophiobolus, see also under Linocarpon
Lidophia, see text
Linocarpon, see text
Linospora, see text
littoralis Cribb & Cribb, Ophiobolus, see Ophiobolus australiensis
littoralis (Crouan) Sacc., Ophiobolus, see Sphaeria littoralis
littoralis, Sphaeria, exact identity unknown
livistonae, Linocarpon, see also under Ophiobolus livistonae
livistonae, Ophiobolus, see also under Linocarpon livistonae
Lophiostoma, see under Leptospora implexa
Lophodermium, see text
Lulworthia, see text

magellanica, Linospora, syn. of Lophodermium magellanicum
magellanicum, Lophodermium
Magnaporthe salvinii, see note on hyphopodia and appressoria, and list of unplaced Gaeumannomyces specimens, under Oryza
manihotis, Linocarpon, see under Ophiobolus manihotis

manihotis, Ophiobolus, exact identity not known
maritima, Rhaphidophora, type sterile; see under Ophiobolus maritimus
maritimum, Linocarpon, see under Ophiobolus maritimus
maritimus, Ophiobolus, type sterile; exact identity not known
maydicus, Pithomyces, see list of specimens under Ophiobolus sp.
medusae, Linocarpon, see also under Lulworthia
medusae, Lulworthia
medusae, Ophiobolus, see also under Lulworthia and Ophiobolus andropogonis
medusae f. bromi, Ophiobolus, syn. of Ophiosphaerella herpotricha
medusae var. minor, Ophiobolus, exact identity not known; see under Ophiobolus andropogonis and Ophiosphaerella herpotricha
Meliola panici, see under Ophiobolus stipae
michotii, Paraphaeosphaeria, see list of unplaced Gaeumannomyces specimens under Gramineae undet.
Microdochium bolleyi, see under Phialophora radicicola
Microstelium, doubtful genus
moravica, Plagiosphaera, syn. of Plagiosphaera immersa; type species of Plagiosphaera
(For further "m" names, see Addendum at end of paper)

Nakatea sigmoidea, see note on hyphopodia and appressoria
narmari, Leptosphaeria, see also note on hyphopodia and appressoria
nipae, Linocarpon, see also under Ophiobolus nipae
nipae, Ophiobolus, see also under Linocarpon nipae
Nodulosphaeria, see under Sphaeria penicillus
Nodulosphaeria erythrospora, see under Ophiobolus pellitus

oedema, Ophiobolus, see also under Linocarpon
oedema, Rhaphidospora, see also under Ophiobolus oedema
oedema, Sphaeria, see also under Ophiobolus oedema
ophioboloides, Leptosphaeria, syn. of Ophiobolus ophioboloides
ophioboloides, Leptosphaeriopsis, syn. of Ophiobolus ophioboloides
ophioboloides, Ophiobolus
Ophiobolus, see text
Ophioceras, see text
Ophiochaeta, see discussion; a syn. of Acanthophiobolus
Ophiosphaerella, see text
Ophiosphaeria, syn. of Acanthophiobolus
Ophiotrichia, not validly published
oryzae, Ophiobolus, see also under Ophiosphaerella herpotricha
oryzae, Phaeosphaeria, type species of Phaeosphaeria
oryzae, Pyrenochaeta, see list of unplaced Gaeumannomyces specimens, under Oryza
oryzinum, Linocarpon, syn. of Gaeumannomyces graminis var. graminis
oryzinus, Gaeumannomyces, invalid; syn. of Gaeumannomyces graminis var. graminis
oryzinus, Ophiobolus, syn. of Gaeumannomyces graminis var. graminis

palmetto, Linocarpon
palmetto, Linospora, syn. of Linocarpon palmetto
paludosa, Leptosphaeria, see under Gaeumannomyces spp. on Cyperaceae
paludosus, Ophiobolus, see under Gaeumannomyces spp. on Cyperaceae
pandani, Linocarpon, type species of Linocarpon

rubellus, Ophiobolus, see also Leptospora rubella
rubra (Fragi similis), Sphaeria

salinus, Ophiobolus, new name for Ophiobolus medusae var. minor; see under Ophiobolus andropogonis
salvinii, Magnaporthe, see note on hyphopodia and appressoria and list of unplaced Gaeumannomyces specimens, under Oryza
Schizacrospermum, exact identity not known
Scolecosporiella, see under Ophiosphaerella herpotricha
sigmoidea, Nakatea, see note on hyphopodia and appressoria
solani, Rhizoctonia, see note on hyphopodia and appressoria
sorghi, Ophioceras, exact identity uncertain
sp.(lobed hyphopodia), Phialophora
spartinae, Buergenerula, see note on hyphopodia and appressoria
Sphaeria, see text
Sphaeropsidales, undetermined, see list of unplaced Gaeumannomyces specimens, under Oryza
Sphaerulina, see text; also under Ophioceras zeae
Sphaerulina pedicellata, see note on hyphopodia and appressoria
spirosporus, Ophiobolus
Stictis, see under Cylindrina and Ophiobolus stictisporus
stictispora, Sphaeria, see Ophiobolus stictisporus
stictisporus, Ophiobolus
stipae, Linocarpon, syn. of Ophiosphaerella stipae
stipae, Ophiobolus, exact identity uncertain; see also under Ophiosphaerella
stipae, Ophiosphaerella
'strictisporus', Ophiobolus, spelling error for stictisporus (q.v.)
'subantarctica', Linospora, herbarium name; see Sphaerulina antarctica

tanaceti, Leptosphaeria
tanaceti, Ophiobolus, syn. of Leptosphaeria tanaceti; see also under Leptosporopsis
tax sp. 1, Gaeumannomyces, on Cyperaceae
tax sp. 2, Gaeumannomyces, now Gaeumannomyces caricis
tax sp. 3, Gaeumannomyces, on Cyperaceae
tenella, Ophiosphaeria, syn. of Acanthophiobolus helicosporus
tortilis, Ophiobolus, exact identity unknown
'trechisporus', Ophiobolus, spelling error for trichisporus
trichella, Ophiochaeta, exact identity unknown; see also under Ophiobolus
trichellus, Ophiobolus, exact identity unknown; see also under Ophiochaeta
trichisporus, Ophiobolus, syn. of Leptospora rubella
'Trichospermella' platensis, herbarium name; see Plagiosphaera platensis
Trichospermella pulchella, type species of Trichospermella; see under Plagiosphaera platensis
'trichosporus', Ophiobolus, spelling error for trichisporus

umbelliferarum, Linocarpon, syn. of Plagiosphaera umbelliferarum
umbelliferarum, Plagiosphaera, see also under Ophioceras leptosporum
Urohendersoniella, see under Ophiosphaerella herpotricha

vagans, Phaeosphaeria, see under Ophiosphaerella
verminosa, Rhaphidophora, see under Ophiobolus verminosus
verminosa, Sphaeria, see under Ophiobolus verminosus
verminosum, Linocarpon, see under Ophiobolus verminosus
verminosus, Ophiobolus
versisporum, Linocarpon
versisporus, Ophiobolus, syn. of Linocarpon versisporum
verrucosa, Phialophora, type species of Phialophora

williamsii, Linocarpon, syn. of Ophiosphaerella williamsii
williamsii, Ophiosphaerella
Winterella, see also under Plagiosphaera platensis

Ypsilonia, see under Acanthotheciella

'zeae, Cochliobolus', see under Ophiobolus zeae
zeae, Ophiobolus, syn. of Ophiosphaerella herpotricha
zeae, Ophioceras, exact identity unknown

HOST AND SUBSTRATE INDEX

The hosts are listed in alphabetical order under families and the fungi recorded on each species noted. The list includes all specimens examined and also host-parasite associations noted in the literature when these are mentioned in the text. These literature records are marked (L) and, as specimens have not been seen, their accuracy cannot be verified here. The name 'Ophiobolus graminis' in the list refers to unplaced specimens listed under Gaeumannomyces or to literature records of take-all where the variety of G. graminis cannot be determined.

ARALIACEAE
  Heptapleurum venulosum
    Acrospermum parasiticum (L)
AVICENNIACEAE
  Avicennia sp.
    Ophiobolus australiensis (L)
CAPRIFOLIACEAE
  Lonicera quinquelocularis
    Plagiosphaera bhargavai (L)
COMPOSITAE
  Artemisia austriaca
    Leptosphaeria compressa
  Cirsium arvense
    Ophiobolus acuminatus
  Erechtites prenanthoides
    Leptospora rubella
  Erigeron sp.
    Leptosphaeria compressa
CYPERACEAE
  Carex acutiformis
    Acanthophiobolus helicosporus
    Gaeumannomyces caricis
    Gaeumannomyces tax.sp.1
  Carex elata
    Acanthophiobolus helicosporus
    Sclerotia and lobed hyphopodia
  Carex paniculata
    Acanthophiobolus helicosporus
    Gaeumannomyces caricis
  Carex pendula
    Acanthophiobolus helicosporus
    'Sphaeria eucrypta' (L)
  Carex pseudocyperus
    Gaeumannomyces tax. sp.1
  Carex riparia
    Acanthophiobolus helicosporus
    Gaeumannomyces tax. sp.1
  Carex vesicaria
    Leptosphaeria paludosa (L)
  Carex sp. (aff. C.bichenoviana)
    Sclerotia and lobed hyphopodia

Carex sp.
Gaeumannomyces tax. sp.1
Carpha schoenoides
Sphaerulina antarctica
Cladium mariscus
Acanthophiobolus helicosporus
Ophiochaeta cladii (L)
Lepidosperma sp.
Acanthophiobolus helicosporus
Scirpus lacustris
Sphaeria culmorum Wallr. (L)
Scirpus sp.
Ophiosphaerella leptosperma
Undetermined
Acanthophiobolus helicosporus
Gaeumannomyces tax. sp. 3

FAGACEAE
Quercus glauca
Plagiosphaera sp. (L)
Quercus salicina
Plagiosphaera quercicola (L)

GRAMINEAE
Agropyron scabrum
'Ophiobolus graminis'
Agrostis palustris
Gaeumannomyces graminis var. avenae
Agrostis stolonifera
Gaeumannomyces graminis var. avenae
Agrostis tenuis
Gaeumannomyces graminis var. avenae
Phialophora graminicola
Agrostis sp.
Gaeumannomyces graminis var. avenae
Ammophila arenaria
Ophiobolus trichellus (L)
Plejobolus arenarius (L)
Andropogon muricatus
see under Vetiveria zizanioides
Andropogon sp.
Leptospora implexa (L)
Aristida sp.
Gaeumannomyces graminis var. graminis
Avena byzantina
Gaeumannomyces graminis var. tritici
Avena fatua
Gaeumannomyces graminis var. tritici
Avena sativa
Gaeumannomyces graminis var. avenae
Gaeumannomyces graminis var. graminis
Gaeumannomyces graminis var. tritici
'Axonopus africanus'
Ophiosphaerella herpotricha
Axonopus compressus
Gaeumannomyces graminis var. graminis
Axonopus sp.
Gaeumannomyces graminis var. graminis
Bromus inermis
Ophiosphaerella herpotricha
Bromus sterilis
Gaeumannomyces graminis var. tritici
Bromus unioloides
Gaeumannomyces graminis var. graminis
Lophodermium gramineum
Phialophora graminicola
Bromus vulgaris
Gaeumannomyces graminis var. tritici
'Ophiobolus graminis'
Calamagrostis neglecta
Ophiosphaerella erikssonii
Chloris gayana
Gaeumannomyces graminis var. graminis
Ophiosphaerella herpotricha (immature)
Chrysopogon sp.
Ophiosphaerella sp.
Cynodon dactylon
Gaeumannomyces graminis var. graminis
Ophiobolus sp. (L)
Deschampsia bottnica
Gaeumannomyces graminis var. avenae
Deschampsia danthonioides
Gaeumannomyces graminis var. avenae
'Ophiobolus graminis'
Echinochloa crus-galli
Ophiosphaerella herpotricha
Elymus sp.
Lophodermium alpinum (L)
Festuca purpurascens
Lophodermium magellanicum

Festuca subulata
'Ophiobolus graminis'
Festuca sp.
Lophodermium alpinum (L)
Glyceria maxima
Acanthophiobolus helicosporus
Lejosphaerella
'Ophiobolus graminis'
Glyceria spectabilis
Acanthophiobolus helicosporus (L)
Holcus sp.
Gaeumannomyces graminis var. avenae
Hordeum vulgare
Gaeumannomyces graminis var. tritici
Microdochium bolleyi (L)
'Ophiobolus graminis'
Phialophora sp. (lobed hyphopodia)
Leptochloa virgata
Ophiosphaerella graminicola
Lolium perenne
Phialophora graminicola
Microlaena stipoides
Gaeumannomyces graminis var. graminis
Molinia japonica
Gaeumannomyces graminis var. graminis
Nardus stricta
Lophodermium alpinum (L)
Oryza sativa
Cochliobolus sp.
Gaeumannomyces graminis var. graminis
Gaeumannomyces graminis var. tritici
'Ophiobolus graminis'
Ophiobolus sp. (L)
Ophiosphaerella herpotricha
Pyrenochaeta oryzae
Sclerotia undet.
Sphaeropsidales undet.
Panicum curtisii
'Ophiobolus graminis'
Panicum maximum
Leptospora implexa
Paspalidium geminatum
'Ophiobolus graminis'
Paspalidium sp.
Gaeumannomyces graminis var. graminis
Pennisetum americanum
'Ophiobolus graminis'
Pennisetum clandestinum
Gaeumannomyces graminis var. graminis
Phalaris aquatica
'Ophiobolus graminis'
Phalaris arundinacea
Leptosphaeria paludosa (L)
Phalaris minor
'Ophiobolus graminis'
Phalaris sp.
Gaeumannomyces graminis var. graminis
Phragmites australis
Acanthophiobolus helicosporus
Poa aquatica
see Glyceria maxima
Poa pratensis
Dinemasporium graminum
'Ophiobolus graminis'
Phaeosphaeria herpotrichoides
Psamma arenaria
see Ammophila arenaria
Pucciniella sp.
Lophodermium alpinum (L)
Saccharum spontaneum
Ophiobolus spirosporus
Sasa kurilensis
Plagiosphaera muroiana
Secale cereale
Phialophora sp.(lobed hyphopodia)
Sorghum halepense
Leptospora implexa
'Ophiobolus graminis' (L)
Sorghum vulgare
'Ophiobolus graminis (L)
Ophiobolus leptosporus (L)
Ophioceras sorghi (L)
Spartina sp.
Lulworthia medusae
Stipa aristiglumis
Gaeumannomyces graminis var. graminis
Stipa dregeana
Meliola panici
Ophiobolus stipae
Stipa sp.
Ophiosphaerella stipae
Trisetum cernuum
'Ophiobolus graminis'
Triticum aestivum
Gaeumannomyces cylindrosporus
Gaeumannomyces graminis var. avenae
Gaeumannomyces graminis var. graminis

Gaeumannomyces graminis
var. tritici
'Ophiobolus graminis'
Phialophora graminicola (L)
Wojnowicia graminis
Vetiveria zizanioides
Ophiobolus andropogonis (L)
Ophiobolus medusae var.
minor (L)
Ophiobolus tortilis (L)
Ophiosphaerella herpotricha
Vulpia bromoides
'Ophiobolus graminis'
Zea mays
'Ophiobolus graminis' (L)
Ophioceras zeae (L)
Ophiosphaerella herpotricha
Phaeosphaeria sp.
Phialophora radicicola Cain
Phialophora sp. (lobed
hyphopodia)
Pithomyces aff. maydicus
Zizania aquatica
Gaeumannomyces graminis
var. graminis
Zostera marina
Lulworthia halima (L)
Gramineae (Cynodon or Agropyron)
Gaeumannomyces graminis
var. graminis
Undetermined Gramineae
Leptospora rubella
Lidophia graminis
Mycosphaerella sp.
'Ophiobolus graminis'
Ophiosphaerella herpotricha
Ophiosphaerella williamsii
Paraphaeosphaeria michotii
Phialophora graminicola
Phialophora spp.
Pleospora sp.

GROSSULARIACEAE
Ribes sp.
Ophiochaeta incompta (L)

IRIDACEAE
Iris foetidissima
Plagiosphaera sp.
Iris pseud'acorus
Acanthophiobolus helicosporus

JUNCACEAE
'Juncus laevis'
Sphaeria culmorum Wallr. (L)
Juncus subnodulosus
Acanthophiobolus helicosporus
Juncus sp.
Ophiobolus junci (L)

ORCHIDACEAE
Liparis liliiflora
Cylindrina delavayi

PALMAE
Elaeis guineensis
Linocarpon cajani (L)
Linocarpon elaeidis
Livistona sp.
Ophiobolus livistonae
Mauritia flexuosa
Ophiobolus oedema
Sabal spp.
Linocarpon palmetto (L)
Ophiobolus versisporus (L)
Undetermined
Ophiobolus licualae (L)
Ophiobolus nipae (L)
Ophiobolus verminosus (L)

PANDANACEAE
Pandanus laevis
Linocarpon pandani
Pandanus sabotan
Linocarpon pandani
Pandanus utilissimus
Linocarpon pandani

PAPILIONACEAE
Cajanus cajan
Linocarpon cajani
Glycine max
Gaeumannomyces graminis
var. graminis

PHYTOLACCACEAE
Phytolacca dioica
Plagiosphaera platensis

RANUNCULACEAE
Aconitum napellus
Plagiosphaera immersa

SALICACEAE
Salix sp.
Linospora capreae (L)

TYPHACEAE
Typha latifolia
Gaeumannomyces graminis
var. graminis (L)

UMBELLIFERAE
  Heracleum lanatum
    Plagiosphaera umbelliferarum
  Undetermined
    Ophioceras leptosporum

URTICACEAE
  Urtica dioica
    Plagiosphaera immersa

ZINGIBERACEAE
  Amomum sp.
    Schizacrospermum filiforme

Dead scale insects on branches
  Acanthotheciella barbata

Bark
  Microstelium hyalinum

Cloth
  Acanthophiobolus helicosporus

Leaves, waterlogged
  Ophioceras leptosporum

Stems, herbaceous
  Sphaeria penicillus

Wood, waterlogged
  Ophioceras dolichostomum (L)

ACKNOWLEDGEMENTS

The help of all the people and institutions who contributed to this work is gratefully acknowledged. Special thanks are given to the curators of the following herbaria who lent many specimens, searched for others, provided working space in some cases and often traced references: ADW, B, BPI, BRIP, C, CBS, CO, DAOM, E, FH, ILLS, IMI, K, L, LPS, M, NSW, NY, PAD, PC, PNG, PR, S, TNS, TRTC, UPS, VPRI, W, WSP and YAM. Many cultures and some specimens were also provided by Drs. J.W. Deacon (Edinburgh), D. Hornby (Rothamsted), D. Huber (West Lafayette), G.C. MacNish (Perth), K.W. Roy (West Lafayette), D.E. Shaw (Brisbane), K. Sivasithamparam (Perth), J.P. Skou (Roskilde), P.T.W. Wong (Tamworth) and J. Yeates (Perth). Miss C. Nuzum (DAR) assisted with cultural and inoculation studies. I am especially grateful to the following who discussed (often in voluminous correspondence) various aspects of the work or gave detailed advice on particular points: Drs. J.W. Deacon, R.W.G. Dennis (K), O. Eriksson (Umeå), J.M. Hirst (Long Ashton), L. Holm (UPS), D. Hornby, W.E. McKeen (London, Ont.), D. Reid (K), P.R. Scott (Cambridge), D.E. Shaw (Brisbane), D.F. Wadsworth (Oklahoma) and J. Webster (Exeter). Drs. M.J.C. Asher (Roslin) and P.J. Shipton (Aberdeen), as editors of the take-all book, have helped with editorial advice on material to be included. Dr. Margaret Barr Bigelow (MASS) and Dr. C. Booth (IMI) kindly refereed the paper before publication. Finally, I must thank Mrs. A. Adams and Mrs. D. Crompton for the long and exacting job of typing the drafts and final copy.

REFERENCES

Ainsworth, G.C. 1971. Ainsworth and Bisby's Dictionary of the Fungi. 6th Ed. x + 663 pp. Commonwealth Mycological Institute, Kew.

Arnaud, G. 1912. Contribution à l'étude des Fumagines (Troisième Partie). Annales de l'Ecole nationale d'Agriculture de Montpellier (N.S.) 12, 23-54.

Arnaud, G. 1918. Les Astérinées. Annales de l'Ecole nationale d'agriculture de Montpellier (N.S.) 16, 288 pp.

Arx, J.A.von 1979. Ascomycetes as Fungi Imperfecti, Chapter 13, pp.201-213, in Kendrick, B. (Ed.). The Whole Fungus, Vol.1, Proceedings of the Second International Mycological Conference, Kananaskis. National Museums of Canada, Ottawa.

Arx, J.A. von & Müller,E. 1975. A re-evaluation of the bitunicate Ascomycetes with keys to families and genera. Studies in Mycology (Baarn) No.9, 159 pp.

Arx, J.A.von & Olivier, D.L. 1952. The taxonomy of Ophiobolus graminis Sacc. Transactions of the British Mycological Society 35, 29-33.

Asher, M.J.C. & Shipton, P.J. (Eds.) 1980. Biology and Control of Take-all. Academic Press, London (in the press)

Ballantyne, B.J. 1975. Powdery mildew on Cucurbitaceae : identity, distribution, host range and sources of resistance. Proceedings of the Linnean Society of New South Wales 99, 100-120.

Barr, M.E. 1961. Northern Pyrenomycetes. II. Gaspesian Park. Canadian Journal of Botany 39, 307-325.

Barr, M.E. 1967. Northern Pyrenomycetes.III. Western species. Canadian Journal of Botany 45, 1041-1046.

Barr, M.E. 1972. Preliminary studies on the Dothideales in temperate North America. Contributions from the University of Michigan Herbarium 9 (8), 523-638.

Barr, M.E. 1976a. Perspectives in the Ascomycotina. Memoirs of the New York Botanical Garden 28, 1-8.

Barr, M.E. 1976b. Buergenerula and the Physosporeliaceae. Mycologia 68, 611-621.

Barr, M.E. 1978. The Diaporthales in North America with emphasis on Gnomonia and its segregates. Mycological Society of America Mycological Memoir No.7, 232 pp. J. Cramer, Lehre.

Bartholomew, J. and Son Ltd. 1943 (reprinted 1966). Gazetteer of the British Isles 9th Ed. xxxii + 763 pp. J. Bartholomew & Son, Edinburgh.

Berkeley, M.J. & Broome, C.E. 1852. Notices of British fungi. Annals and Magazine of Natural History, ser.2, 9, 377-387.

Berkeley, M.J. & Broome, C.E. 1861. Notices of British fungi. Annals and Magazine of Natural History, ser.3, 7, 449-456.

Berlese, A.N. 1892. Descrizione di alcuni nuovi generi di Pirenomiceti. Reprint from Atti del Congresso Botanico Internazionale 1892, pp. 1-10, dated August 1892.

Berlese, A.N. 1890-1900. Icones fungorum omnium hucusque cognitorum ad usum Sylloges Saccardianae adcommodatae. Vols.1 (1890-1894) and 2 (1895-1900). Publication dates of the relevant pages cited in the text are taken from Stafleu & Cowan (1976).

Bolay, A. 1971. Contribution à la connaissance de Gnomonia comari Karsten. Étude taxonomique, phytopathologique et recherches sur sa croissance in vitro. Berichte der Schweizerischen Botanischen Gesellschaft 81, 398-482.

Butler, F.C. 1961. Root and foot rot diseases of wheat. New South Wales Department of Agriculture Science Bulletin No.77, 98 pp. Government Printer, Sydney.

Cain, R.F. 1952. Studies of Fungi Imperfecti. I. Phialophora. Canadian Journal of Botany 30, 338-343.

Carroll, G.C. & Munk, A. 1964. Studies on lignicolous Sordariaceae. Mycologia 56, 77-98.

Cash, E.K. 1972. Saccardo's Sylloge fungorum omnium hucusque cognitorum. Vol.26, Supplementum universale Part II, ix + 1563 pp. Johnson Reprint Corporation, New York.

Chesters, C.G.C. & Bell, A. 1970. Studies in the Lophiostomataceae Sacc. C.M.I. Mycological Paper No.120, 55 pp.

Clare, B.C. 1964. Erysiphaceae of south-eastern Queensland. University of Queensland Department of Botany Papers 4 (10), 111-144.

Clements, F.E. & Shear, C.L. 1931. The genera of fungi. iv + 496 pp. The H.W. Wilson Company, New York.

Conway, K.E. & Barr, M.E. 1977. Classification of Ophioceras dolichostomum. Mycotaxon 5, 376-380.

Cooke, M.C. 1889. Synopsis Pyrenomycetum. Grevillea 18 (85), 13-17.

Cribb, A.B. & Cribb, J.W. 1955. Marine fungi from Queensland. I. University of Queensland Department of Botany Papers 3 (10),77-81.

Crouan, P.L. & Crouan, H.M. 1867. Florule du Finistère contenant les descriptions de 360 espèces nouvelles de sporogames. F.Klincksieck, Paris and J.B. & A. Lefournier, Brest.

Cruchet, D. 1923. Recherches mycologiques à Montagny et aux environs d'Yverdon. Bulletin de la société vaudoise des sciences naturelles 55, 155-177 (original not seen; from Müller, 1952).

Darker, G.D. 1967. A revision of the genera of the Hypodermataceae. Canadian Journal of Botany 45, 1399-1444.

Davies, D.L.G. 1950. Ophiobolus graminis Sacc.var.avenae E.M.Turner in mid-Wales in 1948. Transactions of the British Mycological Society 33, 352-353.

Deacon, J.W. 1973. Phialophora radicicola and Gaeumannomyces graminis on roots of grasses and cereals. Transactions of the British Mycological Society 61, 471-485.

Deacon, J.W. 1974a. Interactions between varieties of Gaeumannomyces graminis and Phialophora radicicola on roots, stem bases and rhizomes of the Gramineae. Plant Pathology 23, 85-92.

Deacon, J.W. 1974b. Further studies on Phialophora radicicola and Gaeumannomyces graminis on roots and stem bases of grasses and cereals. Transactions of the British Mycological Society 63, 307-327.

Deacon, J.W. 1980. Ecological relationships with other fungi: competitors and hyperparasites. Chapter in Asher & Shipton (1980).

Dennis, R.W.G. 1944. Occurrence of Ophiobolus graminis var. avenae on wheat crops in the field. Annals of applied Biology 31, 100-101.

Dennis, R.W.G. 1960. British cup fungi and their allies. An introduction to the Ascomycetes. Ray Society, London.

Dennis, R.W.G. 1968. British Ascomycetes. xxxii + 455 pp. J. Cramer, Lehre.

Dennis, R.W.G. 1975. New or interesting British microfungi, III. Kew Bulletin 30, 345-365.

Deverall, B.J., Wong, P.T.W. & McLeod, S. 1979. Failure to implicate antifungal substances in cross-protection of wheat against take-all. Transactions of the British Mycological Society 72, 233-236.

Dodman, R.L., Barker, K.R. & Walker, J.C. 1968a. Modes of penetration by different isolates of Rhizoctonia solani. Phytopathology 58, 31-33.

Dodman, R.L., Barker, K.R. & Walker, J.C. 1968b. A detailed study of the different modes of penetration by Rhizoctonia solani. Phytopathology 58, 1271-1276.

Doidge, E.M. 1941. South African Ascomycetes in the National Herbarium. Bothalia 4, 193-217.

Doidge, E.M. 1950. The South African fungi and lichens to the end of 1945. Bothalia 5, 1-1094.

Drechsler, C. 1934. Phytopathological and taxonomic aspects of Ophiobolus, Pyrenophora, Helminthosporium and a new genus Cochliobolus. Phytopathology 24, 953-983.

Ellis, J.B. & Everhart, B.M. 1887. New species of fungi. Journal of Mycology 3, 41-45.

Ellis, J.B. & Everhart, B.M. 1888. New species of fungi from various localities. Journal of Mycology 4, 73-81.

Ellis, J.B. & Everhart, B.M. 1890. New North American fungi. Proceedings of the Academy of Natural Sciences of Philadelphia 1890, 219-249.

Ellis, J.B. & Everhart, B.M. 1892. The North American Pyrenomycetes. iii + 793 pp. Ellis & Everhart, Newfield.

Ellis, J.B. & Everhart, B.M. 1894. New species of fungi from various localities. Proceedings of the Academy of Natural Sciences of Philadelphia 1893, 440-466 (publ. April, 1894).

Ellis, J.B. & Martin, G. 1885. New Florida fungi. Journal of Mycology 1, 97-101.

Ellis, M.B. 1971. Dematiaceous Hyphomycetes. 608 pp. Commonwealth Mycological Institute, Kew.

Ellis, M.B. 1976. More Dematiaceous Hyphomycetes. 507 pp. Commonwealth Mycological Institute, Kew.

Emmett, R.W. & Parbery, D.G. 1975. Appressoria. Annual Review of Phytopathology 13, 147-167.

Eriksson, O. 1967. On graminicolous Pyrenomycetes from Fennoscandia. 2. Phragmosporous and scolecosporous species. Arkiv för Botanik Ser.2, 6 (9), 381-440 (see also Studies on graminicolous Pyrenomycetes from Fennoscandia, Acta Universitatis Upsaliensis, Abstracts of Uppsala Dissertations in Science No.88).

Farr, M.L. 1973. An annotated list of Spegazzini's fungus taxa. 2 Vols. Bibliotheca Mycologica No.35, J. Cramer, Lehre.

Feltgen, J. 1901. Vorstudien zu einer Pilzflora des Grossherzogthums Luxemburg. Nachträge II, 243 pp. (original not seen; from Lindau & Sydow, 1908).

Ferdinandsen, C.C.F. & Winge, O. 1909. Mycological notes II. Botanisk Tidsskrift 29, 305-319 (original not seen; from Lindau & Sydow, 1908 and Shoemaker, 1976).

Fitzpatrick, H.M., Thomas, H.E. & Kirby, R.S. 1922. The Ophiobolus causing take-all of wheat. Mycologia 14, 30-37.

Foëx, E. 1935. Quelques observations sur les maladies du pied des céréales. Compte rendu hebdomadaire des séances de l'Académie d'Agriculture de France 21, 501-505.

Foëx, E. & Rosella, E. 1934. Étude sur les pietins des céréales. Compte rendu hebdomadaire des séances de l'Académie d'Agriculture de France 20, 480-483.

Fries, E. 1823. Systema mycologicum 2, 275-620.

Fuckel, L. 1870. Symbolae mycologicae. Beiträge zur Kenntniss der rheinischen Pilze. Jahrbücher des Nassauischen Vereins für Naturkunde 23-24, 1-459.

Garrett, S.D. & Dennis, R.W.G. 1943. Note on the occurrence of Ophiobolus graminis Sacc. var. avenae E.M. Turner in Scotland in 1942. Transactions of the British Mycological Society 26, 146-147.

Goos, R.D. & Gessner, R.V. 1975. Hyphal modifications of Sphaerulina pedicellata: appressoria or hyphopodia? Mycologia 67, 1035-1038.

Hansford, C.G. 1954. Australian fungi II. New records and revisions. Proceedings of the Linnean Society of New South Wales 79, 97-141.

Hansford, C.G. 1961. The Meliolineae. A monograph. Sydowia, Beiheft 2, 806 pp.

Hansford, C.G. 1963. Iconographia Meliolinearum. Sydowia, Beiheft 5, 1814 illustrations.

Harris, E., Pyne, C.T. & Fatmi, A.S. 1962. In Annual Report Research and Specialist Services Ministry of Agriculture Northern Nigeria 1961-1962, pp.16-20.

Hedjaroude, G.-A. 1969. Études taxonomiques sur les Phaeosphaeria Miyake et leurs formes voisines (Ascomycètes). Sydowia 22 (1968), 57-107.

Hino, I. & Katumoto, K. 1966. Notes on bambusicolous fungi (2). Journal of Japanese Botany 41, 292-297.

Höhnel, F.von 1907. Fragmente zur Mykologie (IV. Mitteilung, Nr. 156 bis 168). Sitzungsberichte der kaiserlichen Akademie der Wissenschaft in Wien. Mathematisch-naturwissenschaftliche Klasse,116, 615-647.

Höhnel, F. von 1911. Fragmente zur Mykologie (XIII. Mitteilung, Nr.642 bis 718). Sitzungsberichte der kaiserlichen Akademie der Wissenschaft in Wien. Mathematisch-naturwissenschaftliche Klasse, 120, 379-484.

Höhnel, F. von 1920. Fragmente zur Mykologie (XXIV. Mitteilung, Nr. 1189 bis 1214). Sitzungsberichte der kaiserlichen Akademie der Wissenschaft in Wien. Mathematisch —naturwissenschaftliche Klasse, 129, 137-184.

Holm, L. 1948. Taxonomical notes on Ascomycetes. I. The Swedish species of the genus Ophiobolus Riess sensu Sacc. Svensk botanisk tidskrift 42, 337-347.

Holm, L. 1957. Études taxonomiques sur les Pléosporacées. Symbolae botanicae upsalienses 14 (3), 1-188.

Holmgren, P.K. & Keuken, W. 1974. Index Herbariorum. Part 1. The herbaria of the world. vii + 397 pp. International Bureau for Plant Taxonomy and Nomenclature, Utrecht.

Holmgren, P.K. & Keuken, W. 1976. Additions to 'The herbaria of the world' ed. 6. Taxon 25, 517-524.

Holmgren, P.K. & Keuken, W. 1977. Additions to 'The herbaria of the world' ed. 6 (II). Taxon 26, 483-491.

Holmgren, P.K. & Keuken, W. 1978. Additions to 'The herbaria of the world' ed. 6 (III). Taxon 27, 427-432.

Homma, Y. 1937. Erysiphaceae of Japan. Journal of the Faculty of Agriculture Hokkaido University 38, 183-461.

Hornby, D., Henden, D.R. & den Toom, A. 1979. Gaeumannomyces-Phialophora complex: isolates from a site with little take-all, in Rothamsted Experimental Station Report for 1978, Part 1, 213-214.

Hornby, D., Slope, D.B., Gutteridge, R.J. & Sivanesan, A. 1977. Gaeumannomyces cylindrosporus, a new Ascomycete from cereal roots. Transactions of the British Mycological Society 69, 21-25.

Hughes, S.J. 1978. New Zealand fungi 25. Miscellaneous species. New Zealand Journal of Botany 16, 311-370.

Iqbal, S.H. 1972. Gaeumannomyces leptosporus, a new aquatic ascomycete. Transactions of the British Mycological Society 58, 346-348.

Jones, S.G. 1926. The development of the perithecium of Ophiobolus graminis, Sacc. Annals of Botany 40, 607-629.

Kirby, R.S. 1925. The take-all disease of cereals and grasses caused by Ophiobolus cariceti (Berkeley & Broome) Saccardo. Memoirs of the Cornell University Agricultural Experiment Station No.88, 1-45.

Kirschstein, W. 1907. Neue märkische Ascomyceten. Verhandlungen des Botanischen Vereins der Provinz Brandenburg 48 (1906), 39-61.

Kirschstein, W. 1936. Beiträge zur Kenntnis der Ascomyceten und ihrer Nebenformen besonders aus der Mark Brandenburg und dem Bayerischen Walde. Annales Mycologici 34, 180-210.

Kobayashi, T. 1970. Taxonomic studies of Japanese Diaporthaceae with special reference to their life histories. Bulletin of the Government Forest Experiment Station (Tokyo) No.226, 242 pp.

Kobayashi, T. 1976. New fungi parasitic to woody plants in Yakii Island. Memoirs of the National Science Museum Tokyo 9, 85-94.

Kohlmeyer, J. 1972. A revision of Halosphaeriaceae. Canadian Journal of Botany 50, 1951-1963.

Kohlmeyer, J. & Gessner, R.V. 1976. Buergenerula spartinae sp. nov., an Ascomycete from salt marsh cordgrass, Spartina alterniflora. Canadian Journal of Botany 54, 1759-1766.

Krause, R.A. & Webster, R.K. 1972. The morphology, taxonomy, and sexuality of the rice stem rot fungus, Magnaporthe salvinii (Leptosphaeria salvinii). Mycologia 64, 103-114.

Larsen, P. 1952. Studies in Danish Pyrenomycetes. Dansk Botanisk Arkiv 14 (7), 1-61.

Lindau, G. & Sydow, P. 1908-1917. Thesaurus litteraturae mycologicae et lichenologicae. Vols.1 (1908), 2 (1909), 3 (1913), 4 (1915) and 5 (1917). Borntraeger Bros., Leipzig.

Lundell, S. & Nannfeldt, J.A. 1953. Fungi exsiccati Suecici, praesertim Upsalienses, Fasc. XLIII-XLIV (nr.2101-2200). Almquist and Wiksells, Uppsala.

Luttrell, E.S. 1973. Loculoascomycetes. In The Fungi. An advanced Treatise (Ainsworth, G.C., Sparrow, F.K. & Sussman, A.S., eds.), Vol. 4A, Chapter 7, 135-219.

McKeen, W.E. 1952. Phialophora radicicola Cain, a corn rootrot pathogen. Canadian Journal of Botany 30, 344-347.

Malbranche, A. & Niel, E. 1890. Essai monographique sur les Ophiobolus observés en Normandie. Bulletin de la Société des Amis des Sciences Naturelles de Rouen 1890, 47-61.

Mangin, L. 1899. Contribution à l'étude de quelques parasites du blé. Oversigt over det Kongelige Danske Videnskabernes Selskabs fordhandlinger 1899, pp.213-272.

Meyers, S.P. 1957. Taxonomy of marine Pyrenomycetes. Mycologia 49, 475-528.

Miller, J.H. & Burton, G. 1942. Georgia Pyrenomycetes. Mycologia 34, 1-7.

Miyake, I. 1909. Studies on the parasitic fungi of rice in Japan. Botanical Magazine (Tokyo) 23 (266), 85-97 (Japanese)

Montagne, J.F.C. 1856. Sylloge generum specierumque Cryptogamarum. xxiv + 498 pp. J.-B. Baillière, Paris.

Mounce, I. & Diehl, W.W. 1934. A new Ophiobolus on eelgrass. Canadian Journal of Research 11, 242-246.

Müller, E. 1950. Die schweizerischen Arten der Gattung Leptosphaeria und ihrer Verwandten. Sydowia 4, 185-319.

Müller, E. 1952. Die schweizerischen Arten der Gattung Ophiobolus Riess. Bericht der Schweizerischen Botanischen Gesellschaft 62, 307-339.

Müller, E. & Arx, J.A. von 1973. Pyrenomycetes: Meliolales, Coronophorales, Sphaeriales. In The Fungi. An Advanced Treatise (Ainsworth, G.A., Sparrow, F.K. & Sussman, A.S., eds.). Vol. 4A, Chapter 6, 87-132.

Munk, A. 1953a. The system of the Pyrenomycetes. A contribution to a natural classification of the group Sphaeriales sensu Lindau. Dansk Botanisk Arkiv 15 (2), 1-163.

Munk, A. 1953b. The system of the Pyrenomycetes. A contribution to a natural classification of the group Sphaeriales sensu Lindau. Additions and corrections. Botanisk Tidsskrift 50, 86-90.

Munk, A. 1957. Danish Pyrenomycetes. A preliminary flora. Dansk Botanisk Arkiv 17 (1), 1-491.

Mussat, E. 1901. Synonymia generum, specierum subspecierumque in Vol. I-XIV descriptorum. Sylloge fungorum 15, viii + 455 pp.

Nag Raj, T.R. 1977. Ypsilonia, Acanthotheciella, and Kazulia gen. nov. Canadian Journal of Botany 55, 1599-1622.

Niessl, G. von 1876. Notizen über neue und kritische Pyrenomyceten. Verhandlungen des Naturforschenden Vereins in Brünn 14, 165-218.

Nilsson, H.E. 1969. Studies of root and foot rot diseases of cereals and grasses. I. On resistance to Ophiobolus graminis Sacc. Annals of the Agricultural College of Sweden 35, 275-807.

Nilsson, H.E. 1972. The occurrence of lobed hyphopodia on an isolate of the take-all fungus, 'Ophiobolus graminis Sacc.', on wheat in Sweden. Swedish Journal of Agricultural Research 2, 105-118.

Nilsson, H.E. & Drew Smith, J. 1980. Take-all of grasses. Chapter in Asher & Shipton (1980).

Ou, S.H. 1972. Rice diseases. xix + 368 pp. Commonwealth Mycological Institute, Kew.

Padwick, G.W. 1950. Manual of rice diseases. viii + 198 pp. Commonwealth Mycological Institute, Kew.

Parbery, D.G. & Emmett, R.W. 1977. Hypotheses regarding appressoria, spores, survival and phylogeny in parasitic fungi. Revue de Mycologie 41, 429-447.

Patouillard, N. & Gaillard, A. 1888. Champignons du Vénézuéla et principalement de la région du Haut-Orénoque, récoltés en 1887 par M.A. Gaillard II. Bulletin de la Société Mycologique de France 4, 92-129.

Penzig, O. & Saccardo, P.A. 1897. Diagnoses fungorum novorum in insula Java collectorum. Ser. 1. Malpighia 11, 387-409 (original not seen; from Lindau & Sydow, 1909).

Petrak, F. 1921. Mykologische Notizen. II. Annales Mycologici 19, 17-128.

Petrak, F. 1924. Mykologische Notizen. VII. Annales Mycologici 22, 1-182.

Petrak, F. 1941. Mykologische Notizen. XIV. Annales Mycologici 39, 251-349.

Petrak, F. 1952. Über die Gattungen Gaeumannomyces v. Arx et Olivier, Halophiobolus Linder und Linocarpon Syd. Sydowia 6, 383-388.

Petrak, F. 1957. Mykologische Bemerkungen. Sydowia 10 (1956), 296-305.

Petrak, F. 1960. Ergebnisse einer Revision der Grundtypen verschiedener Gattungen der Askomyzeten and Fungi Imperfecti. Sydowia 14, 347-354.

Petrak, F. & Deighton, F.C. 1952. Beiträge zur Pilzflora von Sierra Leone. Sydowia 6, 309-322.

Petrak, F. & Sydow, H. 1936. Kritisch-systematische Originaluntersuchungen über Pyrenomyzeten, Sphaeropsideen and Melanconieen. Annales Mycologici 34, 11-52.

Pirozynski, K.A. 1972. Microfungi of Tanzania. I. Miscellaneous fungi on oil palm. II. New Hyphomycetes. C.M.I. Mycological Paper No. 129, 64 pp.

Rehm, H. 1881. Ascomyceten. Fasc. I-XI. Bericht des naturhistorischen Vereins in Augsburg 26, 1-132 (original not seen; from Holm,1957).
Rehm, H. 1882. Beiträge zur Ascomyceten - Flora der deutschen Alpen und Voralpen. Hedwigia 21, 113-123.
Rehm, H. 1916. Ascomycetes Philippinenses - VIII. Leaflets of Philippine Botany 8, 2935-2961.
Riess, H. 1854. Neue Kernpilze. Hedwigia 1, 25-28.
Roumeguère, C. & Saccardo, P.A. 1881. Reliquiae mycologicae Libertianae, Series altera (1). Revue mycologique 3, 39-59.
Roy, K.W., Abney, T.S. & Huber, D.M. 1976. Isolation of Gaeumannomyces graminis var. graminis from soybeans in the midwest. Proceedings of the American Phytopathological Society 3, 284 (abs.378).
Russell, R.C. 1934. Studies of take-all and its causal organism, Ophiobolus graminis Sacc. Dominion of Canada Department of Agriculture Bulletin No.170 (N.S.), 64 pp. J.O. Patenaude, Ottawa.
Saccardo, P.A. 1875. Fungi veneti novi vel critici. Ser.II. Nuovo giornale botanico italiano 7, 299-329.
Saccardo, P.A. 1878. Fungi novi ex herbario Professoris Doct.P. Magnus Beroliensis. Michelia 1 (2), 117-132.
Saccardo, P.A. 1883-1899. Sylloge fungorum omnium hucusque cognitorum. Vols. 2 to 14 inclusive (dates for individual volumes given in text).
Saccardo, P.A. 1916. Notae mycologicae: XX. Nuovo giornale botanico italiano (N.S.), 23, 185-234.
Saccardo, P.A. & Saccardo, D. 1905. Sylloge fungorum omnium hucusque cognitorum 17, cvii + 991 pp. R. Friedländer & Son, Berlin.
Saccas. A.M. 1951. A propos de quelques champignons nouveaux parasites et saprophytes sur maïs. Revue de Pathologie végétale et d'Entomologie agricole de France 30, 161-196.
Saccas, A.M. 1954. Les champignons parasites des sorghos (Sorghum vulgare) et des pénicillaires (Pennisetum typhoideum) en Afrique Equatoriale Francaise. L'Agronomie Tropicale 9, 135-173, 263-301, 647-686.
Saccas, A.M. & Fernier, H. 1954. Une grave maladie du riz due à Ophiobolus oryzinus Sacc. L'Agronomie Tropicale 9, 7-20.
Savile, D.B.O. 1959. The botany of Somerset Island, District of Franklin. Canadian Journal of Botany 37, 959-1002.
Sawada, K. 1959. Descriptive Catalogue of Taiwan (Formosan) Fungi, Part XI, i + 268 pp. National Taiwan University, Taipei.
Schrantz, J.P. 1961. Recherches sur les Pyrénomycètes de l'ordre des Diatrypales, sensu M. Chadefaud, 1957. Bulletin trimestriel de la Société Mycologique de France 76 (1960), 305-407.
Scott, P.R. 1970. Phialophora radicicola, an avirulent parasite of wheat and grass roots. Transactions of the British Mycological Society 55, 163-167.
Shaw, D.E. 1977. Gaeumannomyces leptosporus in Papua New Guinea. Papua New Guinea Agricultural Journal 28, 33-38.
Sherwood, M.A. 1977. The Ostropalean fungi. Mycotaxon 5, 1-277.
Shoemaker, R.A. 1974. Gaeumannomyces graminis var. tritici. Fungi Canadenses No.37, National Mycological Herbarium, Ottawa.
Shoemaker, R.A. 1976. Canadian and some extralimital Ophiobolus species. Canadian Journal of Botany 54, 2365-2404.
Sivasithamparam, K. 1975. Phialophora and Phialophora-like fungi occurring in the root region of wheat. Australian Journal of Botany 23, 193-212.

Spegazzini, C. 1880. Fungi argentini. Pugillus secundus. Anales de sociedad cientifica Argentina 10, 5-33 (original not seen; from Farr, 1973).
Spegazzini, C. 1909. Mycetes Argentinenses. Ser.IV. Anales del Museo Nacional de Buenos Aires 19, (Ser.3, 12), 257-458.
Spegazzini, C. 1912. Mycetes Argentinenses. Ser.VI. Anales del Museo Nacional de Buenos Aires 23, 1-129.
Spegazzini, C. 1924. Relación de un paseo hasta el Cabo de Hoorn. Boletín de la Academia de Ciencias de la República Argentina 27, 321-404.
Sprague, R. & Halisky, P.M. 1955. Take-all in the Olympic National Park. Plant Disease Reporter 39, 989.
Stafleu, F.A. & Cowan, R.S. 1976. Taxonomic literature, 2nd Ed.Volume 1: A-G. xl + 1136 pp. Bohn, Scheltema & Holkema, Utrecht.
Stafleu, F.A. et al.(Eds.) 1972. International Code of Botanical Nomenclature, 426 pp. International Association for Plant Taxonomy, Utrecht.
Stetter, S. & Leroul, N. 1979. Continuous barley growing. II. Influence on the fungal population of the roots. Statens Planteavisforsog Beretning Nr. 1440, 50-72, Copenhagen (Danish).
Sutton, B.C. 1968. The appressoria of Colletotrichum graminicola and C. falcatum. Canadian Journal of Botany 46, 873-876.
Sutton, B.C. 1977. Coelomycetes VI. Nomenclature of generic names proposed for Coelomycetes. C.M.I. Mycological Paper No.141, 253 pp.
Sydow, H.& P. 1913. Novae fungorum species - IX. Annales Mycologici 11, 54-65.
Sydow, H.& P. 1917. Beitrag zur Kenntnis der Pilzflora der Philippinen - Inseln. Annales Mycologici 15, 165-268.
Sydow, H.& P. & Butler, E.J. 1911. Fungi Indiae orientalis. Pars. III. Annales Mycologici 9, 372-421.
Sydow, P. 1897. Index to Saccardo's Sylloge fungorum Vols. I-XI. Sylloge fungorum 12, viii + 1053 pp.
Tanaka, T. 1917. New Japanese fungi. Notes and translations: 1. Mycologia 9, 167-172.
Tarr, S.A.J. 1962. Diseases of sorghum, sudan grass and broom corn. xi + 380 pp. Commonwealth Mycological Institute, Kew.
Tehon, L.R. 1935. A monographic rearrangement of Lophodermium. Illinois Biological Monographs 13 (4), 1-151.
Tehon, L.R. & Daniels, E.Y. 1927. Notes on the parasitic fungi of Illinois - III. Mycologia 19, 110-129.
Terrier, C.-A. 1942. Essai sur la systématique des Phacidiaceae (Fr.) sensu Nannfeldt (1932). Matériaux pour la flore cryptogamique Suisse 9 (2), 1-99.
Theissen, F. 1913. Die Gattung Asterina in systematischer Darstellung. Abhandlungen der K.K. Zoologisch - Botanischen Gesellschaft in Wien 7 (3), 1-130.
Trail, J.W.H. 1889. Enumeration of fungi collected in Hardanger in 1887. Transactions of the Botanical Society of Edinburgh 17, 487-495 (original not seen; from Dennis, 1975 and Lindau & Sydow, 1909).
Tulasne, L.-R. & Tulasne, C. 1863. Selecta fungorum carpologia, Vol.II, Paris.
Tullis, E.C. 1951. Diseases of rice. United States Department of Agriculture Farmers Bulletin 1854, 16 pp.

Turner, E.M. 1940. Ophiobolus graminis Sacc. var. avenae n.var., as the cause of take-all or whiteheads of oats in Wales. Transactions of the British Mycological Society 24, 269-281.

Wadsworth, D.F. 1967. Etiology of spring dead spot, a root rot complex of Bermuda grass. Dissertation Abstracts 28 (1) B, 18.

Walker, J. 1972. Type studies on Gaeumannomyces graminis and related fungi. Transactions of the British Mycological Society 58, 427-457.

Walker, J. 1973. Gaeumannomyces graminis var. graminis, var. avenae, var. tritici. C.M.I. Descriptions of Pathogenic Fungi and Bacteria Nos. 381, 382 & 383.

Walker, J. 1975. Take-all diseases of Gramineae: A review of recent work. Review of Plant Pathology 54, 113-144.

Walker, J. 1980. Taxonomy of take-all fungi and related genera and species. Chapter in Asher & Shipton (1980).

Walker, J. & Smith, A.M. 1972. Leptosphaeria narmari and L. korrae spp. nov., two long-spored pathogens of grasses in Australia. Transactions of the British Mycological Society 58, 459-466.

Walker, J. & Sutton, B.C. 1974. Dilophia Sacc. and Dilophospora Desm. Transactions of the British Mycological Society 62, 231-241.

Webster, J. & Hudson, H.J. 1957. Graminicolous pyrenomycetes VI. Conidia of Ophiobolus herpotrichus, Leptosphaeria luctuosa, L. fuckelii, L. pontiformis and L. eustomoides. Transactions of the British Mycological Society 40, 509-522.

Weese, J. 1921. Über die Gattungen Ophiosphaeria W. Kirschst., Acanthophiobolus Berl. und Ophiochaeta Sacc. Berichte der Deutschen Botanischen Gesellschaft 39, 114-120.

Wehmeyer, L.E. 1961. A world monograph of the genus Pleospora and its segregates. ix + 451 pp. University of Michigan Press, Ann Arbor.

Wong, P.T.W. 1975. Cross-protection against the wheat and oat take-all fungi by Gaeumannomyces graminis var. graminis. Soil Biology and Biochemistry 7, 189-194.

Wong, P.T.W. 1980. Biological control of take-all by cross-protection. Chapter in Asher & Shipton (1980).

Wong, P.T.W. & Walker, J. 1975. Germinating phialidic conidia of Gaeumannomyces graminis and Phialophora-like fungi from Gramineae. Transactions of the British Mycological Society 65, 41-47.

ADDENDUM

The following "m" names were inadvertently omitted from the Synopsis of Fungi and should be added:-

moravicus, Ophiobolus, syn. of Plagiosphaera immersa
muroiana, Plagiosphaera
muroianum, Linocarpon, syn. of Plagiosphaera muroiana
mutabilis, Phialophora, see under Phialophora
Mycosphaerella, see list of unplaced Gaeumannomyces species, under Gramineae undet.
myriadea, Sphaerulina, type species of Sphaerulina

MYCOTAXON

Vol. XI, No. 1, pp. 130-138 April-June 1980

GENERIC DELIMITATION IN THE LICHEN FAMILY THELOTREMATACEAE

Mason E. Hale, Jr.

Department of Botany, Smithsonian Institution
Washington, D.C. 20560, U.S.A.

ABSTRACT

Three genera in the lichen family Thelotremataceae, Thelotrema *Ach.,* Myriotrema *Fée, and* Ocellularia *Meyer, are delimited on the basis of excipular structure and new combinations for 135 species are made.*

The lichen family Thelotremataceae is a largely tropical group of about 450 species. There are four spore types, colorless-transversely septate, brown-transversely septate, colorless-muriform, and brown-muriform, which J. Müller Argoviensis (1887) recognized as four distinct genera: *Ocellularia* Meyer, *Phaeotrema* Müll. Arg., *Thelotrema* Ach., and *Leptotrema* Mont. & v. d. Bosch, respectively. Most lichenologists have in fact adopted these "spore genera." At the same time, when the species are examined without reference to spore characters, one finds significant differences in excipular structure, unrelated to spore septation and pigmentation, which Salisbury (1971, 1972, 1978) has recently argued to be a more natural basis for generic classification in the family. His conclusions follow logically from the increased emphasis being given to ontogenetic characters at both the generic and family level (Henssen & Jahns, 1974).

Salisbury recognizes one genus (*Thelotrema*), which he subdivides into three sections, reflecting the nature of the exciple: sect. *Thelotrema* (exciple colorless, with periphysoids), sect. *Myriotrema* (Fée) G. Salisbury (exciple colorless, without periphysoids), and sect. *Ascidium* (Fée) G. Salisbury (exciple carbonized, without periphysoids). While the four spore genera are more or less equally represented in each of these sections (much as the three excipular types are represented in each of the spore genera), an alignment according to exciple is obviously a more natural one since it places in close proximity species with identical apothecial and cortical structure and chemistry, even though the spores are different. By using spores the same species are dispersed in widely separated genera.

I propose to recognize the three main excipular types at the generic level, much as Fée had unwittingly done in 1824, although his classification was not adopted by any later workers. Thus, *Thelotrema* sect. *Thelotrema* becomes *Thelotrema*, sect. *Myriotrema Myriotrema*, and sect. *Ascidium Ocellularia*. These three genera are amply distinguished by the excipular structures as well as correlating anatomical and

chemical characters (Hale, 1981) with virtually no intermediate states, providing a convenient breakdown of the 450 species known at the world level.

Many species described in *Ocellularia* and *Thelotrema* or transferred to these genera on the basis of spore characters are in fact already correctly recognized in the new generic delimitation. However, a number of species must be transferred to *Myriotrema*, which no authors since Fée have accepted, and all species formerly classified under the brown-spored genera *Leptotrema* and *Phaeotrema* must be transferred to the appropriate excipular genera. The following 135 new combinations are being made here for species which I have already examined and typified (Hale, 1973, 1974a, 1974b, 1975, 1978a, 1978b). Full synonymy and more detailed discussions of the genera will be presented in another article (Hale, 1981).

THELOTREMA

Thelotrema Ach., Meth. Lich. 130 (1803).
Type species: *Lichen lepadinus* Ach.
Thelotrema sect. *Thelotrema*
Number of species: 100

Thelotrema africanum (Hale) Hale, comb. nov.
Basionym: *Leptotrema africanum* Hale, Mycotaxon 7:382 (1978).
Thelotrema aggregatum (Hale) Hale, comb. nov.
Basionym: *Phaeotrema aggregatum* Hale, Smith. Contr. Bot. 16:29 (1974).
Thelotrema astroideum (Berk. & Broome) Hale, comb. nov.
Basionym: *Platygrapha astroidea* Berk. & Broome, J. Linn. Soc. 14:109 (1875).
Thelotrema coccineum (Leight.) Hale, comb. nov.
Basionym: *Platygrapha coccinea* Leight. Trans. Linn. Soc. 25:456 (1866).
Thelotrema dilatatum (Müll. Arg.) Hale, comb. nov.
Basionym: *Ocellularia dilatata* Müll. Arg. J. Linn. Soc., Bot. 30:452 (1895).
Thelotrema dissutum (Hale) Hale, comb. nov.
Basionym: *Ocellularia dissuta* Hale, Smith. Contr. Bot. 38:20 (1978).
Thelotrema esslingeri (Hale) Hale, comb. nov.
Basionym: *Ocellularia esslingeri* Hale, Smith. Contr. Bot. 38:20 (1978).
Thelotrema hawaiiense (Hale) Hale, comb. nov.
Basionym: *Leptotrema hawaiiense* Hale, Phytol. 27:490 (1974).
Thelotrema hypoprotocetraricum (Hale) Hale, comb. nov.
Basionym: *Leptotrema hypoprotocetraricum* Hale, Smith. Contr. Bot. 38:52 (1978).
Thelotrema kamatii (Patw. & Kulk.) Hale, comb. nov.
Basionym: *Ocellularia kamatii* Patw. & Kulk. Norw. J. Bot. 24:130 (1977).
Thelotrema leprieurii (Mont.) Hale, comb. nov.
Basionym: *Stictis leprieurii* Mont. Ann. Sci. Nat. Bot., sér. 4, 3:97 (1855).
Thelotrema magnificum (Berk. & Broome) Hale, comb. nov.
Basionym: *Platygrapha magnifica* Berk. & Broome, J. Linn. Soc.

14:110 (1875).

Thelotrema mirabile (Zahlbr.) Hale, comb. nov.
Basionym: *Phaeographina mirabilis* Zahlbr. in Handel-Mazzetti, Symb. Sin. 3:60 (1930).

Thelotrema neei (Hale) Hale, comb. nov.
Basionym: *Ocellularia neei* Hale, Smith. Contr. Bot. 38:25 (1978).

Thelotrema phlyctidioides (Müll. Arg.) Hale, comb. nov.
Basionym: *Ocellularia phlyctidioides* Müll. Arg. Hedw. 32:130 (1893).

Thelotrema pseudoexanthismocarpum (Patw. & Kulk.) Hale, comb. nov.
Basionym: *Ocellularia pseudoexanthismocarpa* Patw. & Kulk. Norw. J. Bot. 24:130 (1977).

Thelotrema pseudoschizostomum (Hale) Hale, comb. nov.
Basionym: *Ocellularia pseudoschizostoma* Hale, Smith. Contr. Bot. 38:28 (1978).

Thelotrema refertum (Hale) Hale, comb. nov.
Basionym: *Ocellularia referta* Hale, Smith. Contr. Bot. 38:29 (1978).

Thelotrema rockii (Zahlbr.) Hale, comb. nov.
Basionym: *Phaeotrema rockii* Zahlbr. Ann. Mycol. 10:370 (1912).

Thelotrema stellatum (Hale) Hale, comb. nov.
Basionym: *Leptotrema stellatum* Hale, Smith. Contr. Bot. 38:54 (1978).

Thelotrema turgidulum (Müll. Arg.) Hale, comb. nov.
Basionym: *Ocellularia turgidula* Müll. Arg. J. Botanique 7:94 (1893).

MYRIOTREMA

Myriotrema Fée, Essai Crypt. 103 (1824).
Type species: *Myriotrema olivaceum* Fée
Thelotrema sect. *Myriotrema* (Fée) G. Salisbury
Number of species: 150

Myriotrema albidulum (Nyl.) Hale, comb. nov.
Basionym: *Thelotrema albidulum* Nyl. Ann. Sci. Nat. Bot., sér 4, 15:46 (1861).

Myriotrema anamalaiense (Patw. & Kulk.) Hale, comb. nov.
Basionym: *Thelotrema anamalaiense* Patw. & Kulk. Norw. J. Bot. 24:127 (1977).

Myriotrema andamanicum (Nyl.) Hale, comb. nov.
Basionym: *Thelotrema andamanicum* Nyl. Bull. Soc. Linn. Normandie, sér. 2, 7:167 (1873).

Myriotrema bahianum (Ach.) Hale, comb. nov.
Basionym: *Thelotrema lepadinum* var. *bahianum* Ach. Meth. Lich. 132 (1803).

Myriotrema barroense (Hale) Hale, comb. nov.
Basionym: *Ocellularia barroensis* Hale, Smith. Contr. Bot. 38:14 (1978).

Myriotrema calvescens (Fée) Hale, comb. nov.
Basionym: *Thelotrema calvescens* Fée, Essai Crypt. Suppl. 89 (1837).

Myriotrema cinereoglaucescens (Vain.) Hale, comb. nov.
Basionym: *Thelotrema cinereoglaucescens* Vain. Suomal. Tiedeakat. Toim., ser. A, 15:189 (1921).

Myriotrema cinereum (Müll. Arg.) Hale, comb. nov.
Basionym: *Thelotrema cinereum* Müll. Arg. Flora 74:112 (1891).

Myriotrema clandestinum (Fée) Hale, comb. nov.
Basionym: *Thelotrema clandestinum* Fée, Essai Crypt. Suppl. 90 (1837).
Myriotrema compunctum (Ach.) Hale, comb. nov.
Basionym: *Urceolaria compuncta* Ach. Meth. Lich. 143 (1803).
Myriotrema concretum (Fée) Hale, comb. nov.
Basionym: *Thelotrema concretum* Fée, Essai Crypt. Suppl. 90 (1837).
Myriotrema configuratum (Hale) Hale, comb. nov.
Basionym: *Ocellularia configurata* Hale, Smith. Contr. Bot. 38:17 (1978).
Myriotrema congestum (Hale) Hale, comb. nov.
Basionym: *Ocellularia congesta* Hale, Smith. Contr. Bot. 38:17 (1978).
Myriotrema costaricense (Müll. Arg.) Hale, comb. nov.
Basionym: *Ocellularia costaricensis* Müll. Arg. Bull. Soc. Roy. Bot. Belg. 30:75 (1891).
Myriotrema dactyliferum (Hale) Hale, comb. nov.
Basionym: *Ocellularia dactylifera* Hale, Smith. Contr. Bot. 38:19 (1978).
Myriotrema deceptum (Hale) Hale, comb. nov.
Basionym: *Leptotrema deceptum* Hale, Smith. Contr. Bot. 16:39 (1978).
Myriotrema desquamans (Müll. Arg.) Hale, comb. nov.
Basionym: *Anthracothecium desquamans* Müll. Arg. Flora 71:48 (1888).
Myriotrema elachistoteron (Leight.) Hale, comb. nov.
Basionym: *Thelotrema elachistoteron* Leight. Trans. Linn. Soc. Lond. 27:169 (1870).
Myriotrema eminens (Hale) Hale, comb. nov.
Basionym: *Thelotrema eminens* Hale, Mycotaxon 3:177 (1975).
Myriotrema exile (Hale) Hale, comb. nov.
Basionym: *Thelotrema exile* Hale, Mycotaxon 7:381 (1978).
Myriotrema foliicola (Hale) Hale, comb. nov.
Basionym: *Phaeotrema foliicola* Hale, Mycotaxon 3:175 (1975).
Myriotrema fragile (Hale) Hale, comb. nov.
Basionym: *Ocellularia fragilis* Hale, Phytol. 27:492 (1974).
Myriotrema glaucescens (Nyl.) Hale, comb. nov.
Basionym: *Thelotrema glaucescens* Nyl. Ann. Sci. Nat. Bot., sér. 4, 19:332 (1863).
Myriotrema glaucophaenum (Kremplh.) Hale, comb. nov.
Basionym: *Thelotrema glaucophaenum* Kremplh. Nuov. G. Bot. Ital. 7:19 (1875).
Myriotrema glauculum (Nyl.) Hale, comb. nov.
Basionym: *Thelotrema glauculum* Nyl. in Triana & Planchon, Ann. Sci. Nat. Bot., sér. 4, 19:332 (1863).
Myriotrema granulosum (Leight.) Hale, comb. nov.
Basionym: *Ascidium granulosum* Leight. Trans. Linn. Soc. Lond. 27:171 (1870).
Myriotrema halei (Tuck.) Hale, comb. nov.
Basionym: *Porina halei* Tuck. & Mont. in Mont. Ann. Sci. Nat. Bot., sér. 4, 8:295 (1857).
Myriotrema hartii (Müll. Arg.) Hale, comb. nov.
Basionym: *Thelotrema hartii* Müll. Arg. Flora 69:311 (1886).
Myriotrema immersum (Eschw.) Hale, comb. nov.
Basionym: *Thelotrema immersum* Eschw. in Mart. Fl. Bras. 1:177 (1833).
Myriotrema insigne (Zahlbr.) Hale, comb. nov.
Basionym: *Thelotrema insigne* Zahlbr. Denkschr. Math.-nat. Cl.

Myriotrema laeviusculum (Nyl.) Hale, comb. nov.
Basionym: *Thelotrema laeviusculum* Nyl. in Triana & Planchon, Ann. Sci. Nat. Bot., sér. 4, 19:335 (1863).
Myriotrema leiostomum (Tuck.) Hale, comb. nov.
Basionym: *Thelotrema leiostomum* Tuck. Proc. Amer. Acad. Arts Sci. 5:407 (1862).
Myriotrema mammiculum (Hale) Hale, comb. nov.
Basionym: *Leptotrema mammiculum* Hale, Mycotaxon 7:382 (1978).
Myriotrema mammilare (Hale) Hale, comb. nov.
Basionym: *Phaeotrema mammilare* Hale, Phytol. 27:494 (1974).
Myriotrema masonhalei (Patw. & Kulk.) Hale, comb. nov.
Basionym: *Thelotrema masonhalei* Patw. & Kulk. Norw. J. Bot. 24:128 (1977).
Myriotrema maximum (Hale) Hale, comb. nov.
Basionym: *Thelotrema maximum* Hale, Smith. Contr. Bot. 38:45 (1978).
Myriotrema microporellum (Nyl.) Hale, comb. nov.
Basionym: *Thelotrema microporellum* Nyl. in Triana & Planchon, Ann. Sci. Nat. Bot., sér. 4, 19:327 (1863).
Myriotrema microporum (Mont.) Hale, comb. nov.
Basionym: *Thelotrema microporum* Mont. Ann. Sci. Nat. Bot., sér. 3, 10:130 (1848).
Myriotrema microstomum (Müll. Arg.) Hale, comb. nov.
Basionym: *Thelotrema microstomum* Müll. Arg. Flora 74:113 (1891).
Myriotrema minutulum (Hale) Hale, comb. nov.
Basionym: *Ocellularia minutula* Hale, Smith. Contr. Bot. 38:24 (1978).
Myriotrema minutum (Hale) Hale, comb. nov.
Basionym: *Ocellularia minuta* Hale, Mycotaxon 7:379 (1978).
Myriotrema myriocarpum (Fée) Hale, comb. nov.
Basionym: *Thelotrema myriocarpum* Fée, Essai Crypt. 94 (1824).
Myriotrema myrioporoides (Müll. Arg.) Hale, comb. nov.
Basionym: *Thelotrema myrioporoides* Müll. Arg. in Durand & Pittier, Bull. Soc. Roy. Bot. Belg. 32:147 (1893).
Myriotrema myrioporum (Tuck.) Hale, comb. nov.
Basionym: *Thelotrema myrioporum* Tuck. Proc. Amer. Acad. Arts Sci. 5:412 (1862).
Myriotrema myriotremoides (Nyl.) Hale, comb. nov.
Basionym: *Thelotrema myriotremoides* Nyl. Ann. Sci. Nat. Bot., sér. 4, 11:221 (1859).
Myriotrema norstictícum (Hale) Hale, comb. nov.
Basionym: *Thelotrema norstictícum* Hale, Phytol. 26:417 (1978).
Myriotrema occultum (Eschw.) Hale, comb. nov.
Basionym: *Thelotrema occultum* Eschw. in Martius, Fl. Bras. 174 (1833).
Myriotrema pachystomum (Nyl.) Hale, comb. nov.
Basionym: *Thelotrema pachystomum* Nyl. in Triana & Planchon, Ann. Sci. Nat. Bot., sér. 4, 19:325 (1863).
Myriotrema phaeosporum (Nyl.) Hale, comb. nov.
Basionym: *Thelotrema phaeosporum* Nyl. Ann. Sci. Nat. Bot., sér. 4, 11:242 (1859).
Myriotrema porinaceum (Müll. Arg.) Hale, comb. nov.
Basionym: *Thelotrema porinaceum* Müll. Arg. Nuov. G. Bot. Ital. 23:130 (1891).
Myriotrema protocetraricum (Hale) Hale, comb. nov.
Basionym: *Ocellularia protocetrarica* Hale, Smith. Contr. Bot. 38:28 (1978).

Myriotrema pulverulentum (Hale) Hale, comb. nov.
Basionym: *Ocellularia pulverulenta* Hale, Smith. Contr. Bot. 38:29 (1978).
Myriotrema pycnoporellum (Nyl.) Hale, comb. nov.
Basionym: *Thelotrema pycnoporellum* Nyl. Flora 59:562 (1876).
Myriotrema reclusum (Kremplh.) Hale, comb. nov.
Basionym: *Thelotrema reclusum* Kremplh. in Nyl. Bull. Soc. Linn. Normandie, sér. 2, 7:168 (1873).
Myriotrema rugiferum (Harm.) Hale, comb. nov.
Basionym: *Thelotrema rugiferum* Harm. Bull. Séanc. Soc. Sci. Nancy, sér. 3, 13:44 (1912).
Myriotrema santessonii (Hale) Hale, comb. nov.
Basionym: *Thelotrema santessonii* Hale, Phytol. 26:417 (1973).
Myriotrema scabridum (Hale) Hale, comb. nov.
Basionym: *Phaeotrema scabridum* Hale, Mycotaxon 7:380 (1978).
Myriotrema schizostomum (Tuck.) Hale, comb. nov.
Basionym: *Thelotrema schizostomum* Tuck. Proc. Amer. Acad. Arts Sci. 5:411 (1862).
Myriotrema secernendum (Harm.) Hale, comb. nov.
Basionym: *Thelotrema secernendum* Harm. Bull. Séanc. Soc. Sci. Nancy, sér. 3, 13:40 (1912).
Myriotrema sphinctrinellum (Nyl.) Hale, comb. nov.
Basionym: *Thelotrema sphinctrinellum* Nyl. Acta Soc. Sci. Fenn. 7:449 (1863).
Myriotrema steyermarkii (Hale) Hale, comb. nov.
Basionym: *Thelotrema steyermarkii* Hale, Phytol. 27:496 (1974).
Myriotrema subcompunctum (Nyl.) Hale, comb. nov.
Basionym: *Thelotrema subcompunctum* Nyl. Bull. Soc. Linn. Normandie, sér. 2, 2:76 (1868).
Myriotrema subconforme (Nyl.) Hale, comb. nov.
Basionym: *Thelotrema subconforme* Nyl. J. Linn. Soc. Bot. 20:53 (1883).
Myriotrema subwrightii (Hale) Hale, comb. nov.
Basionym: *Ocellularia subwrightii* Hale, Smith. Contr. Bot. 38:32 (1978).
Myriotrema terebrans (Nyl.) Hale, comb. nov.
Basionym: *Thelotrema terebrans* Nyl. Bull. Soc. Linn. Normandie, sér. 2, 7:166 (1873).
Myriotrema terebratulum (Nyl.) Hale, comb. nov.
Basionym: *Thelotrema terebratulum* Nyl. Ann. Sci. Nat. Bot., sér 5, 7:315 (1867).
Myriotrema trypaneoides (Nyl.) Hale, comb. nov.
Basionym: *Thelotrema trypaneoides* Nyl. in Triana & Planchon, Ann. Sci. Nat. Bot., sér. 4; 19:335 (1863).
Myriotrema uniseptatum (Hale) Hale, comb. nov.
Basionym: *Ocellularia uniseptata* Hale, Smith. Contr. Bot. 38:33 (1978).
Myriotrema urceolare (Ach.) Hale, comb. nov.
Basionym: *Thelotrema urceolare* Ach. Kongl. Vetensk. Acad. Nya Handl. 1812:90 (1812).
Myriotrema viridialbum (Krempl.) Hale, comb. nov.
Basionym: *Thelotrema viridialbum* Krempl. Flora 59:221 (1876).
Myriotrema vulcani (Hale) Hale, comb. nov.
Basionym: *Phaeotrema vulcani* Hale, Smith. Contr. Bot. 38:37 (1978).
Myriotrema wightii (T. Tayl.) Hale, comb. nov.
Basionym: *Endocarpon wightii* T. Tayl. in Hook. Lond. J. Bot. 6:155 (1847).

Myriotrema wrightii (Tuck.) Hale, comb. nov.
Basionym: *Thelotrema wrightii* Tuck. Proc. Amer. Acad. Arts Sci. 5:409 (1862).

OCELLULARIA

Ocellularia Meyer, Nebenstunden 327 (1825) (generic name conserved over *Ascidium* Fée ex anno 1824)
Type species: *Thelotrema obturatum* Ach.
Thelotrema sect. *Ascidium* (Fée) G. Salisbury
Number of species: 200

Ocellularia arecae (Vain.) Hale, comb. nov.
Basionym: *Thelotrema arecae* Vain. Hedwigia 46:174 (1907).
Ocellularia asiatica (Vain.) Hale, comb. nov.
Basionym: *Thelotrema asiaticum* Vain. Hedwigia 46:175 (1907).
Ocellularia auberiana (Mont.) Hale, comb. nov.
Basionym: *Thelotrema auberianum* Mont. in Sagra, Hist. Phys. Pol. Nat. Cuba, Bot. 163 (1842).
Ocellularia aurata (Tuck.) Hale, comb. nov.
Basionym: *Thelotrema auratum* Tuck. Proc. Amer. Acad. Arts Sci. 5:408 (1862).
Ocellularia caledoniensis (Hale) Hale, comb. nov.
Basionym: *Phaeotrema caledoniense* Hale, Phytol. 27:494 (1974).
Ocellularia chiriquiensis (Hale) Hale, comb. nov.
Basionym: *Leptotrema chiriquiense* Hale, Smith. Contr. Bot. 38:50 (1978).
Ocellularia conformis (Fée) Hale, comb. nov.
Basionym: *Thelotrema conforme* Fée, Essai Crypt. Suppl. 89 (1837).
Ocellularia confusa (Hale) Hale, comb. nov.
Basionym: *Thelotrema confusum* Hale, Smith. Contr. Bot. 16:32 (1974).
Ocellularia crassa (Müll. Arg.) Hale, comb. nov.
Basionym: *Leptotrema crassum* Müll. Arg. Flora 65:332 (1882).
Ocellularia depressa (Mont.) Hale, comb. nov.
Basionym: *Thelotrema depressum* Mont. Ann. Sci. Nat. Bot., sér. 3, 16:73 (1851).
Ocellularia epitrypa (Nyl.) Hale, comb. nov.
Basionym: *Thelotrema epitrypum* Nyl. Acta Soc. Sci. Fenn. 7:454 (1863).
Ocellularia erumpens (Magn.) Hale, comb. nov.
Basionym: *Thelotrema erumpens* Magn. Ark. Bot., ser. 2, 3(10):279 (1955).
Ocellularia eumorpha (Stirt.) Hale, comb. nov.
Basionym: *Thelotrema eumorphum* Stirt. Proc. Phil. Soc. Glasgow 10:158 (1877).
Ocellularia fissa (Nyl.) Hale, comb. nov.
Basionym: *Thelotrema fissum* Nyl. Ann. Sci. Nat. Bot., sér. 4, 11:258 (1859).
Ocellularia glyphica (Nyl.) Hale, comb. nov.
Basionym: *Thelotrema glyphicum* Nyl. Acta Soc. Sci. Fenn. 7:453 (1863).
Ocellularia grandis (Hale) Hale, comb. nov.
Basionym: *Thelotrema grande* Hale, Phytol. 26:416 (1973).

Ocellularia interponenda (Nyl.) Hale, comb. nov.
Basionym: *Ascidium interponendum* Nyl. Sert. Lich. Trop. Labuan Singapore, 20 (1891).
Ocellularia interposita (Nyl.) Hale, comb. nov.
Basionym: *Ascidium interpositum* Nyl. in Triana & Planchon, Ann. Sci. Nat. Bot., sér. 4, 19:336 (1863).
Ocellularia leucina (Müll. Arg.) Hale, comb. nov.
Basionym: *Thelotrema leucinum* Müll. Arg. Rev. Mycol. 35:10 (1887).
Ocellularia leucomelaena (Nyl.) Hale, comb. nov.
Basionym: *Thelotrema leucomelaenum* Nyl. in Triana & Planchon, Ann. Sci. Nat. Bot., sér. 4, 19:329 (1863).
Ocellularia lirelliformis (Tuck.) Hale, comb. nov.
Basionym: *Thelotrema lirelliforme* Tuck. Proc. Amer. Acad. Arts Sci. 6:270 (1864).
Ocellularia marivelensis (Vain.) Hale, comb. nov.
Basionym: *Thelotrema marivelense* Vain. Suomal. Tiedeakat. Toim., ser. A, 15:176 (1921).
Ocellularia massalongi (Mont.) Hale, comb. nov.
Basionym: *Ascidium massalongi* Mont. Ann. Sci. Nat. Bot., sér. 4, 14:174 (1860).
Ocellularia meiosperma (Nyl.) Hale, comb. nov.
Basionym: *Thelotrema meiospermum* Nyl. Ann. Sci. Nat. Bot., sér. 4, 19:333 (1863).
Ocellularia metaphorica (Nyl.) Hale, comb. nov.
Basionym: *Thelotrema metaphoricum* Nyl. Acta Soc. Sci. Fenn. 7:455 (1863).
Ocellularia microspora (Zahlbr.) Hale, comb. nov.
Basionym: *Leptotrema microsporum* Zahlbr. Sitzb. Akad. Wiss. Math.-nat. Abt. 1(111):392 (1902).
Ocellularia monosporoides (Nyl.) Hale, comb. nov.
Basionym: *Thelotrema monosporoides* Nyl. Lich. New Zealand, 76 (1888).
Ocellularia neodominicana Hale, nom. nov.
Basionym: *Thelotrema dominicanum* Hale, Smith. Contr. Bot. 16:33 (1974) (non *Ocellularia dominicana* Hale ex anno 1974).
Ocellularia obscura (Hale) Hale, comb. nov.
Basionym: *Phaeotrema obscurum* Hale, Smith. Contr. Bot. 16:31 (1974).
Ocellularia panamensis (Hale) Hale, comb. nov.
Basionym: *Leptotrema panamense* Hale, Smith. Contr. Bot. 38:54. (1978).
Ocellularia planaria (Hale) Hale, comb. nov.
Basionym: *Thelotrema planarium* Hale, Mycotaxon 7:382 (1978).
Ocellularia praestans (Müll. Arg.) Hale, comb. nov.
Basionym: *Thelotrema praestans* Müll. Arg. J. Linn. Soc. Lond. 30:453 (1895).
Ocellularia psoromica (Hale) Hale, comb. nov.
Basionym: *Phaeotrema psoromicum* Hale, Mycotaxon 7:380 (1978).
Ocellularia sanfordiana (Zahlbr.) Hale, comb. nov.
Basionym: *Thelotrema sanfordianum* Zahlbr. Ann. Mycol. 33:41 (1935)
Ocellularia stictica (Hale) Hale, comb. nov.
Basionym: *Phaeotrema stictieum* Hale, Mycotaxon 3:176 (1975).
Ocellularia straminea (Vain.) Hale, comb. nov.
Basionym: *Thelotrema stramineum* Vain. Suomal. Tiedeakat. Toim., ser. A, 5:181 (1921).

Ocellularia subpraestans (Hale) Hale, comb. nov.
Basionym: *Thelotrema subpraestans* Hale, Phytol. 27:497 (1974).
Ocellularia subsimilis (Hale) Hale, comb. nov.
Basionym: *Thelotrema subsimile* Hale, Phytol. 27:497 (1974).
Ocellularia tenuis (Hale) Hale, comb. nov.
Basionym: *Thelotrema tenue* Hale, Smith. Contr. Bot. 16:38 (1974).
Ocellularia thelotremoides (Leight.) Hale, comb. nov.
Basionym: *Ascidium thelotremoides* Leight. Trans. Linn. Soc. Lond. 27:170 (1870).
Ocellularia virens (Müll. Arg.) Hale, comb. nov.
Basionym: *Phaeotrema virens* Müll. Arg. Flora 70:398 (1887).

REFERENCES

Hale, M. E., Jr. 1973. Studies on the lichen family Thelotremataceae. 1. Phytol. 26:413-420.

_____. 1974a. Morden-Smithsonian expedition to Dominica: The lichens (Thelotremataceae). Smith. Contr. Bot. 16:1-46.

_____. 1974b. Studies on the lichen family Thelotremataceae. 2. Phytol. 27:490-501.

_____. 1975. Studies on the lichen family Thelotremataceae. 3. Mycotaxon 3:173-181.

_____. 1978a. A revision of the lichen family Thelotremataceae in Panama. Smith. Contr. Bot. 38:1-60.

_____. 1978b. Studies on the lichen family Thelotremataceae. 4. Mycotaxon 7:377-385.

_____. 1981. A revision of the lichen family Thelotremataceae in Sri Lanka. Bull. Brit. Mus. Nat. Hist. (Bot.). 8 (in press).

Henssen, A., and H. M. Jahns. 1974. Lichenes. Eine Einführung in die Flechtenkunde. Stuttgart.

Müller Argoviensis, J. 1887. Graphideae Féeanae. Mém. Soc. Phys. Hist. Nat. Genève 29(8):1-80.

Salisbury, G. 1971. *Thelotrema wightii* (T. Tayl.) Nyl. Port. Acta Biol. (B) 11:35-37.

_____. 1972. *Thelotrema* Ach. section *Thelotrema*. 1. The *T. lepadinum* group. Lichenol. 5:262-274.

_____. 1978. *Thelotremata* Achariana et Féeana. Nova Hedwigia 29:405-427.

MYCOTAXON

Vol. XI, No. 1, pp. 139-149 April-June 1980

SONORAN DESERT MYXOMYCETES[1]

Meredith Blackwell

Department of Biology, Hope College, Holland, Michigan 49423

R. L. Gilbertson

Department of Plant Pathology
University of Arizona, Tucson 85721

SUMMARY

Thirty-three species of Myxomycetes are reported from the Sonoran Desert of Arizona; 46 species are now known from this region. This unexpected variety includes some seldom collected species such as *Licea fimicola*, *Fuligo megaspora*, *Physarum straminipes*, *Didymium* sp. (in press), and *D. karstensii*, and three undescribed species. Field observations and cultural studies indicate that sclerotial formation and production of small plasmodia are important in the life cycle of some of these organisms which are common on dead plant and dung substrates. Spore-to-spore agar culture of *Badhamia affinis*, *Physarum notabile*, and *P. straminipes* is reported for the first time.

Myxomycetes are known primarily as inhabitants of temperate hardwood and coniferous forests and boreal forests (Martin and Alexopoulos, 1969). Some are known from rain forests and other tropical vegetation types (Alexopoulos, 1970; Farr, 1974; Reynolds and Alexopoulos, 1971; Alexopoulos and Saenz, 1975; Braun and Keller, 1976; Keller and Braun, 1977). But few field collected specimens have been reported from desert regions (Table 1).

Ramon (1968) reported three species of Myxomycetes from the Saharan-Sindian phytogeographical territory, and she attributed the small number of total species in Israel to the arid character of the country. In a more comprehensive report of North African Myxomycetes, Faurel et al. (1965) reported species for Morocco, Algeria, and Tunisia, including twelve desert species from moist chamber-cultured dung of Saharan animals (Table 1).

The small number of Myxomycetes (24) previously known from the Sonoran Desert (almost all from moist chamber cultures) is probably due to the fact that almost no collecting of slime molds has been done there (Evenson, 1961) (Table 1). Several fungal groups are now known to be well represented in the Sonoran Desert. These include rusts

[1]/University of Arizona Agricultural Experiment Station Journal Article No. 3096.

Table 1. Myxomycete species previously reported from desert habitats.

Species	Locality	References
Comatricha laxa Rost.	Arizona	Evenson (1961)
C. lurida A. Lister	*Arizona	Evenson (1961)
C. nigra (Pers.) Schroet.	*Algeria	Faurel et al. (1965)
C. pulchella (C. Bab.) Rost.	*Algeria *Arizona	Faurel et al. (1965) Evenson (1961)
Stemonitis flavogenita Jahn	*Arizona	Evenson (1961)
Echinostelium colliculosum Whitney et Keller	*Arizona	Whitney and Keller (1980)
Licea fimicola Dearness et Bisby	*Arizona	Evenson (1961)
L. pseudoconica Brooks et Keller	*Arizona	Keller and Brooks (1977)
Perichaena chrysosperma (Curry) A. Lister	*Arizona	Evenson (1961)
P. corticalis (Batsch) Rost.	*Arizona *Algeria	Evenson (1961) Faurel et al. (1965)
P. depressa Libert	*Arizona	Evenson (1961)
P. vermicularis (Schw.) Rost.	*Arizona	Evenson (1961)
Arcyria cinerea (Bull.) Pers.	*Arizona *Algeria	Evenson (1961)
A. insignis Kalchbr. et Cooke	*Arizona	Evenson (1961)
Badhamia macrocarpa (Ces.) Rost.	Arizona Israel	Evenson (1961) Ramon (1968)
B. panicea (Fries) Rost.	*Arizona	Evenson (1961)
Fuligo cinerea (Schw.) Morgan	Mexico	Braun and Keller (1976)
F. megaspora Sturgis	New Mexico	Martin and Alexopoulos (1969)

Table 1. Myxomycete species previously reported from desert habitats - (continued).

Species	Locality	References
Craterium leucocephalum (Pers.) Ditmar	*Algeria	Faurel et al. (1965)
Physarum compressum Alb. et Schw.	*Algeria *Arizona	Faurel et al. (1965) Evenson (1961)
P. didermoides (Pers.) Rost.	*Algeria	Faurel et al. (1965)
P. leucopus Link	*Algeria	Faurel et al. (1965)
P. mutabile (Rost.) G. Lister	*Arizona	Evenson (1961)
P. notabile Macbr.	Arizona	Evenson (1961)
P. nucleatum Rex	*Algeria	Faurel et al. (1965)
P. pusillum (Berk. et Curt.) G. Lister	*Arizona Israel	Evenson (1961) Ramon (1968)
Physarum sp.	*Arizona	Ranzoni (1968)
Colloderma oculatum (Lippert) G. Lister	*Algeria	Faurel et al. (1965)
Diderma simplex (Schroet.) G. Lister	*Algeria	Faurel et al. (1965)
Didymium anellus Morgan	*Arizona	Evenson (1961)
D. difforme (Pers.) S. F. Gray	Israel	Ramon (1968)
D. dubium Rost.	*Arizona	Evenson (1961)
D. nigripes (Link) Fries	*Arizona	Raper and Alexopoulos (1973)
D. vaccinium (Dur. et Mont.) Buchet	*Arizona	Evenson (1961)
unidentified plasmodium	*Arizona	Ranzoni (1968)

*Known only from moist chamber culture at this locality.

(Cummins, 1979), wood-rotting fungi (Lindsey and Gilbertson, 1975; Gilbertson et al., 1976; Nakasone and Gilbertson, 1978), and downy mildews (Solheim and Gilbertson, 1970).

Recent field collections and moist chamber cultures of substrates have yielded 33 myxomycete species for a total of 46 species from the Sonoran Desert of Arizona including *Licea fimicola* Dearness et Bisby, *Fuligo megaspora* Sturgis, *Physarum straminipes* Lister, *Didymium* sp. (Blackwell and Gilbertson, 1980), and *D. karstenii* Nann.-Brem., and three undescribed species. *Badhamia gracilis* (Macbr.) Macbr., *Physarum leucophaeum* Fries, *P. straminipes* Lister, and *Comatricha laxa* Rost. are common. This unexpected variety and abundance is of great interest in a group known primarily from more mesic habitats.

Sonoran Desert localities commonly receive four to six inches of precipitation during the two month period of July and August. A winter rainy season during December and January (Smith, 1956) also provides conditions favorable for fruiting of Myxomycetes. A variety of substrates which supports fungal growth is provided by the large number of species of vascular plants in the Sonoran Desert (Shreve and Wiggins, 1964). All field collections and plant moist chamber developments reported here are from fallen dead plants or dead parts of living plants in contact with the ground. The most common substrates for field collections are cacti which have a thickened outer tissue covering the cortex and vascular tissue. Our field observations show that these plants retain some moisture up to a month after the last precipitation, and the temperature beneath them is sometimes 20°C cooler than that of the bare soil surface in summer. Only occasional specimens are collected in the field on hardwoods. In addition dung of herbivorous animals is abundant and is another important substrate for Myxomycetes. Of approximately 80 species of Myxomycetes known to occur on dung (Eliasson and Lundqvist, 1979), twenty species (Table 2) are reported from moist chamber cultures of dung of desert animals.

Two or more species of slime molds fruiting in a small area on the same substrate was common. The presence of inconspicuous sporangia of additional species often was not discovered until the collections were examined in the laboratory under a dissecting microscope. The letter after the collection number denotes specimens from the same collection. We believe that this close sympatry indicates a limited number of favorable microhabitats for myxomycete growth and fruiting.

Moist chamber culture observations and limited agar culture studies indicate that sclerotia play an important part in the life of these desert-inhabiting organisms. Sclerotia are also frequently found in field collections either associated with sporangia or as the only stage present. The ability to sclerotize quickly and for sclerotia to germinate and produce plasmodia and fruiting bodies quickly would be an important attribute for survival under desert conditions.

Alexopoulos (1964) discussed the rapid sporulation of some Myxomycetes in moist chamber culture. Sporangia produced in fewer than five days usually belonged to species with proto- or aphanoplasmodia. We have observed fruiting of *Echinostelium minutum* deBary within 7 to 8 days of wetting moist chamber material. In addition, *Didymium* sp. (Blackwell and Gilbertson, 1980) and an undescribed species of

Table 2. Myxomycete species known from herbivorous animal dung collected in deserts.

Species	References
Comatricha nigra (Pers.) Schroet.	Faurel et al. (1965)
C. pulchella (C. Bab.) Rost.	Faurel et al. (1965)
Licea fimicola Dearn. et Bisby	Angel and Wicklow (1975); cited here
Perichaena corticalis (Batsch) Rost.	Faurel et al. (1965)
Arcyria cinerea (Bull.) Pers.	Faurel et al. (1965)
Echinostelium minutum deBary	cited here
Badhamia gracilis (Macbr.) Macbr.	cited here
Badhamia sp.	cited here
Fuligo cinerea (Schw.) Morgan	cited here
F. septica (L.) Wiggers	cited here
Physarum compressum Alb. et Schw.	Faurel et al. (1965)
P. didermoides (Pers.) Rost.	Faurel et al. (1965)
P. leucopus Link	Faurel et al. (1965)
P. nucleatum Rex	Faurel et al. (1965)
P. pusillum (Bert. et Curt.) G. Lister	Faurel et al. (1965); cited here
Craterium leucocephalum (Pers.) Ditmar	Faurel et al. (1965)
Diderma simplex (Schroet.) G. Lister	Faurel et al. (1965)
Didymium anellus Morgan	cited here
D. iridis (Ditmar) Fries	cited here
Collodema oculatum (Lippert) G. Lister	Faurel et al. (1965)

Didymium fruited within five days. In agar culture these two species have extremely small phaneroplasmodia which produce single sporangia (Blackwell and Gilbertson, 1980) and form sclerotia of discrete macrocysts similar to those reported by Alexopoulos (1964) for species of *Comatrichia, Stemonitis, Arcyria,* and *Perichaena.* An even more intriguing observation was the appearance of one to four sporangia of *Badhamia gracilis* within one to three days after wetting and numerous sporangia within six days in *B. gracilis* and *Physarum straminipes.* The large phaneroplasmodia of these two species were often observed the day after wetting, and almost certainly formed from sclerotia although none was observed on the substrates.

The records on which this paper is based were taken from specimens in the University of Arizona Herbarium and specimens collected in the field by the authors during the spring, summer, and winter of 1979. Additional specimens which are indicated were obtained from moist chamber cultures of various desert substrates (Gilbert and Martin, 1933). The myxomycete classification of Martin and Alexopoulos (1969) is followed. Plant substrate nomenclature follows Kearny and Peebles (1966). All specimens are deposited in the University of Arizona Herbarium. Collecting localities in Arizona are listed below.

> Tucson environs, Pima Co., 2400 ft; Saguaro National Monument, West Unit (SNMW), Tucson Mtn. foothills, Pima Co., 2600 ft; Sil Nakya Hills (SNH), Papago Indian Reservation, Pima Co., 2400 ft; Molino Basin, Santa Catalina Mts., Pima County, 4500 ft; Santa Rosa Valley, Papago Indian Reservation, Pinal Co., 2000 ft; Organ Pipe National Monument, Quitoboquito Spring, Pima Co., 1500 ft; Saguaro National Monument, East Unit (SNME), Rincon Mtn. foothills, Pima Co., 3100 ft; Redington Pass Rd. (RPR), Rincon Mtn. foothills, Pima Co., 5300 ft; Orange Grove Rd. (OGR), Santa Catalina Mtn. foothills, Pima Co., 2700 ft; Camino Padre Isidoro (CPI), Santa Catalina Mtn. foothills, Pima Co., 2800 ft; Santa Rita Experimental Range (SRER), Santa Rita Mtn. foothills, Pima Co., 3500 ft; Mt. Lemmon Hwy., Old Federal Prison Camp (Head of Soldier Canyon), Pima Co., 5000 ft; Superior, Dripping Springs Mtns., Pinal Co., 2600 ft.

COMATRICHA LAXA Rost. - OGR, on corrugated cardboard, 25 Aug. 1979, 79-054; SNME, on *Carnegiea gigantea* (Engelm.) Britt. et Rose (saguaro), 28 Aug. 1979, 79-068; SNME on *Cercidium microphyllum* (Torr.) Rose et Johnst. (yellow palo verde), 28 Aug. 1979, 79-067B; CPI on *Prosopis juliflora* (SW.) DC. (mesquite), 26 Aug. 1979, 79-056B; ORG, on *Opuntia fulgida* Engelm. (jumping cholla), 25 Aug. 1979, 79-058C; SRER, on jumping cholla, 24 Aug. 1979, 79-045B.

The genus *Comatricha* is well represented in alpine habitats of Arizona (Evenson, 1961; Gilbertson and Blackwell, unpublished). Although *C. laxa* was the only species collected by us in the desert it was common in several localities. Collection 79-054 occupied a 2 x 4 ft area on three layers of a discarded corrugated cardboard box which had been rain-soaked three weeks before collection.

LICEA FIMICOLA Dearness et Bisby - Tucson, on goat (?) dung, U. of Arizona Mycology class, moist chamber, Feb. 1977.

LICEA PARASITICA (Zukal) Martin - SNMW nature trail, on *Olneya tesota* Gray (ironwood), 21 Aug. 1979, 79-041B; OGR, on jumping cholla, 25 Aug.

BADHAMIA GRACILIS (Macbr.) Macbr. - Tanque Verde Rd., on deer dung, moist chamber, substrate collected May 1979, wet 14 May 1979, fruited 29 May 1979, 79-012; SNMW, on saguaro, moist chamber, substrate collected July 1973, wet 14 May 1979, fruited 22 May 1979, 79-017A; SNH, on *Lemaireocereus thurberi* (Engelm) Britt. et Rose (organ pipe cactus), 8 June 1979, RLG 12069A; SNH, on saguaro, moist chamber, substrate collected 8 June 1979, wet 21 June 1979, fruited 27 June 1979, 79-019B; SNH, on saguaro, 8 June 1979, RLG 12072C; SNH, on saguaro, moist chamber, substrate collected 8 June 1979, wet 21 June 1979, fruited 24 June - 26 June 1979, 79-021; SNH, on jack rabbit dung, moist chamber, substrate collected 8 June 1979, wet 21 June 1979, fruited 23 June - 30 June 1979, 79-027; *CPI, on unidentified herbivorous dung, moist chamber, substrate collected Oct. 1978, wet 20 Nov. 1978, fruited 8 Dec. 1978, 79-031C; SNMW, Signal Hill, on saguaro, 22 Aug. 1979, 79-033B, 79-035, 79-037, 79-038, 79-039; CPI, on *Opuntia phaeacantha* Engelm. (Engelmann prickly pear), 26 Aug. 1979, 79-049, 79-051; OGR, on jumping cholla, 25 Aug. 1974, 79-052B; OGR, on Engelmann prickly pear, 25 Aug. 1979, 79-053; OGR, on *Ferocactus wislizenii* (Engelm.) Britt et Rose (barrel cactus) 25 Aug. 1979, 79-055; OGR, on *Fouquieria splendens* Engelm. (ocotillo), 25 Aug. 1979, 79-057; OGR, on jumping cholla, 25 Aug. 1979, 79-059; OGR, on Engelmann prickly pear, 25 Aug. 1979, 79-060, 79-062; SNME, nature trail, on saguaro, 28 Aug. 1979, 79-065, 79-066; Organ Pipe National Monument, Quitoboquito Spring, on *Populus fremontii* S. Wats. (Fremont cottonwood), 31 Mar. 1979, RLG 11947; SRV, on saguaro, 11 Nov. 1971, Elmer R. Canfield No. 71-364; Old Federal Prison Camp, on Parry agave, 20 Nov. 1979, RLG 12277; RLG 12279; RLG 12282B; RLG 12281; OGR, on Engelmann prickly pear, 11 Nov. 1979, RLG 12251; RLG 12252; RLG 12253; CPI, on *Aloe saponaria* Haw. (aloe) 11 Nov. 1979, RLG 12244; CPI, on *Agave americana*L. (American agave) 11 Nov. 1979, RLG 12245; SNMW, on saguaro, 14 Nov. 1979, RLG 12270; SNMW, on Engelmann prickly pear, 14 Nov. 1979, RLG 12273; Molino Basin, on Parry agave, 13 Nov. 1979, RLG 12261; SNH, on saguaro, 7 Nov. 1979, RLG 12238; SNH, on organ pipe cactus, 7 Nov. 1979, RLG 12235; RLG 12239.

This species was collected in all localities where dead cacti were examined and was one of the few species found in large fruitings. Spore markings (Scheetz and Alexopoulos, 1971) were consistent in all collections and in agar-cultured material, and spore color was generally dark but somewhat variable.

BADHAMIA MACROCARPA (Ces.) Rost. - SNMW, nature trail, on ironwood, 21 Aug. 1979, 79-041A.

BADHAMIA SP. - *RPR, on old cow dung, moist chamber, substrate collected May 1979, wet 14 May 1979, fruited 24 May 1979, 79-014B.

In culture this species consistently had distinctly oval spores with spines at one end and side with the other end and side smooth. Except for the spore ornamentation this specimen is similar to *B. ovispora* Racib. and *B. apiculospora* (Härkönen) U. Eliass. et Lundq.

BADHAMIA PANICEA (Fries) Rost. - SRER, on jumping cholla, 24 Aug. 1979, 79-046; SNH, Papago Indian Reservation, on saguaro, 8 June 1979, RLG 12072A.

PHYSARUM AURISCALPIUM Cooke - Santa Rita Exp. Range, on jumping cholla, 24 Aug. 1979, 79-045D.

PHYSARUM COMPRESSUM Alb. et Schw. - SNMW, Signal Hill, on saguaro, 22 Aug. 1979, 79-033A, 79-034, 79-036.

PHYSARUM LATERITIUM (Berk. et Rav.) Morgan - SNH, on organ pipe cactus, moist chamber, substrate collected 8 June, 1979, wet 2 June 1979, (red sclerotium), fruited 23 July 1979, 79-026A.

This specimen was collected as a yellow plasmodium which formed a red sclerotium before being placed in moist chamber culture. The plasmodium did not fruit until it was placed in direct light from a window.

PHYSARUM LEUCOPHAEUM Fries - SNMW, nature trail, on saguaro, 21 Aug. 1979, 79-042A; SNMW, Loop Rd., on jumping cholla, 21 Aug. 1979, 79-044; SRER, on jumping cholla, 24 Aug. 1979, 79-045C; OGR, on jumping cholla, 25 Aug. 1979, 79-052, 79-058B; OGR, on Engelmann prickly pear, 25 Aug. 1979, 79-061; SNME, nature trail, on yellow palo verde, 28 Aug. 1979, 79-063B; 79-067A.

PHYSARUM LUTEOLUM Peck - Molino Basin, on Parry agave, 13 Nov. 1979, RLG 12274.

PHYSARUM NOTABILE Macbr. - SNMW, nature trail, on saguaro, 21 Aug. 1979, 79-042B.

PHYSARUM PUSILLUM (Berk. et Curt.) G. Lister - *CPI, on unidentified herbivorous dung, moist chamber, substrate collected Oct. 1978, wet Nov. 1978, fruited 2 Dec. 1978, 79-031B.

PHYSARUM STRAMINIPES Lister - SNMW, on saguaro, moist chamber, substrate collected July 1973, wet 14 May 1979, 79-017C; SNH, on saguaro, moist chamber, substrate collected 8 June 1979, wet 21 June 1979, fruited 27 June, 1979, 79-019C; SNH, on organ pipe cactus, moist chamber, substrate collected 8 June 1979, wet 21 June 1979, fruited 26 June 1979, 79-023; SNH, on saguaro, 8 June 1979, RLG *12069B, 12071, 12072B; SNH, on saguaro, 7 Nov. 1979, RLG 12234; RLG 12257.

This is the third report of *P. straminipes* from the Western Hemisphere. Spore and sporangial morphology agreed with the description of Martin and Alexopoulos (1969). Sporangial stalks were short and stout in moist chamber developments and lacking in field collected specimens. Spores were distinctly ornamented with pale lines due to absence of spines. These pale areas were usually the site of wrinkles forming an overlying reticulum (Sheetz and Alexopoulos, 1976).

PHYSARUM VERNUM Somm. ex Fries - *CPI, cultivated sedge debris, 26 Aug. 1979, 79-050; CPI, on American agave, 11 Nov. 1979, RLG 12244; SNME, nature trail, on yellow palo verde, 28 Aug. 1979, 79-063A; Old Federal Prison Camp, on dead leaves of *Agave schottii*, 10 Sept. 1979, RLG 12151.

DIDYMIUM ANELLUS Morgan - *CPI, unidentified herbivorous dung, moist chamber, substrate collected Oct. 1978, wet 20 Nov. 1978, fruited 2 Dec. 1978, 79-031E.

This specimen grew easily from spore to spore in agar culture.

DIDYMIUM DUBIUM Rost. - SNME, nature trail, on yellow palo verde, 28 Aug. 1979, 79-064.

1979, 79-058A.

LICEA PEDICELLATA (H. C. Gilbert) H. C. Gilbert - SRER, on jumping cholla, 24 Aug. 1979, 79-045E.

PERICHAENA CORTICALIS (Batsch) Rost. - SNMW nature trail, on saguaro, 21 Aug. 1979, 79-040; SNH, on saguaro, moist chamber, substrate collected 8 June 1979, wet 21 June 1979, fruited ?, 79-019E; Dripping Springs Mtns., 10 mi S. Superior, on saguaro, RLG 10549, 4 Nov. 1971.

PERICHAENA DEPRESSA Libert - Molino Basin, on *Agave parryi* Engelm. (Parry agave) 13 Nov. 1979, RLG 12262.

PERICHAENA VERMICULARIS (Schw.) Rost. - SNH, on *Opuntia* sp. (cholla), moist chamber, substrate collected 8 June 1979, wet 21 June 1979, fruited 2 July 1979, 79-018B; SNH, on saguaro, moist chamber, substrate collected 8 June 1979, wet 21 June 1979, fruited 2 July 1979, 79-019D. Old Federal Prison Camp, on Parry agave, 20 Nov. 1979, RLG 12278; RLG 12280; RLG 12282A.

ECHINOSTELIUM MINUTUM deBary - Tucson, on unidentified dung, moist chamber, substrate collected Oct. 1978, wet 14 May 1979, fruited 29 May 1979, 79-010; RPR, on cow dung, moist chamber, substrate collected May 1979, wet 14 May 1979, fruited 22 May 1979, 79-014A; SNH, on cholla, moist chamber, substrate collected 8 June 1979, wet 21 June 1979, fruited 28 June 1979, 79-018A.

FULIGO CINEREA (Schw.) Morgan - *CPI, Tucson, on unidentified herbivorous dung, moist chamber, substrate collected Oct. 1978, wet 20 Nov. 1978, fruited 2 Dec. 1978, 79-031D.

In agar culture this isolate of *F. cinerea* grew easily. Some plasmodial fragments always sclerotized when the main part of the plasmodium fruited.

FULIGO MEGASPORA Sturgis - Tucson Rose Garden, on soil, 26 June 1950, R. B. Streets.

This specimen is typical of the description given by Martin and Alexopoulos (1969), except that spore size is smaller (13-15 µm).

FULIGO SEPTICA (L.) Wiggers - SNMW nature trail, on soil, 21 Aug. 1979, 79-043; Circle O Worm Ranch (brought into plant clinic), on horse dung, 24 June 1976; SNH, on soil, 7 Nov. 1979, RLG 12241; on leaf mold in flower bed, Sept. 1979, RLG 12248.

A single well-matured aethalium (79-043) was collected on bare unshaded desert soil. Soil temperature was approximately 62 C (130 F).

BADHAMIA AFFINIS Rost. - *CPI, Tucson, on mesquite, 26 Aug. 1979, 79-056A; SNH, on saguaro, 8 June 1979, RLG 12069C; SNMW, on saguaro, 14 Nov. 1979, RLG 12271.

One specimen was grown from spore-to-spore on half strength corn meal agar, and sporangial morphology was consistent with field collected material.

---

*Denotes spore-to-spore culture on half strength corn meal agar (Gray and Alexopoulos, 1968).

DIDYMIUM SP. (Blackwell and Gilbertson, 1980) - *SNMW, on saguaro, moist chamber, substrate collected July 1973, wet 14 May 1979, fruited 22 May 1979, 79-017B (Type); SNH, on saguaro, moist chamber, substrate collected 8 June 1979, wet 21 June 1979, fruited 26 June 1979, 79-019A.

The minute sporangia of this species fruited abundantly on the moist chamber-cultured saguaro from Saguaro National Monument. Only four sporangia were produced from Sil Nakya Hills, but they were similar in all respects to the SNM collection. In half strength corn meal agar culture plasmodia formed numerous sclerotia (Blackwell and Gilbertson, 1980).

DIDYMIUM IRIDIS (Ditmar) Fries - *CPI, unidentified herbivorous dung, moist chamber, substrate collected Oct. 1978, wet 20 Nov. 1978, fruited 6 Dec. 1978, 79-031A.

Mass spore, single-spore, and sclerotial cultures on agar produced numerous phaneroplasmodia which remained small and produced up to five or six sporangia upon fruiting.

DIDYMIUM KARSTENSII Nann.-Brem. -*SNMW, nature trail, on ironwood, 21 Aug. 1979, 79-041C.

Didymium karstensii is similar to *D. squamulosum* except for spore morphology. Spores have a rough overlying reticulum like that of *Badhamia gracilis* and *Physarum straminipes*. The presumptive phaneroplasmodium of this species developed from field collected spores sown on half strength corn meal agar was colorless to slightly creamy. Sclerotia formed abundantly, but sporulation was aberrant and prevented positive identification.

DIDYMIUM SP. - *SNH, on organ pipe cactus, moist chamber, substrate collected 8 June 1979, wet 21 June 1979, fruited 26 June 1979, 79-026B.

This undescribed species produced small, pulvinate sporangia. Distinctive capillitial ornamentation of bell-shaped enlargements in moist chamber developments was not present in agar-cultured sporangia. Minute phaneroplasmodia similar to those found in *D. eremophilum* produced a single sporangium. In culture the plasmodia sclerotized readily.

DIDERMA EFFUSUM Link - SRER, on jumping cholla, 24 Aug. 1979, 79-048.

DIDERMA SP. - SRER, on jumping cholla, 24 Aug. 1979, 79-045A.

This specimen consists of pale pink effused plasmodiocarps with highly branched, dark, thick capillitium, and spores paler on one side. The spores germinated, but did not produce plasmodia in agar culture.

ACKNOWLEDGMENTS

We thank Dr. D. H. Pfister of the Farlow Herbarium of Cryptogamic Botany, Harvard University, for providing some of the literature cited. Field work by Blackwell was supported by a Hope College Mellon Faculty Development Grant.

LITERATURE CITED

ALEXOPOULOS, C. J. 1964. The rapid sporulation of some Myxomycetes in moist chamber culture. Southwestern Naturalist 9:155-159. ALEXOPOULOS, C. J. 1970. The rain forest Myxomycetes. *In* A tropical rain forest. (R. T. Odum, ed.). Ch. F-3:F-21-23. ALEXOPOULOS, C. J., and J. A. SÁENZ R. 1975. The Myxomycetes of Costa Rica. Mycotaxon 2:223-271. BLACKWELL, M., and R. L. GILBERTSON. 1980. *Didymium eremophilum*; A new myxomycete from the Sonoran Desert. Mycologia 72: in press. BRAUN, K. L., and H. W. KELLER. 1976. Myxomycetes of Mexico I. Mycotaxon 3:297-317. CUMMINS, G. B. 1979. Rust fungi of the Sonoran Desert. Mycotaxon 10:1-20. ELIASSON, U., and N. LUNDQVIST. 1979. Fimicolous Myxomycetes. Bot. Notiser 132:551-568. EVENSON, A. E. 1961. A preliminary report of the Myxomycetes of southern Arizona. Mycologia 53:137-144. FARR, M. L. 1974. Some new myxomycete records from the neotropics and some taxonomic problems in the Myxomycetes. Proc. Iowa Acad. Sci. 81:37-40. FAUREL, L., J. FELDMANN, and G. SCHOTTER. 1965. Catalogue des Myxomycètes de l'Afrique du Nord. Bull. Soc. Hist. Nat. de l'Afrique du Nord. 55:7-39. GILBERT, H. C., and G. W. MARTIN. 1933. Myxomycetes found on the bark of living trees. Univ. Iowa Stud. Nat. Hist. 15:3-8. GILBERTSON, R. L., H. H. BURDSALL, JR., and E. R. CANFIELD. 1976. Fungi that decay mesquite in southern Arizona. Mycotaxon 3:487-551. GRAY, W. D., and C. J. ALEXOPOULOS. 1968. *Biology of the Myxomycetes*. Ronald Press, N. Y. 288 p. KEARNY, T. H., and R.H. PEEBLES. 1969. *Arizona flora*. Univ. California Press. Berkeley and Los Angeles. 1032 p. plus supplement. KELLER, H. W., and K. L. BRAUN. 1977. Myxomycetes of Mexico II. Bol. Soc. Mex. Mic. 11:167-180. KELLER, H. W., and T. E. BROOKS. 1976. Corticolous Myxomycetes V: Observations on the genus *Echinostelium*. Mycologia 68:1204-1220. KELLER, H. W., and T. E. BROOKS. 1977. Corticolous Myxomycetes VII: Contribution toward a monograph of *Licea*, five new species. Mycologia 69:667-684. LINDSEY, J. P., and R. L. GILBERTSON. 1975. Wood-inhabiting homobasidiomycetes on saguaro in Arizona. Mycotaxon 2:83-103. MARTIN, G. W., and C. J. ALEXOPOULOS. 1969. *The Myxomycetes*. Univ. of Iowa Press. 560 p. NAKASONE, K. K., and R. L. GILBERTSON. 1978. Cultural and other studies of fungi that decay ocotillo in Arizona. Mycologia 70:266-299. NANNENGA-BREMEKAMP, N. E. 1964. Notes on Myxomycetes VIII. A new species of *Didymium* from the Netherlands. Acta Bot. Neerl. 13:246-249. RAMON, E. 1968. Myxomycetes of Israel. Israel J. Bot. 17:207-211. RANZONI, F. V. 1968. Fungi isolated in culture from soils of the Sonoran Desert. Mycologia 60:356-371. RAPER, K. B., and C. J. ALEXOPOULOS. 1973. A myxomycete with a singular myxamoebal encystment stage. Mycologia 65:1284-1295. REYNOLDS, D. R., and C. J. ALEXOPOULOS. 1971. Southeast Asian Myxomycetes. I. Thailand and Burma. Pacific Science 15:33-38. SCHEETZ, R. W., and C. J. ALEXOPOULOS. 1971. The spores of *Badhamia gracilis* (Myxomycetes). Trans. Am. Micro. Soc. 90: 473-475. SCHEETZ, R. W., and C. J. ALEXOPOULOS. 1976. Studies on the spores of Myxomycetes. II. *Physarum straminipes*. Mycotaxon 4:335-339. SHREVE, F., and I. L. WIGGINS. 1964. *Vegetation and flora of the Sonoran Desert*. Stanford Univ. Press, Stanford, Calif. 2 vol. 1740 p. SMITH, H. V. 1956. The climate of Arizona. Univ. Ariz. Agric. Exp. Sta. Bull. 279. 99 p. SOLHEIM, W. G., and R. L. GILBERTSON. 1973. *Peronospora* species in Arizona. Mycopathol. et Mycol. Appl. 49:153-159. WHITNEY, K. D., and H. W. KELLER. 1980. A new species of *Echinostelium*. Mycologia 72: in press.

MYCOTAXON

Vol. XI, No. 1, pp. 150-164 April-June 1980

DIDYMIUM ATRICHUM, A NEW MYXOMYCETE FROM SOUTH-CENTRAL TEXAS

MARY R. HENNEY

Northrop Services, Inc., P. O. Box 34416
Houston, Texas 77034

CONSTANTINE J. ALEXOPOULOS

Cell Research Institute and Department of Botany
University of Texas at Austin
Austin, Texas 78712

and

RAYMOND W. SCHEETZ

Biology Department, University of Southern Mississippi
Hattiesburg, Mississippi 39401

SUMMARY

Didymium atrichum M. R. Henney and Alexopoulos is described from south-central Texas. Because of the presence of crystalline lime on its peridium, the organism is placed in the genus Didymium despite its lack of capillitium. The sporangia are produced either singly or in heaped clusters resembling pseudoaethalia. The spores, under the oil immersion objective of the light microscope, appear to be minutely verrucose or faintly reticulate, but the scanning electron microscope reveals a conspicuous, if sometimes broken, reticulation. The often clustered sessile sporangia, the complete absence of capillitium and the reticulate spores, all characters which have proved to be stable on various natural and artificial substrata under three conditions of temperature and after numerous subcultures in the last 16 years, make Didymium atrichum difficult to confuse with any previously known myxomycete. The organism completes its life cycle from spore to spore in mass-spore culture within seven days under favorable conditions, and in monosporous culture in about 14 days. Light is not required

by the milky white phaneroplasmodium to sporulate.

INTRODUCTION

On December 29 and 30, 1962, one of us (MRH) collected various materials in south-central Texas for moist chamber cultures, hoping to develop myxomycete fructifications for a continuing project which aims to assemble a list of Myxomycetes occurring in Texas (Alexopoulos, 1965; Alexopoulos and Henney, 1971). This material was placed in moist chambers a few days later according to the method of Gilbert and Martin (1933). Several minute, sessile myxomycete sporangia (Figure 10)[1] devoid of capillitium, but with fully matured spores, which developed on a leaf that had fallen from a Bauhinia sp. tree, could not be placed in any known species, but appeared to belong to the genus Didymium because of the crystalline lime on their peridia (Figures 11-14). Spores were well developed and their markings were quite different from those of any known species of Didymium. Under the phase contrast oil immersion objective they appear to be faintly reticulate in some specimens and punctate or spiny in others. The scanning electron microscope, however, revealed a very conspicuous reticulation (Figure 19) in all spores examined. No columella was present in any of the sporangia examined, except for a small calcareous dome in some sporangia, which might be interpreted as a rudimentary columella. Energy dispersive x-ray spectrometry[2] has demonstrated (Figure 20) the presence of phosphorus in the sporangia. Schoknecht (1975) reported traces of phosphorus in Didymium trachysporum G. Lister.

MATERIALS, METHODS, AND RESULTS

Isolation. Spores from several sporangia were suspended in about 3 ml of sterile distilled water in a small screw cap tube, which was shaken vigorously for a few seconds to disperse the spores. Monosporous cultures were prepared by spreading a few loopfuls of the spore suspension and of a suspension of Enterobacter aerogenes cells over the

[1]All material for SEM was prepared according to standard procedures (Scheetz & Alexopoulos, 1976).

[2]Procedure described in Nelson, Scheetz, and Alexopoulos, (1977).

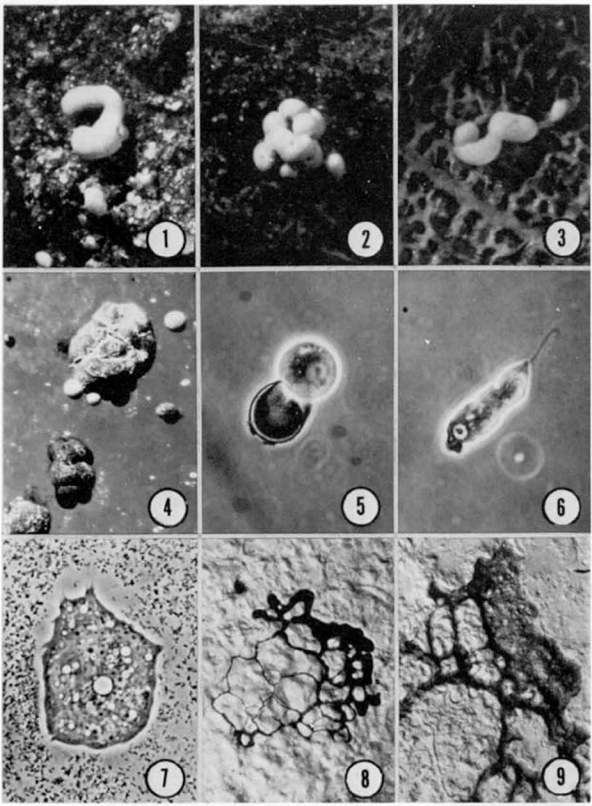
surface of three Petri dishes containing lactose-yeast (LY) 3% agar and allowing them to dry. Well-separated spores were cut out under a dissecting microscope at 90X magnification and transplanted to a plate containing five or six glass rings embedded in LY agar, one spore to a ring. Each ring was then checked under the low power of a compound microscope to insure that it contained but a single spore.

As it turned out, the organism completed its life cycle in monosporous culture, and mass spore transfers were routinely made thereafter to perpetuate the organism in culture. Smart (1937) indicated that germination of single myxomycete spores is more difficult than germination in mass spore sowings. This presented no serious problem with our organism, as 54.8% of the isolated spores germinated in our experiments.

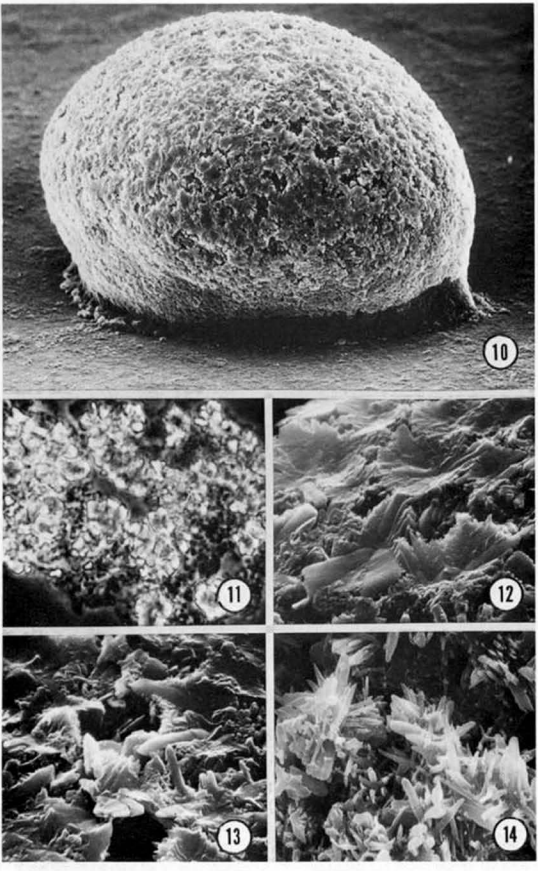
Spore germination. Spore germination was observed many times in hanging drops prepared as follows: Melted, hot LY agar was poured onto a large (45 X 50 mm) cover slip and the excess agar was drained off leaving a thin film on the cover glass. After a few seconds when the agar was dry, two drops of sterile water were placed on the agar in the middle of the cover slip and inoculated with spores from a 14-day old culture that had sporulated freely. This preparation was inverted over a small, plastic Petri dish half filled with sterile water.

Spore germination could be observed in the hanging drop through the cover slip and the thin layer of agar, under the low and high powers of the microscope and often under the oil immersion objective. Spores were examined every hour from the time of inoculation until the germination process had been completed.

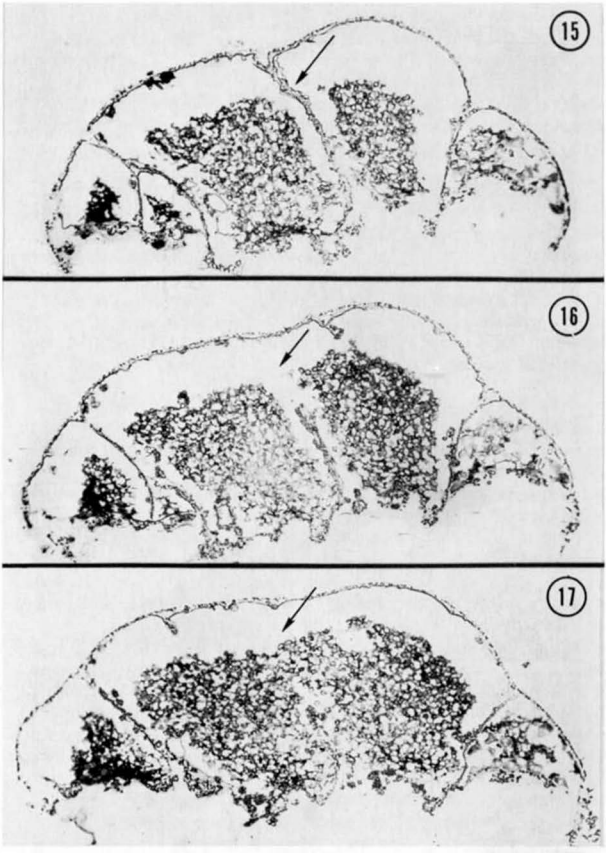
Spores germinate by the cracking method as described by Gilbert (1928) for Fuligo septica (L) Wiggers and as is characteristic of the Physarales in general. The first indication of germination is a slight crack in the spore wall. This is soon followed by a flow of protoplasm through the V-shaped opening. At first myxamoebal (Figure 5), the protoplast becomes very active, produces flagella, and swims away as a swarm cell (Figure 6). Two hours after inoculation many swarm cells could be seen in the hanging drop. Maximum germination occurs in two to five hours. Never was more than one protoplast seen emerging from a spore.



Figures 1-9. Didymium atrichum. 1. Sporangia on bark. SEM X 56. 2. Clustered sporangia on bark. SEM X 32. 3. Sporangia on leaf. SEM X 32. 4. Clustered sporangia on agar. SEM X 27. 5. Germinating spore. Phase contrast X 9,950. 6. Swarm cell. Phase contrast X 1,000. 7. Young plasmodium. Phase contrast. X 90. 8. Plasmodium at a later stage. X 16. 9. Almost full grown plasmodium X 16.



Figures 10-14. Didymium atrichum. 10. Mature sporangium. Note hypothallus. SEM X 555. 11. Aggregate of lime crystals. Phase contrast X 1,400. 12. Peridium. SEM X 10,250. 13. Peridium. SEM X 4,700. 14. Peridium. SEM X 2,500.



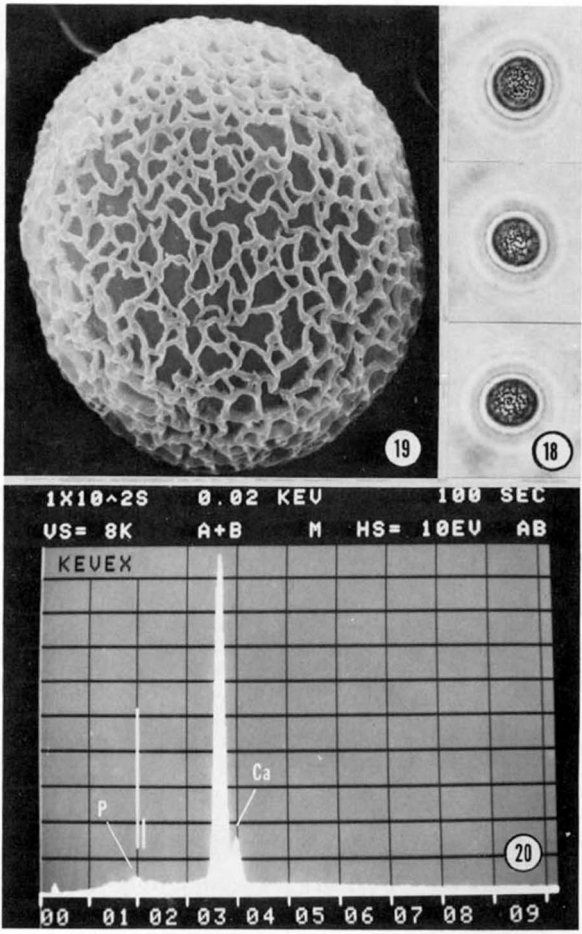
Figures 15-17. Didymium atrichum. Sequential sections through a cluster of sporangia. Note incomplete partitions at arrows. X 121.

Syngamy and Plasmodial Formation. Fusion of swarm cells at their posterior ends was seen on a few occasions, but karyogamy was not observed. It is, therefore, impossible to state whether this strain of the organism is homothallic or apogamic. Because only a single protoplast was seen ever to issue from a spore, however, it appears probable that heterothallism is not involved.

Plasmodia apparently develop through the enlargement of a single protoplast -- myxamoeba or possibly zygote. These never grow very large, but appear to split after reaching a certain size. Although remaining very small, the plasmodia develop veins and terminal fans characteristic of phaneroplasmodia (Figures 7-9). Their protoplasm is highly vacuolate and very granular, characters also typical for this type of plasmodium. At first colorless, the plasmodia become milky white as they grow.

Sporulation. At 25 C, on LY agar, this organism completes its life cycle from spore to spore in seven days from mass spore sowings, but in 14 days in monosporous culture. Each plasmodium becomes concentrated and, depending on its size at the time of sporulation, forms one to several single or closely grouped fruiting bodies (Figure 4). In the latter case, the sporangia form mounds and appear to be actually fused as is evident in the three sections through one such mass in which incomplete walls separate individual sporangia (Figures 15-17). Whether such masses are simple aggregations of sporangia, pseudoaethalia, or aethalia, is a matter of interpretation. The fact remains that both single and massed sporangia are formed under all conditions studied and on all substrata. The proportion of single and massed sporangia varies in different cultures, but at no time could it be correlated with either type of substratum or temperature. We believe that the size a plasmodium attains by the time it sporulates is a factor that influences the type of fructification produced, the larger plasmodia tending, perhaps, to produce masses of fruiting bodies.

Effect of Temperature and Substrate on Plasmodial Formation and Sporulation. Plasmodial formation and sporulation were studied under three conditions of temperature on five agar media in triplicate. A single spore was planted, allowed to germinate and complete the life cycle on agar, forming a multitude of tiny sporangia. The spores of 150 of these sporangia were placed in 50 ml of sterile



Figures 18-20. Didymium atrichum. 18. Spores. Phase contrast X 1,050. 19. Spore. SEM X 9,700. 20. Energy dispersive x-ray spectrum of the peridium.

distilled water. The number of spores was determined to be 250/0.1 ml, by the use of a bright-line hemocytometer. Twenty determinations were made and the average computed. Five different media were used and three temperatures. One-tenth ml of a spore suspension was plated onto 100 X 20 mm Petri dishes containing the following media: lactose-yeast, corn meal, half-strength corn meal, Bristol's, and plain agar. Enterobacter aerogenes was used as the associated organism. All experiments were performed in triplicate.

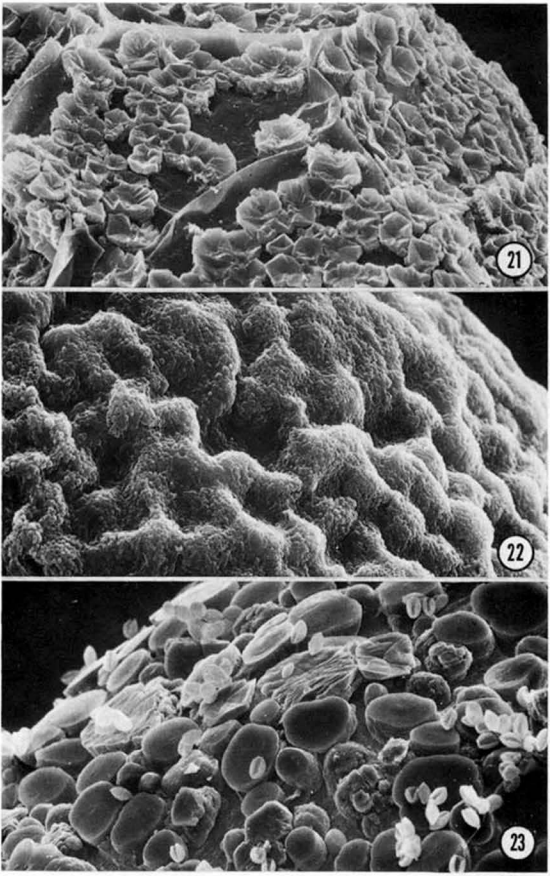
Table 1 indicates the average number of plasmodia and sporangia (or sporangial groupings) per plate at each temperature, on the five media employed, eight days after the spores were sown.

TABLE 1. EFFECT OF TEMPERATURE AND SUBSTRATUM ON PLASMODIAL FORMATION AND SPORULATION.

(Numbers of plasmodia and sporophores are averages for three plates.)

Medium	Structure	15 C	20 C	25 C
Lactose yeast agar	Plasmodia	--	14.6	20.6
	Sporophores	--	--	10.6
Plain agar	Plasmodia	--	--	2.0
	Sporophores	--	--	--
Bristol's agar	Plasmodia	--	3.0	10.3
	Sporophores	--	--	2.6
Corn meal agar	Plasmodia	--	12.3	18.6
	Sporophores	--	--	6.6
Half strength corn meal agar	Plasmodia	--	--	--
	Sporophores	--	--	--

Lactose yeast agar (LY) -- Lactose 1 g, Yeast extract 0.5 g, Agar 30 g.
Bristol's agar -- for formula see Bristol (1919).
Corn meal agar (CM) -- Difco corn meal agar prepared according to directions.
Half strength corn meal agar (CM/2) -- Equal quantities of Difco corn meal agar and plain agar.



Figures 21-23. SEMs of peridia of three species of Myxomycetes. 21. Didymium trachysporum G. Lister. X 1,060. 22. Squamuloderma nullifila Kowalski. X 1,800. 23. Lepidoderma chailletii Rost. X 325.

A number of natural substrata were also inoculated. These were pieces of bark or leaves from living trees as follows: bark of Quercus virginiana, Pinus taeda, Carya pecan; leaves of Bauhinia sp. All natural substrata were placed on filter paper in Petri dishes and, after autoclaving, were inoculated with a spore suspension of the myxomycete under study and with a few drops of Enterobacter aerogenes cell suspension. Sporangia were seen developing on these substrata eight days after inoculation; they had the same characteristics when mature as those developed on agar (Figures 1-3).

Effect of Light on Sporulation. The statement is often found in the literature that pigmented plasmodia require light for sporulation, but that white plasmodia do not (Gray and Alexopoulos, 1968). Gustafson (1973), however, showed that the white plasmodia of the particular strain of Didymium squamulosum (Alb. & Schw.) Fries he was studying would not form fruiting bodies in the dark. An experiment was performed, therefore, to determine whether our slime mold required light for sporulation.

One-tenth ml of an aqueous spore suspension containing 2.5×10^3 spores/ml was plated onto each of eight 60 X 20 mm Petri dishes together with a few drops of Enterobacter aerogenes cell suspension. Four of these contained LY agar and the other four CM/2 agar (Difco corn meal agar mixed with equal quantities of plain agar). All eight plates were placed in a light-tight box together with a small strip of unexposed 35 mm fast film to test for possible light leakage. The film was still unexposed at the end of the experiment. The box was placed in an incubator equipped with cool-white fluorescent tubes and programmed to maintain a temperature of 25 C. An identical set of plates was incubated next to the box on the shelf of the incubator.

All plates were examined after two weeks. Each was found to contain many sporangia. No significant differences were found in either the number or the morphology of the sporophores in the two sets of plates. It was concluded that this organism requires no light for sporulation. It will be remembered that in the experiment summarized in Table 1 the organism did not sporulate on CM/2 agar. In the light/dark experiment a number of sporophores were formed on this medium. We have no explanation for this discrepancy.

Effect of Substratum and Temperature on Taxonomic Characters. In accordance with the recommendations of Alexopoulos (1969) it was now imperative to test the stability of the major characters of the fructification and the spores before describing a new species.

A comparative study of the sporangia and spores produced on various substrata at 15, 20, and 25 C was undertaken to determine if the distinguishing characteristics of this organism remained stable under different conditions prevailing at the time of sporulation. Three types of agar and several natural substrata (bark and leaves from three species of trees, and pieces of wheat straw) were inoculated in triplicate and incubated at the three different temperatures listed above, in lighted incubators, after the spores had germinated at room temperature. Escherichia coli was used in these experiments as the associated organism.

Spore size and markings were quite uniform under all these conditions. The proportion of single sporangia to sporangial aggregates and the size of the sporophores varied in different plates but could not be correlated either with substratum or temperature, nor could differences in sporangial dimensions. Columella and capillitium were absent from all sporangia examined.

TAXONOMY

In view of the fact that the major characters used in classification were found to remain stable under a variety of environmental conditions on various substrata and have remained stable after more than 30 subcultures over 16 years, and inasmuch as the characteristics of this organism do not correspond to those of any known species of myxomycete, the description of a new species seems warranted.

Didymium atrichum M. R. Henney & Alexopoulos, sp. nov.

Sporangia sessilia, globosa vel plasmodiocarpa, dispersa vel fasciculata, 80-250 µm longa; hypothallus conspicuus, parce elevatus; peridium membranaceum, crystallis calcis obtectum vel conspersum; columella absens vel rudimentaria; capillitium absens; sporae globosae vel subglobosae, reticulatae, fuscobrunneae, 10-11 µm, diam.; phaneroplasmodium minutum, album. Holotypus = UTMC-1681

(TEX).

Didymium atrichum M. R. Henney & Alexopoulos, sp. nov.

Sporangia sessile, globose to plasmodiocarpous, scattered or clustered, 80-250 µm across; hypothallus conspicuous, gelatinous at first, slightly elevated when dry, sometimes resembling a short stipe; peridium membranaceous, sprinkled or covered with lime crystals; columella mostly absent, but sometimes rudimentary and then calcareous; capillitium totally lacking; spores mostly globose to subglobose, spinulose or faintly reticulate under the light microscope, but conspicuously reticulate under the scanning electron microscope, black in mass, dark brown by transmitted light, 10-11 µm diam., phaneroplasmodium remaining minute, milky white.

Etymology: Gr. a = without + thrix (trichos) = hair, i.e. without capillitium.

Holotype in the University of Texas at Austin Myxomycete Collection (TEX) as UTMC-1681. Cultotypes (mass spore transfers from a monosporous culture) in the National Fungus Collections (BPI); New York Botanical Garden (NY); American Type Culture Collection; Royal Botanical Gardens, Kew (K); Department of Botany, University of Helsinki; Facultad de Sciencias Naturales y Museo, La Plata, Argentina; and in the private collections of Dr. D. T. Kowalski, Chico, CA; Mme. E. N. Nannenga-Bremekamp, Doorwerth, Holland; and D. W. Mitchell, East Sussex, England.

In some sporangia of Didymium atrichum a calcareous mass at the base suggests a rudimentary columella reminiscent of that found sometimes in Didymium trachysporum G. Lister. This, and the fact that the latter species often has a scanty capillitium and spores on which the warts are often arranged in lines to form an inconspicuous reticulation, suggests a possible relationship between the two species.

There may be a difference of opinion among myxomycete taxonomists as to whether one of the Physarales without capillitium should be included in the genus Didymium. Kowalski (1972), for example, described the genus Squamuloderma chiefly on the basis of absence of capillitium from its didymioid sporangia. Alexopoulos (1976) criticized Kowalski's decision, pointing out that there are a number

of Didymium species known to have a scanty capillitium and at least two species of Perichaena in which the capillitium is often scanty and occasionally lacking altogether (Martin and Alexopoulos, 1969). Our species could conceivably be classified in Squamuloderma, if that genus is recognized, except for the difference in the structure of the peridial lime. Kowalski (1972) described the lime of Squamuloderma as consisting of scalelike squamules, as the name of the genus indicates. We decided, therefore, to compare the lime of Didymium atrichum (cultotype), D. trachysporum (southwest Texas isolate by Mary R. Henney), Squamuloderma nullifila (subculture from a culture supplied by Dr. Kowalski), and Lepidoderma chailletii (UTMC-1110). Our results are depicted in the SEMs of Figures 12-14 and 21-23.

It was surprising to find that the lime of Squamuloderma was not in the form of scales, squamules, or crystals. The lime of Didymium atrichum in no way resembles that of Squamuloderma or Lepidoderma. It is closer to that of Didymium trachysporum in that both these species have lime crystals united laterally into flattened discs. This again supports the inclusion of D. atrichum in the genus Didymium.

We have decided that our species has its affinities with Didymium. We leave it to future taxonomists to rule whether our decision is the correct one.

ACKNOWLEDGMENTS

We thank Dr. Marie L. Farr for help with the Latin diagnosis, for suggesting the designation of cultotypes for specimens to be distributed, and for reviewing the manuscript before submittal to Mycotaxon. We also thank Dr. R. K. Benjamin, who was the second reviewer, for his critical comments.

LITERATURE CITED

ALEXOPOULOS, C. J. 1965. First list of Myxomycetes from Texas with notes on some rarely reported species. Southwest Natural. 10:221-226.

ALEXOPOULOS, C. J. 1969. The experimental approach to the

taxonomy of the Myxomycetes. Mycologia 61:219-239.

ALEXOPOULOS, C. J. 1976. Absence of capillitium as a taxonomic character in the Myxomycetes. Trans. Brit. Mycol. Soc. 66:2.

ALEXOPOULOS, C. J., and MARY R. HENNEY. 1971. Myxomycetes from Texas. II. Additions and corrections. Southwest Natural. 16:143-150.

BRISTOL, B. M. 1919. On the retention of vitality by algae from old stored soils. New Phytol. 18:92-107.

GILBERT, F. A. 1928. A study of the method of spore germination in Myxomycetes. Am. J. Bot. 15:345-352.

GILBERT, F. A., and G. W. MARTIN. 1933. Myxomycetes found on the bark of living trees. Univ. Iowa Stud. Nat. Hist. 15:3-8.

GRAY, W. D., and C. J. ALEXOPOULOS. 1968. Biology of the Myxomycetes. Ronald Press, New York. 288 pp.

GUSTAFSON, R. A. 1973. The life cycle of Didymium squamulosum. An ultrastructural and physiological study. Ph.D. Thesis, University of Texas at Austin. 273 pp.

KOWALSKI, D. T. 1972. Squamuloderma: a new genus of Myxomycetes. Mycologia 64:1282-1289.

MARTIN, G. W., and C. J. ALEXOPOULOS. 1969. The Myxomycetes. Univ. Iowa Press, Iowa City. 561 pp. (incl. 61 col. pls.)

NELSON, R. K., R. W. SCHEETZ, and C. J. ALEXOPOULOS. 1977. Elemental composition of Metatrichia vesparium sporangia. Mycotaxon 5:365-375.

SCHEETZ, R. W., and C. J. ALEXOPOULOS. 1976. Studies on the spores of Myxomycetes. Mycotaxon 4:335-339.

SCHOKNECHT, J. D. 1975. SEM and x-ray microanalysis of calcareous deposits in myxomycete fructifications. Trans. Amer. Microsc. Soc. 94:216-223.

MYCOTAXON

Vol. XI, No. 1, pp. 165-172 April-June 1980

ARNIUM APICULATUM (SORDARIACEAE S. LAT.) REDISCOVERED

C.A. SHEARER

Department of Botany, University of Illinois, Urbana, Illinois 61801

D.L. HAWKSWORTH

Commonwealth Mycological Institute, Kew, Surrey TW9 3AF

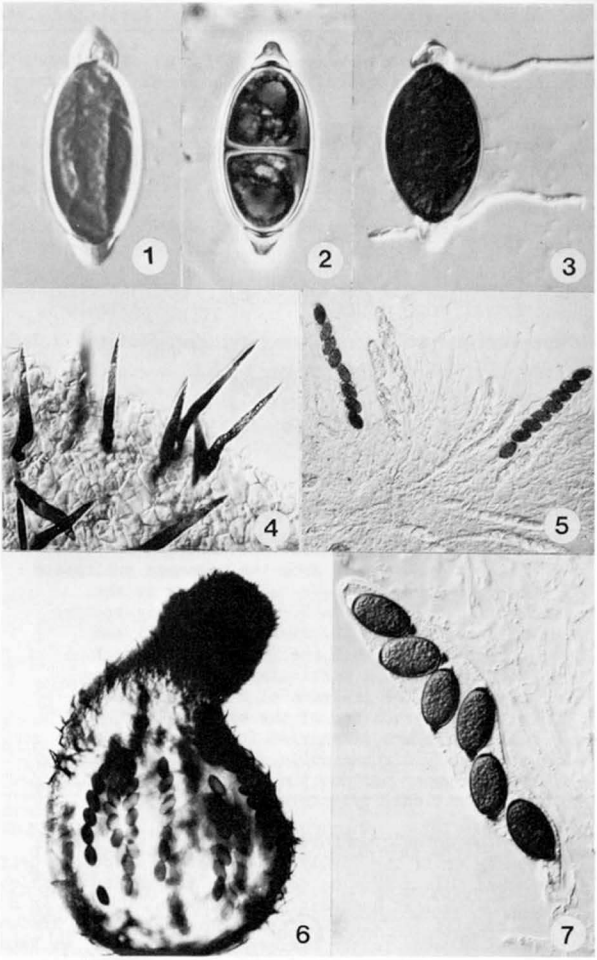
S. VON BODMAN

Department of Botany, University of Illinois, Urbana, Illinois 61801

SUMMARY

Arnium apiculatum (Griffiths) Lundq., a species hitherto known only from the holotype collection made in 1898, has been rediscovered in the British Isles and in N. America. This species is described and illustrated in detail and compared with other species of *Arnium* sect. *Murnia* Lundq. A particular feature of this species is the presence of a conical apical process at each end of the spore. The ascospores are discharged forcibly by a subapical, circumcissile splitting and shedding of the upper part of the ascus (inclusive of a non-functional cylindrical apical apparatus).

Arnium apiculatum (Griffiths) Lundq. was first described by Griffiths (1901) as *Delitschia apiculata* Griffiths. He collected this fungus on dead stems of Russian thistle (*Salsola kali* L.) at Aberdeen, South Dakota, U.S.A., in March 1898. Lundqvist (1972) transferred this species to *Arnium* sect. *Murnia* Lundq. in the Lasiosphaeriaceae Chen. ex Nannf. (Sordariaceae s. lat.). *Arnium* Nitschke ex Winter is


1
2
3
4
5
6
7

distinguished from *Podospora* Ces. nom. cons. primarily by the ellipsoid to fusiform shape of the young ascospores; in sect. *Murnia* the spores are finally transversely 1-septate and bicaudate. Lundqvist noted that only three of the original slides, which are in poor condition, remain of the type material of *Arnium apiculatum*. This species was, however, isolated from ascospores of a perithecium on a dead stem of *Equisetum* sp. collected from an Illinois stream in 1978 and then incubated in a moist chamber. A further collection, evidently conspecific with these specimens, was discovered on dead *Heracleum sphondylium* L. stems in a marsh in Devon, England, the same year.

This paper records the discovery of this species and, with the additional material available, provides a fuller description and discussion of the affinities of this fungus than has hitherto been possible.

Arnium apiculatum (Griffiths) Lundq., *Symb. bot. upsal.* 20 (1): 243 (1972).

Delitschia apiculata Griffiths, *Mem. Torrey bot. Club* 11: 104 (1901).

Figs 1-18. Colonies on half-strength Emerson's yeast, peptone, soluble starch agar (YpSs/2) floccose, white, turning grey to blackish. Perithecia superficial, scattered or aggregated into small clusters, pyriform to subglobose, ostiolate, 0.4-1.3 x 0.2-0.5mm, covered with brown, thick-walled, straight or slightly curved, 0-1 septate hairs, 25-115 x 10-15µm, hairs more numerous in the neck region, with subhyaline to brown flexuose hyphae at the base. Peridium membranous, hyaline to greyish brown, semitransparent except for the dark brown opaque neck; peridial cells angular, pseudoparenchymatous, thin-walled, measuring about 2.5-15µm diam. Neck cylindrical to conical, periphysate, positively phototrophic, 200-550 x 150-250µm. Paraphyses hyaline, filiform, thin-walled, septate, often

Figs 1-13, 15-18. *Arnium apiculatum* (ILLS). *Fig.* 1. Aseptate ascospore with appendages at both ends, x 1300. *Fig.* 2. Mature septate ascospore, x 1000. *Fig.* 3. Germinating ascospore, x 900. *Fig.* 4. Perithecial hairs and angular peridial cells, x 700. *Fig.* 5. Fascicle of asci and paraphyses, x 120. *Fig.* 6. Perithecium with a bent neck produced when under a unidirectional source of light, x 100. *Fig.* 7. Ascus containing non-septate ascospores and illustrating the thickened ascus tip, x 450.

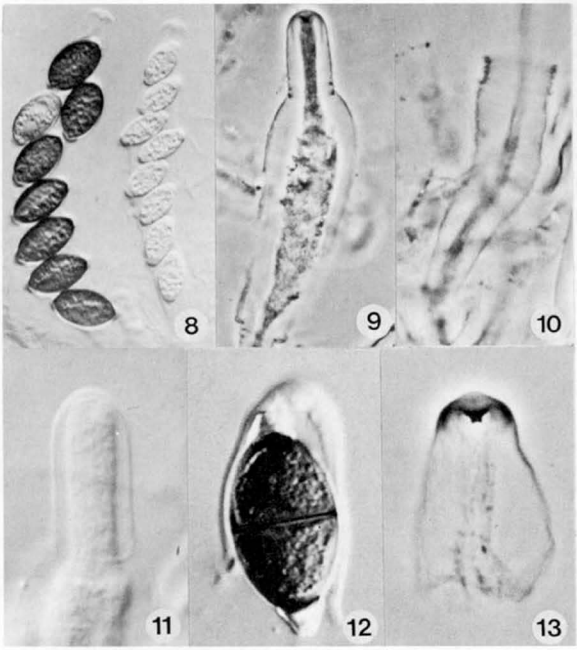


Fig. 8. Mature and immature asci, x 425. *Fig.* 9. Developing ascus illustrating the area of the ascus tip that will rupture, x 650. *Fig.* 10. Ascus after rupture of ascus tip and ejection of ascospores, x 900. *Fig.* 11. Ascus tip showing line of rupture, x 1200. *Fig.* 12. Ejected ascospore carrying the ascus tip, x 1500. *Fig.* 13. Ruptured ascus tip, x 1500.

longer than and mixed with the asci. Asci eight-spored, 150-250 x 15-50μm, unitunicate, cylindrical, narrowed and

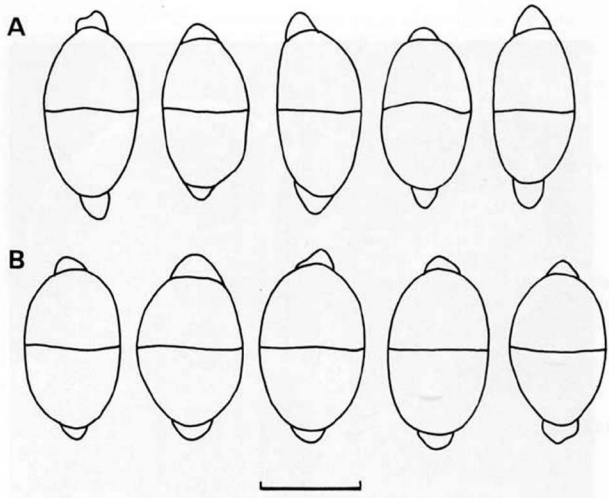


Fig. 14. Ascospore outlines. A, Illinois collection (IMI 238683). B, Devon collection (IMI 232650). Scale = 25μm.

somewhat rounded at the apices, tapering to a slender stipe 50-100μm long, non-amyloid, apical apparatus a cylinder with slightly concave sides, 7-21 x 4-9μm, thicker discharged, upper portion of the ascus rupturing from the basal portion along a predetermined circumcissile line. Ascospores obliquely uniseriate, sometimes biseriate, broadly ellipsoidal, (26-)30-35(-43) x (16-)17-23(-26)μm, hyaline with conspicuous oil droplets when immature, becoming dark brown and (0-)1-septate at maturity, ornamented with small rounded warts (SEM) but appearing smooth by LM; conical processes covering germ pores at both ends, 2.3-7.0μm long.

Specimens Examined: BRITISH ISLES, England: S. Devon, Mamhead, on dead *Heracleum sphondylium* stems, 1 September 1978, *M.B. & J.P. Ellis* (IMI 232650). -- U.S.A., Illinois: Vermilion Co., Jordon Creek, on submerged *Equisetum* sp., 29 May 1978, *C.A. Shearer J-4-1* (ATCC 38020, ILLS, IMI 238683, NY). South Dakota: Aberdeen, on *Salsola kali*, March 1898,

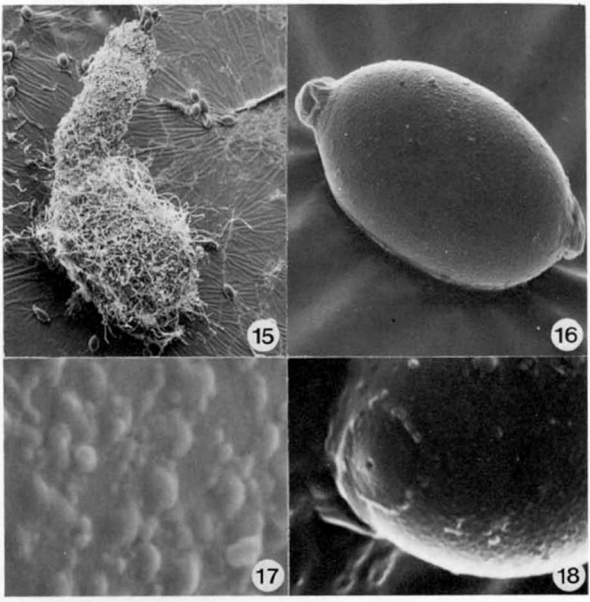


Fig. 15. Perithecium, SEM, x 95. *Fig.* 16. Ascospore, SEM, x 1030. *Fig.* 17. Ascospore surface ornamentation, SEM, x 6350. *Fig.* 18. Ascospore germ pore, the apical process removed, SEM, x 2600.

D. Griffiths (NY (3 slides only), holotype of *Delitschia apiculata* Griffiths).

The Illinois isolate appears to be identical to the type specimen, at least in ascospore morphology and size, although it should be noted that many immature spores in which the central septum has not yet developed occur in the type slides. The perithecia and asci of the type specimen are not well preserved but measurements and general

morphology of this isolate agree well with those of the protologue. This isolate grows very well in culture on Emerson's YpSs/2 agar but reproduces much more abundantly when some type of plant substrate is incorporated into the medium.

Studies of the species in culture also showed that the neck of the perithecium is positively phototophic and will bend towards a unidirectional source of light (Fig. 6). Ascospores are forcibly discharged, usually in groups of eight. Griffiths (1901) described the asci as 'very evanescent' but did not discuss the process of ascospore discharge, which proves to be of particular interest. A circumcissile rupture occurs well below the ascus apex as the spores are forcibly discharged in a mass, often carrying the ascus cap with them (Figs 9, 11). The wall of the ascus is thicker above this line than below it (Fig. 7). Fig. 10 shows an ascus from which the tip has been ruptured, and Fig. 13 a ruptured ascus tip. A distinct apical cylinder can be seen in the tip of the ascus before and after discharge (Figs 7-9, 13). Discharging asci were observed more frequently when perithecia were allowed to dry slightly.

The British collection agrees in most details with the North American specimens, but the length:width ratios of the spores are slightly lower (Fig. 14). Spore measurements of the British material are 31-38 x 20-26µm, and of the N. American 26.5-43 x 15-23µm.

The processes at the ends of the spores were interpreted as gelatinous by Lundqvist (1972). However, they are apparently laid down at a very early stage of spore formation prior to the formation of the rounded ends which include the germ pore. Although rather constant in size and shape, these processes never seem to contain any protoplast material at ascospore maturity, and so we feel that they should not be regarded as cellular. By SEM, the outer covering of the processes appears discontinuous with that of the dark body of the spore (Fig. 16). The development of these processes is perhaps similar to that in other members of the Lasiosphaeriaceae Chen. ex Nannf., e.g. *Zopfiella lundqvistii* Shearer & Crane (Shearer & Crane, 1979). No TEM studies of appendage development in the Lasiosphaeriaceae appear to have been carried out but it would clearly be of interest to ascertain if the caudate appendages originated in a similar way in all genera of the family.

Arnium apiculatum was compared with the extant material of other species placed in sect. *Murnia* by

Lundqvist (1972), viz. *A. imitans* Lundq. (BP, holotype; UPS, isotype; BP and O, paratypes) and *A. septosporum* Lundq. (UPS, holotype; UPS, paratype). Neither of these species is known in culture and it proved impossible to deduce the method of ascus discharge from the slide preparations and very limited material available. The apical cylinder in the ascus tip of *A. apiculatum* is, however, identical to that in *A. imitans*; in *A. septosporum* rather few asci were in a suitable stage to observe the maturing asci in detail, but the apical cylinder appears to be shorter in that species. The appendages in both *A. imitans* and *A. septosporum* appear to lack a distinct internal channel. Further, as in *A. apiculatum* (Fig. 18), the appendages cover the apical germ pores (a single pore in the case of *A. septosporum*). All three species have similar perithecia, perithecial hairs, and spores in which the central dark cell becomes 1-septate at maturity.

These fungi clearly form a reasonably well circumscribed group within *Arnium* distinguished by (a) the apical cylinder of the asci, (b) the septate dark cell, (c) apical rather than excentric germ pores, and perhaps also (d) the unchannelled appendages (seen also in a few species of *Arnium* s. str.), and (e) the ornamented ascospore walls (Fig. 17). If the asci also discharge in a distinctive manner, it could be argued that the group might justify recognition at the generic level. However, we feel that it would be premature to do this until more information is available on the nature of the apical processes and discharge mechanisms in the family.

ACKNOWLEDGEMENTS

We are indebted to Dr N. Lundqvist for reading the manuscript and for his extremely helpful comments on our material, and further to the curators of the herbaria cited in the text (BP, O, UPS) for allowing us to study material in their care.

REFERENCES

Griffiths, D. (1901) The North American Sordariaceae. *Mem. Torrey bot. Club* 11: 1-134.

Lundqvist, N. (1972) Nordic Sordariaceae s. lat. *Symb. bot. upsal.* 20 (1): 1-374.

Shearer, C.A. & Crane, J.L. (1978) Illinois fungi IX. *Zopfiella lundqvistii* sp. nov., a new ascomycete from submerged wood. *Trans. Br. mycol. Soc.* 70: 456-459.

MYCOTAXON

Vol. XI, No. 1, pp. 173-176 April-June 1980

ON AURIPORIA (APHYLLOPHORALES: POLYPORACEAE)

ERAST PARMASTO

Institute of Zoology & Botany
202400 Tartu, Estonian SSR, USSR

The genus *Auriporia* was described as monotypic by Ryvarden for *Poria aurea* Peck in 1973. David, Tortic & Jelic described a new species, *A. aurulenta*, in 1974, and emended the diagnosis of the genus. The third species of the genus was found by the author in East Asia and will be described below. In contrast to the known species, it is pileate and has allantoid spores; consequently, the diagnosis of *Auriporia* must be emended once more.

AURIPORIA PILEATA Parm. sp. nov. - Fig. 1.

Basidiomata pileata, tenuia (ad 3 mm crass.), mollia, in state sicco levia. Superficies cremea, deinde luteo-aurantiaca, in alcalinis (KOH) rufescens. Contextus et tubuli cremei. Pori atrocremei, rotundo-angulati, 3.5-4 per mm. Systema hypharum monomiticum; hyphae generatoriae fibulatae. Cystidia fusoidea, inflata, apice muricellata (ubi ad instar *Inocybarum* concrescint cristalla), crasse tunicata, pedicellata, pedicellus usualiter basiramifer, 25-40 x 8-13 µm. Sporae allantoideae, 4.5-5.2 x 0.8-1.2 µm.

Typus: URSS, regio Primorsk, distr. Ternei, reservatum Sichote-Alinicum, ad caudicem arboris frondosae prolapsum putridum in populeto, leg. 19. IX 1976 E. Parmasto (Herb. Instituti Zoologici et Botanici, Tartu, no. TAA 52807).

Basidiomata pileate, sessile or with a decurrent resupinate base, sometimes attached by narrow base, solitary or imbricate, soft, light, 0.5-2 x 2-3 x 0.15-0.25 cm, when sideways concrescent up to 8 cm broad. Abhymenial surface nearly glabrous, in herbarium specimens slightly radiately rugose, indistinctly zonate, whitish cream or cream colour (Munsell: 2.5 Y 8.5/4; Kornerup & Wanscher: 4A4),[1] at the base or later totally luteous-orange or orange (7.5 -10 YR 7/12; 5A7), becoming vinaceous (2.5 R 5/8; 10C6) in KOH. Context white, slightly fibrous, 0.5-1 mm thick. Tubes 0.5-1.5 mm long, thin-walled, fragile when dry, concolorous with the pore surface. Pores quite regular, subangular, 0.2-0.25-(0.35) mm in diam., 3.5-4 per mm, with entire or only slightly dentate walls; pore surface pale

[1] The colours have been noted according to Munsell, 1976, and Kornerup & Wanscher, 1967; the colur names are given after Rayner, 1970.

luteous or cream (2.5 Y 8.5/4; 4A4).

Hyphal system monomitic; generative hyphae of the context rather densely interwoven, sparsely branched (some at clamps, some in a right angle), thin-walled or thick-walled, some almost solid, with frequent medallion clamps, 3-4.5 µm. Hyphae of the tube trama with thin or thickened walls and ordinary clamps, 2-3.5 µm. Cystidia numerous, of *Inocybe*-type: fusiform or broadly fusoid, sometimes quite irregular, rostrate, capitate-incrusted, thick-walled (walls up to 3 um thick), pedicellate, 25-40 x (6.5)-8-13 µm, projecting 10-20 µm from the hymenium; pedicel 2-3 µm in diam., with a clamp at the basal septum, up to 20-(60) µm long, near the base usually with 1 (rarely 2) short or rarely up to 18 µm long flexuous side branches. Basidia clavate, some slightly utriform, with clamps at basal septa, 15-20 x 4-5.5 µm, with (2) 4 thin, only slightly curved sterigmata 3.5-4 µm long. Spores cylindrical, curved (allantoid), smooth, hyaline, thin-walled, non-amyloid and non-cyanophilous, 4.5-5.2 x 0.8-1.2 µm.

Causes white fibrose rot; in the rotten wood there are scattered small patches of a luteous or orange mycelium.

Type: USSR, Primorskij Region, Ternejskij distr., Sikhote-Alinskij nature reserve area, on a fallen rotten deciduous trunk, coll. 19. Sept. 1967 E. Parmasto (TAA 52807 - holotype; isotypes in O and LY).

The species is related to *A. aurulenta* David, Tortic & Jelic, which differs in a resupinate habit, orange or golden yellow tube layer and pores, hyphae 2-3 µm in diam., only shortly pedicellate cystidia and ellipsoid spores 4.5-6 x 2-3 µm. *Tyromyces inocybe* David & Malenç. has cystidia similar to those of *A. pileata*, but differs in having a resupinate (or slightly reflexed) basidiome, smaller pores (4-5 per mm) and basidia (14.5-16 x 3.5-4 µm), and in slightly different spores 5-5.5-(6) x 1.4-1.6 µm.[2]

Including the new species, the genus *Auriporia* includes three species: *A. aurea* (Peck) Ryv., growing on coniferous wood in North America; *A. aurulenta* on coniferous, rarely on deciduous wood in Europe southwards of 50° N.L., and *A. pileata* on deciduous wood in East Asia; all species are rare or very rare. According to the original description, *Tyromyces inocybe* may also belong to the same genus. However, it was by David & Malençon (1978) compared with *Tyromyces simanii* (Pil.) Parm. The latter has non-inocyboid, non-pedicellate cystidia and seems to be a typical *Tyromyces* (cf. Parmasto, 1961).

Auriporia is a satellite genus of *Tyromyces*; the main difference is in the presence of *Inocybe*-like pedicellate cystidia and (in two species) the change of cream, yellowish or orange colour of basidiomata into red in KOH.

When *Tyromyces* has been revised and its circumscrip-

---

[2] According to the data presented in the paper by David & Malençon, 1978 on p. 396, 406-407; in the table on p. 397 of the same paper the basidia are given as 14-18 (19) x 3.5-4.5 µm and spores as 4.5-5 (6) x 1.5-2 µm.

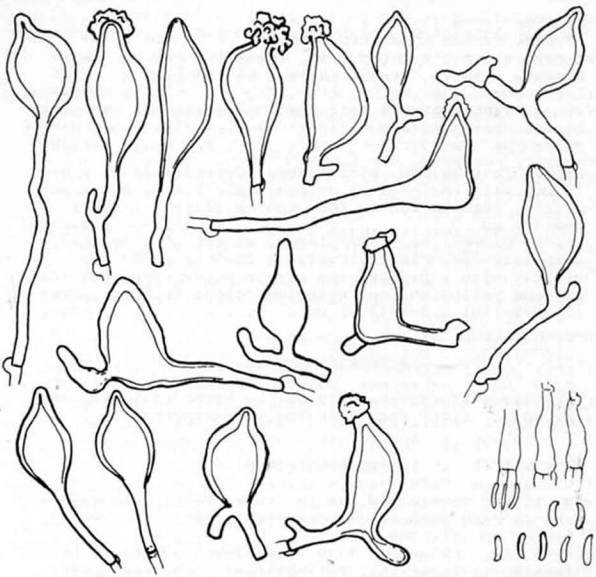


Fig. 1. Cystidia, basidia and spores of *Auriporia pileata*.

tion discussed, it may be that *Auriporia* ultimately will prove to be an arbitrary and superfluous genus, or the limits of *Auriporia* may be changed considerably. *Tyromyces* is still today quite heterogenous in spite of the exclusion of several heteromitic as well as dextrinous species.

The emended description of *Auriporia* and a key to the species known are as follows:

AURIPORIA Ryv., Norw. J. Bot. 20 (1): 2. 1973.
Basidiomata resupinate or pileate, lignicolous. Pores pale luteous, luteous or orange; the colour of basidiomata may turn red in KOH. Hyphal system monomitic; generative hyphae clamped. Cystidia numerous, inocyboid, thick-walled, fusiform, muricate, pedicellate, non-amyloid (and non-dextrinoid). Basidia clavate, with 4 thin sterigmata. Spores hyaline, thin-walled, smooth, non-amyloid, non-cyanophilous, ellipsoidal or allantoid (cylindrical).

1. Spores allantoid, up to 1.6 (? 2) µm in width . . . 2
- Spores ellipsoidal, with flattened side 3

2. Spores 4.5-5.2 x 0.8-1.2 µm. Pores 3-4 per mm. Basidiomata pileate, orange parts turn red in KOH . . . . . *A. pileata.*
- Spores 5-5.5-(6) x 1.4-1.6 µm. Pores 4-5 per mm. Basidiomata resupinate or slightly reflexed, without colour change in KOH (?) . . . . . *Tyromyces inocybe.*

3. Hyphae thin-walled, with clamps. Cystidia 22-35 x 9-15 µm, with one pedicel or non-pedicellate. Basidiome orange, turning red in KOH. Spores (4.5)-5-7-(8) x 2-3-(4) µm . . . . . *A. aurulenta.*
- Hyphae thin-walled, with clamps, others thick-walled, with very rare clamps. Cystidia 20-50 x 14-30 µm, usually with a pedicel and one or several "roots". Basidiome yellowish, not changing colour in KOH. Spores (5)-7-9-(10) x 3-4-(4.5) µm . . . . . *A. aurea.*

ACKNOWLEDGEMENTS

Gratitude is expressed to Dr. L. Ryvarden (Oslo) and Dr. A. David (Lyon) for reviewing the manuscript.

LITERATURE CITED

David, A., M. Tortic & M. Jelic. 1974. Études comparatives de deux espéces d'Auriporia... Bull. Soc. Mycol. France 90 (4): 359-370.

David, A. & G. Malençon. 1978. Tyromyces inocybe et Perenniporia rosmarini, Polyporaceae nouvelles de la région Méditerranéenne. Bull. Soc. Mycol. France 94 (4): 395-408.

Kornerup, A. & J.H. Wanscher. 1967. Methuen Handbook of Colour. 2nd Ed. London.

Munsell Book of Color. Neighbouring Hues Edition, Matte Finish Collection. Baltimore, 1976.

Parmasto, E. 1961. On the Place of Chaetoporellus Šimani (Pil.) Bond. within the Polyporaceae. Eesti NSV Tead. Akad. Toimet., Biol. seer. 10 (2): 118-122. (Russian, with English summary.)

Rayner, R.W. 1970. A Mycological Colour Chart. Kew,Surrey.

Ryvarden, L. 1973. New Genera in the Polyporaceae. Norw. J. Bot. 20 (1): 1-5.

MYCOTAXON

Vol. XI, No. 1, pp. 177-181 April-June 1980

A NEW SPECIES OF CRYPTOPHIALE FROM AMAZONAS

by

M. L. FARR

Mycology Laboratory, Plant Protection Institute
U. S. Department of Agriculture, Agricultural Research,
Beltsville Agricultural Research Center,
Beltsville, Maryland 20705

Among the leaf-inhabiting fungi collected during an expedition of the Projeto Flora Amazonica, there is one which unmistakably belongs to the dematiaceous hyphomycete genus Cryptophiale Pirozynski, but does not fit any known species. The Amazonian fungus is distinguished by its relatively small dimensions (particularly of the conidia) and by variously shaped conidia, and is therefore described as a new species, Cryptophiale minor.

Cryptophiale minor sp. nov.

Etym. L. minor = smaller.

Mycelium reticulatum ex hyphis pallide brunneis vel subhyalinis ad 2 µm diam constans. Phialophora dispersa vel gregaria setiformia recta badia septata, 120-200 µm longa, 68 µm crassa, basi ad 14-20 µm expansa, apice acuta. Zona fecunda in dimidio superiore phialophori, 30-50 µm longa, 12-14(-16) µm lata; cellulis scutelli flavobrunneis cylindraceis vel lobatis 5.5-7.0 µm longis; phialidibus late ovoideis vel ampulliformibus pallide brunneis ca 3.0-5.5 µm diam composita. Phialosporae hyalinae uniseptatae, acerosae, falcatae, angustissime fusiformes, vel angustissime subulatae, 12-14(-16) µm longae, ad ca 1.2 µm latae guttulatae, apice attenuatae, basi attenuatae vel rotundatae.

Mycelium forming small light brown pellicles around the swollen base of the phialophore, elsewhere effusely reticulate, consisting of delicate hyphae nearly 2 µm in diam and pale brown near the phialophore base, becoming progressively narrower and paler. Phialophores scattered

to gregarious, setiform, erect, dark reddish brown, 6- or more-septate (mostly in the upper zone), 120-200 µm long, 6-8 µm thick, flaring to a bulbous, dark basal cell 14-20 µm in diam. Fertile zone extending from just above the middle of the phialophore to within 18-32 µm of the sharply pointed apex, 30-50 µm long, 12-14(-16) µm wide (not including attached conidia); shield cells yellowish brown, cylindric to variously lobed, ca 5.5-7.0 µm long; phialides broadly ovoid to ampulliform, pale brown, ca 3.0-5.5 µm diam; conidia (phialospores) hyaline, 1-septate at or near the middle, straight or slightly curved, acerose to falcate or very narrowly fusiform or subulate, 12-14(-16)µm long, up to ca 1.2 µm wide, guttulate, attenuate at both ends or at the apex and then rounded at the base.

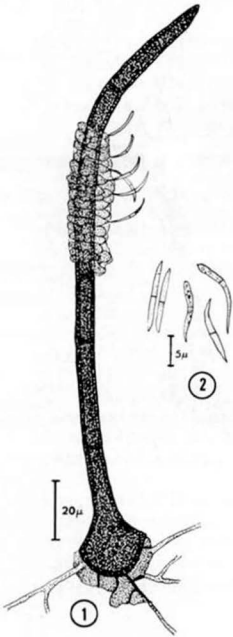
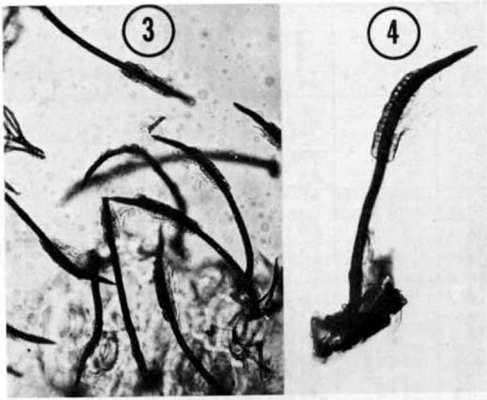


Fig. 1-4. Cryptophiale minor, from BPI isotype. Fig. 1. Fruiting body, semidiagrammatic; shield cells omitted from right edge to show phialides, X500. Fig. 2. Selected conidia, showing variation in shape, X1000 (guttules drawn in two). Both figs. prepared with aid of Leitz drawing tube. Fig. 3. Habit, ca X200, from celloidin strip. Fig. 4. Fruiting body, ca X350.

Holotype. Brazil: Amazonas, along the Rio Negro, near J. Bani (close to Vista Alegre), secondary on large zonate spots on dead leaves of Astrocaryum sp. (Palmaceae) 19 Jan, 1978, coll. I. Araujo & M. L. Farr (Farr AM-155), associated with Acrotheca sp., Brooksia tropicalis Hansf., and other fungi, BPI*; isotype, NY. Known only from the type collection.

The mucilaginous matrix of the conidia, one of the generic characters, was evident mostly as a dried or sticky coating on the fertile zone.

As shown in Table 1, C. minor has smaller conidia than each of the other five known species. In its remaining measurements, as well as in other morphological characteristics, it appears to be closest to C. iriomoteana Mats. The conidia of the latter species, however, are not only larger, but (judged from the illustrations in the protologue) consistently subulate, and



*Originally designated holotype of INPA destroyed by fire while this paper was in preparation.

Table 1. Comparison of Cryptophiale spp.

Species	Phialophores	Fertile Zone	Shield Cells	Phialides	Conidia	Locality	Substrate
kakombensis Pirozynski, Can. J. Bot. 46: 1124-1125. 1968. (type species)	150-260 x 5-8 µm, apex simple	100-110 x 16-22 x 10-15 µm	10-14 x 3.0-3.5 x 11-15 µm	no measurements given; lageniform	22-27.5 x 1.7-2.0 µm, curved, falcate	Tanzania	fallen leaves of Baphia.
udagawae Piroz. & Ichinoe in Pirozynski, Can. J. Bot. 46: 1126. 1968.	to 250 x 5-8 µm, apex 1-3 times dichotomously forked	70-100 x 15-27 x 13-19 µm	10-13 x 3.5 x 13-16 µm	no measurements given; subglobose	15-25 x 1.5-3.0 µm, curved, narrowly subulate, apex drawn out into a short appendage	Japan	fallen leaves of Quercus.
guadalcanalensis Matsushima, Microfungi Solomon Isls. & Papua-New Guinea pp. 15-16. 1971.	170-240 x 6-8 µm, apex 1-2 times forked	70-90 x 13-16 µm	not described	not described	16-24 x 1.3-2.0 µm, curved, subulate	Solomon Isls.; Okinawa	rotten leaves of Pometia Castanopsis
iriomoteanum [sic] Mats. Ic. Fgi. Matsushima Lect. p. 41. 1975.	120-200 x 5-7 µm, apex simple	40-80 x 12-16 µm	not described	hyaline, no shape or measurements given	14-23 x 1.5-2.0 µm, curved, narrowly subulate, with hooked apex ["narrowly obclavate"]	Okinawa	dead hardwood bark
manifesta Sutton & Hodges, Nova Hedwigia 27: 350. 1976.	to 250 x 4.0-6.5 µm, apex simple	31.5-70.0 x 10.5-17.0 x 2-6 µm	not described	4-12 x 2.5-3.5 µm, lageniform w. collarette, polyphialidic, conspicuous	22-27 x 1.5-2.0 µm, straight, narrowly subulate	Brazil	Dead leaves Eucalyptus
minor sp. nov.	120-200 x 6.8 µm, apex simple (but see text)	32-48 x 12-14 (-16) µm	5.5-7.0 µm long	ca 3.0-5.5 µm broadly, ovoid to ampulliform	12-14(16) x up to ca 1.2 µm, acerose or falcate to narrowly fusiform or subulate	Brazil	dead leaves of Astrocaryum Astrocaryum

appear more strongly curved, even hook-like at the apex. The Okinawan species also has a larger fertile zone and is unique in its habit on bark.

The variability of conidial shape shown by C. minor is an unusual feature since conidial shape appears to be uniform in the other species of Cryptophiale.

With respect to structure of the phialophore apex, the species of Cryptophiale fall into two groups (see key). Although the new species definitely belongs to group 1', one phialophore was observed to be split at the very tip into two small branches 10 µm long and 2.0-2.5 µm thick.

The following key is based on the illustrated descriptions of the species of Cryptophiale.

1. Apex of phialophore branched.....2
1'. Apex of phialophore simple, pointed.....3

2. Fertile zone extending into first dichotomy of phialophore apex; conidial apex gradually tapered ..... C guadalcanalensis
2'. Fertile zone confined to unbranched portion of phialophore; conidia abruptly narrowed to an almost appendage-like, curved apex..... C. udagawae

3. Conidia mostly 12-14 µm long..... C. minor
3'. Conidia mostly 14-27 µm long..... 4

4. Conidia 14-23 µm long; on bark..... C. iriomoteana
4'. Conidia 22-28 µm long; on leaves.....5

5. Conidia falcate, tapered toward both ends; fertile region near tip of phialophore, 100-110 x 16-22 x 10-15 µm..... C. kakombensis
5'. Conidia narrowly subulate, tapered toward one end, broadly rounded on the other; fertile region median along phialophore, 31.5-70.0 x 10.5-17.0 x 2-6 µm.... ..... C. manifesta

ACKNOWLEDGMENTS

I thank K. Pirozynski for constructive criticism and most helpful suggestions concerning the manuscript, and G. Papavizas for assistance with Greek etymology. The fungus described in this paper was collected during my participation in Projeto Flora Amazonica, NSF Grant INT77-17704.

MYCOTAXON

Vol. XI, No. 1, pp. 182-184 April-June 1980

A NEW SPECIES OF *EXOPHIALA* RECOVERED FROM LOBLOLLY PINE LITTER

BARRY KATZ[1] AND MICHAEL R. McGINNIS[2]

Department of Botany[1] and Department of Bacteriology and Immunology[2], University of North Carolina, Chapel Hill, North Carolina 27514

ABSTRACT

Exophiala dopicola Katz et McGinnis, sp. nov. is described from *Pinus taeda* L. needle litter in North Carolina.

INTRODUCTION

While studying *Pinus taeda* L. (loblolly pine) needle litter decomposition in age stratified plots, an interesting dematiaceous hyphomycete was repeatedly isolated from two to seven year old litter. A careful study of this hyphomycete, as well as the type cultures of all of the accepted species of *Exophiala* Carmichael, has revealed that this fungus is undescribed.

TAXONOMIC PART

Exophiala dopicola Katz et McGinnis, sp. nov. (figure 1).

Coloniae in agaro cum malto composito satae sub calore 20-23°C die quinto decimo diametrum 7-8 mm attinentes, in medio floccosae, leves prope margines, atro-fuscae vel atro-olivaceae (sensu Ridgway). Hyphae aereae leves, usque ad 3 µm crassae, cellulis 8-18 µm longis; submersae leves, cellulis at 3 µm crassis, 7-15 µm longis, sterilibus. Conidiophori micronemati vel semi-micronemati. Cellulae conidiogenae annellides, proxime in hyphis haud transformatis vel in apicibus catenularum brevium hypharum toruloidearum suffultae. Annellides nonnumquam percurrenter proliferantes. Annellidum venter subglobosus vel ellipticus, 3-5 X 7-12 µm, collum ad 15 µm longum, pallide brunneum. Annelloconidia cylindrica, cicatrici basali stricta notata,

1.5 - 2.5 X 6-11 µm, levia, unicellularia, in globis cumulata, hyalina vel pallide brunnea. Sub calore 37°C nullus auctus et nullae cellulae blastogenae.

Habitat: On decomposing needles of *Pinus taeda* L.

Holotypus: BAK 978, collected from *P. taeda* stand, the Duke Forest, Orange county, North Carolina, October 22, 1977, by B. Katz. The holotype and a living culture will be maintained at the National Fungus Collection, Beltsville, Maryland. Additional living cultures maintained in the Culture Collection, North Carolina Memorial Hospital, Chapel Hill, North Carolina. The epithet *dopicola* was invented and has no historic derivation.

Colonies attaining a diameter of 7-8 mm at 20-23°C on malt agar in 14 days. Colonies floccose in the center, flat at the margins, fuscous-black to olivaceous-black (Ridgeway). Aerial hyphae smooth, up to 3 µm wide, and 7-15 µm long and sterile. Conidiophores micronematous to semimacronematous. Conidiogenous cells are annellides, borne directly on unspecialized hyphae, or at the apices of short chains of toruloid hyphae, or both. Annellides occasionally proliferate percurrently. Annellide venter subglobose to elliptical, 3-5 X 7-12 µm, neck up to 15 µm long, pale brown. Annelloconidia cylindrical, with narrow basal scar, 1.5 - 2.5 X 6-11 µm, smooth, 1-celled, accumulating in balls, hyaline to pale brown. Growth at 37°C and yeast cells are absent.

DISCUSSION

The genus *Exophiala* was established by Carmichael in 1966 (2) to accommodate *E. salmonis*, a pathogen of fish. Subsequently, several additional species have been added to the genus *Exophiala* (1, 3, 5). *Exophiala dopicola* is the only member of this genus that has not been reported to be a pathogen of man or animals (4, 6).

Exophiala dopicola differs from the other species of *Exophiala* by its 1-celled, cylindrical annelloconidia and the absence of yeast-like cells. Isolates of *E. dopicola* have been repeatedly collected from two to seven year old litter throughout the study. In addition to the Duke Forest site, this taxon has also been recovered in a *P. taeda* stand at Saxapahaw, Alamance County, N.C. The fungus is rather common in these sites and is represented by approximately 200 isolates.

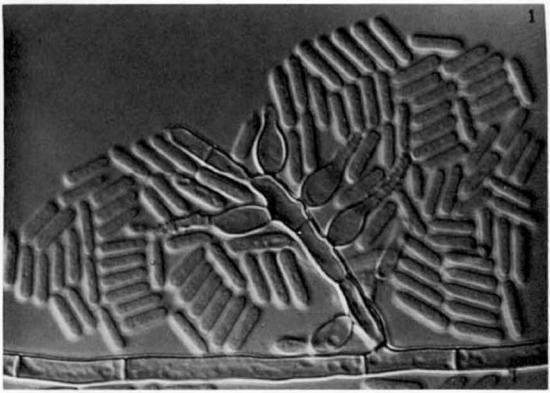


Fig. 1. Annellides of different ages and annelloconidia, 500X.

ACKNOWLEDGEMENT

We would like to thank Dr. D. P. Rogers for reviewing the manuscript and preparing the Latin translation of the diagnosis.

LITERATURE CITED

1. Arx, J. A. von. 1970. The genera of fungi sporulating in pure culture. 1 ed. A. R. Gantner Verlag, Leichtenstein.
2. Carmichael, J. W. 1966. Cerebral mycetoma of trout due to a *Phialophora*-like fungus. Sabouraudia 5:120-123.
3. Hoog, G. S. de and E. J. Hermandies-Nijhof. 1977. The black yeasts and allied Hyphomycetes. Stud. Mycol. 15, Centraalbureau voor Schimmelcultures, Baarn.
4. McGinnis, M. R. 1978. Human pathogenic species of *Exophiala, Phialophora,* and *Wangiella,* Proc. 4th. Int. Cong. Mycoses, PAHO Sci. Pub. No. 356, p. 37-59.
5. McGinnis, M. R. and A. A. Padhye. 1977. *Exophiala jeanselmei,* a new combination for *Phialophora jeanselmei.* Mycotaxon 5:341-352.
6. McGinnis, M. R., D. F. Sorrell, R. L. Miller and G. W. Kaminski. 1980. Subcutaneous phaeohyphomycosis caused by *Exophiala moniliae.* Submitted to Mycopathologia.

MYCOTAXON

Vol. XI, No. 1, pp. 185-188 April-June 1980

LYCOPERDON NETTYANA, A NEW PUFFBALL FROM WESTERN WASHINGTON STATE

By

ROBERT W. RAMSEY

10511 Interlaaken Drive, SW
Tacoma, Washington 98498

DESCRIPTION

Lycoperdon nettyana sp. nov.

Gasterocarpia 2-3 cm lata, 3-4 cm alta, stipitato-subcapitata, ad apicem rotundata, mediobrunnea, pannos granulosos granulis Lycoperdontis pyriformis similibus sed parvioribus et regulatioribus praebens, quos colori brunneo apicis modificationem dilute griseibrunneam donant. Exoperidium e granulis, prominentias breves et conicas, vel globuliformes constans; prominentiae per radandum sed haud terendum effractae, cicatrices rotundatas depressas facientes. Exoperidium in maturitate ad apicem gastero-carpii irregulariter findens et exutum, endoperidium nitentem, laevem, persistentem exhibens; post iacturam exoperidii porus apicalis circularis facitur. Stipes basem versus angustatus, ad substratum per rhizomorphas albas colligatus, pallidus, prominentiis granulisque ad aspectu glandularum reductis, a stipitem pallidum fuscatis videntur.

Gleba omnis pluricellulosa in parte basali sterili et parte apicali fertili divisa. Pars basalis e cellulis minus quam 1 mm diam constans quae inter partes basales et apicales dissepimentum e cellulis complanatis faciunt; dissepimentum in partem fertilem 2 mm ad modum tholi extensum, area fuscata infra tholum ostendens. Gleba fertilis griseibrunnea vel mediobrunnea, e cellulis parvibus et irregularibus, ante aperturiem pori apicalis pseudocolumellam praebens, quam e fasciculum verticalem tubulorum angustorum constat. Sporae globosae, apedicellatae, verruculosae, 4-5 m diam. Capillitium 6 m diam, pariete 1.2 m crasso, foveas circulares parietis et ramulos latiangulos interdum praebens.

Gasterocarpia dispersa vel caespitosa in solo propatulorum sylvarum. Holotypus L-XI ad castram Iron Springs dictam prope Cispus comitato Lewis pagi Washingtonis 22 Oct 77 a Netty Laycock lectus, in herbario Universitatis Washingtonis conservatus.

Gasterocarp 2 to 3 cm broad, 3 to 4 cm high, stipitate-subcapitate with upper portion hemispherical, medium brown, covered with small, (more or less) regular granular patches that impart light grayish brown color (60, see Kelly,1965); granular exoperidium interspersed with short conical spines and rounded buttons about 2 mm apart. Exoperidium at maturity splitting irregularly across the apex and peeling or flaking away. Endoperidium, when exposed, lustrous,smooth, light grayish yellowish brown (79), persistent; apical pore soon forming, circular, less than 1 cm diam. Pseudostipe tapering to base, attached to substrate by white rhizomorphs; surface pallid with scattered dark granules and reduced gland-like projections.

Subgleba whitish, pigmented in uppermost 5 mm, with empty loculae less than 1 mm across; distinctly separated from gleba by a thin layer of collapsed loculae which is centrally elevated about 2 mm at the base of the pseudocolumella. Gleba grayish brown (61) to moderate brown (58) near or at maturity, with a distinct pseudocolumella (see photo) rising to near the apex.. Spores globose, apedicellate, verruculose, 4-4.5 um in diam. Capillitium 6 um in diam., walls up to 1.2 um thick with occasional circular pitting, few wide angle branches.

Collected on soil in woodland clearings, scattered to cespitose, autumn. Holotype, L-X1, collected by Nettie Laycock at Iron Springs Campground 5 miles from Cispus Environmental Learning Center, Lewis Co., Washington, 22 Oct 1977. Stored in University of Washington Herbarium.

DISCUSSION

During the production of a trial key for the Lycoperdales reported for the Pacific Northwest, this puffball was brought to me by Nettie Laycock at the Cispus III Foray. I was not able to match it with any of the reported Northwest species nor with the publications by Dr.Alexander Smith. I sent a sample to Dr. Smith for his opinion and he reported to me that Vincent DeMoulin of Liege, Belgium, has classified it as a western variant of Lycoperdon pyriforme Schaeff per Pers. However, this specimen has significant differences from L. pyriforme which indicate that it should be accorded full rank as a species. These differences are:

1. L. nettyana is covered with granular patches similar to but smaller and more regular in size than L. pyriforme.

2. L. pyriforme does not slough away the exoperidium. The scales and granules dry on the surface of the endoperidium to produce a sandpapery texture.

3. L. pyriforme is always found on wood or wood debris. L. nettyana was found on soil.

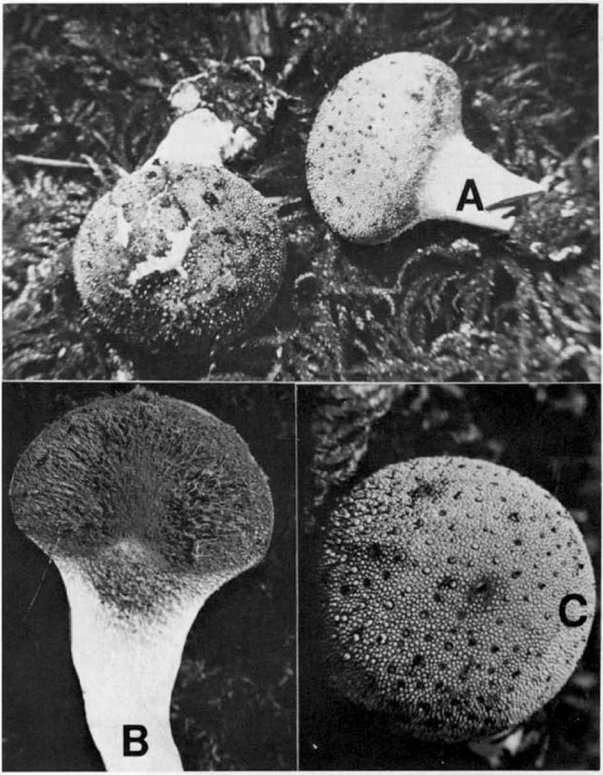


Figure A, left sporocarp with splitting exoperidium.

Figure B, longitudinal section showing discolored area of sterile base and pseudocolumella. Note pore formation at apex.

Figure C, typical exoperidial texture showing spines and buttons. Missing ones were scraped to remove.

Photos by Joy Spurr

4. L. pyriforme does not exhibit a distinct pseudocolumella, nor a sharp division between sterile and fertile tissues, nor a discolored zone below the division.

5. L. pyriforme has spores 2.8 to 3.5 microns while L. nettyana has spores from 4 to 4.5 microns in diam.

6. L. pyriforme forms an irregular pore slowly while L. nettyana forms a circular pore soon after loss of the exoperidium.

Some of these differences could be ascribed to individual variations or climatic and geographic influences, but the second, fourth and fifth points seem unassailable.

There is a superficial resemblance of the exoperidium to Lycoperdon perlatum Pers. but the spines and buttons must be scraped to loosen. Of some two dozen Lycoperdon species described in the U.S., only three others appear to lose the exoperidium by peeling or flaking. L. curtissi Berk. lacks a sterile base. L. rimulatum Peck has a smooth exoperidium. L. marginatum Vitt (L. candidum Pers per Pers.) is not stipitate and its sterile base has much larger loculae. Taken together, all these points lead to the conclusion that Lycoperdon nettyana has heretofore been undescribed.

ACKNOWLEDGMENTS

The author wishes to thank Dr. Daniel Stuntz of the Botany Department of the University of Washington and Dr. David Hosford of Central Washington University for their assistance and criticisms. Also Nettie Laycock for her interest in my area of mycology while engaged in her own study of other genera.

LITERATURE

Smith, Alexander H. (1973) The Non-Gilled Fleshy Fungi.

Smith, Alexander H. (1951) Puffballs & Their Allies in Michigan. Univ. Mich. Press, pages xi & 1-131

Smith, Alexander H. (1978) Personal Communications.

Kelly, K. L. 1965. ISCC - NBS Color-name charts illustrated with Centroid Colors, Standard Sample No. 2106. Suppl. to U.S. Nat. Bur. Standards Circ. 553.

MYCOTAXON

Vol. XI, No. 1, pp. 189-216 April-June 1980

STUDIES IN THE HYALOSCYPHACEAE I: SOME SPECIES OF DASYSCYPHUS ON TROPICAL FERNS

JOHN H. HAINES[1]

Biological Survey
New York State Museum
THE STATE EDUCATION DEPARTMENT
Albany, New York 12230

SUMMARY

The six most common species of *Dasyscyphus* S.F. Gray, on tropical ferns are described and illustrated. They fall into two groups. One contains *D. ulei* and *D. chermisinus*, the other *D. fimbriifer*, *D. varians* and related taxa. *D. fimbriifer* var. *brevisporus* is raised to specific rank, and *D. singerinus* is reduced to a variety of *D. fimbriifer*, *D. pteridophyllus* to a variety of *D. varians* and *Arenaea macrospora* to a variety of *D. oncospermatis*.

Decaying ferns are the preferred substrate for a large number of microfungi (Holm & Holm 1978, Bøhler 1974). Amongst the most prevalent and conspicuous of these are the brightly colored Hyaloscyphaceae on large tropical ferns. During the study of many collections made by the author and others connected with the Flora Neotropica Project, it was found that most collections on ferns are related to *Dasyscyphus varians* Rehm but with wide variations in spore, hair and ascus size and pigmentation of the apothecia. Type specimens of fern inhabiting taxa from all tropical regions were examined, where available, in order to determine the correct names for these taxa. Several species

[1]Published by permission of the Director, New York State Museum/Science Service, Journal Series No. 295.

were reduced to varietal rank and one variety raised to specific rank in an attempt to better reflect natural relationships. A second, smaller natural grouping of species related to *Dasyscyphus ulei* (Wint.) Sacc. is discussed in part here, but other species in this group characterized by bright red discs occur on superficially similar, but phylogenetically unrelated, palm fronds and are outside the scope of this study.

Key to Common Dasyscyphi on Tropical Ferns

1. Species with bright red discs and white hairs.....2
1. Species with cream or yellow discs and white or yellow hairs.....3
   2. Spores 18-30 x 0.6-0.9 µm, on non-living petioles of large ferns.....2. *D. chermisinus*
   2. Spores 10-20 x 1.7-2.3 µm, on pinnae of living *Gleichenia*.....1. *D. ulei*
3. Hairs hyaline, without colored matter at the tips, often over 125 µm long, tapered.....4
3. Hairs straw-colored, with amber to garnet-colored matter at the tips, usually cylindrical, under 100 µm long...6
   4. Hairs up to 600 µm long, spores 10.5-12.7 x 1.8-2.0 µm.....5. *D. brevisporus*
   4. Hairs less than 350 µm long.....5
5. Spores 6-12 µm long.....4. *D. fimbriifer* var. *singerianus*
5. Spores 13-30 µm long.....3. *D. fimbriifer* var. *fimbriifer*
   6. Spores under 18 µm long, stipes not branched, apothecia not convoluted.....7
   6. Spores over 18 µm long, stipes some times branched, apothecia some times with convoluted margins.....8
7. Spores 6-11 µm long with rounded apices..6. *D. varians* var. *varians*
7. Spores 11-18 µm long with acute apices...7. *D. varians* var. *pteridophyllus*
   8. Spores 20-32 µm long...8. *D. oncospermatis* var. *oncospermatis*
   8. Spores 35-65 µm long...9. *D. oncospermatis* var. *macrosporus*

1. *Dasyscyphus ulei* (Wint.) Sacc., Syll. Fung. 8:452. 1889. Fig. 1.

≡*Peziza ulei* Wint., Hedwigia 24:258. 1885.
≡*Atractobolus ulei* (Wint.) O. Kuntze, Revis. Gen. Pl. 3(2):446. 1889.
=*Dasyscyphus dicranopteridis* Seaver & Whetzel, Sci. Surv. Porto Rico 8:74. 1926.
≡*Lachnella dicranopteridis* (Seaver & Whetzel) Seaver, N. Amer. Cup-Fungi, Inoperculates p. 262. 1951.

TYPE COLLECTION - E. Ule, 1884, Sao Francisco, Santa Catharina, Brasil. Distributed as number 3273 in Century XXXIII of Winter's *L. Rabenhorstii Fungi Europaei et Extra-europaei exsiccati*. This exsiccatum was not reexamined by the author as it has been adequately described elsewhere (Dennis, 1954).

Apothecia seated on darkened pinnae of living fern fronds, goblet-shaped, short-stipitate, up to 0.5 mm across, scarlet-red with white to pink hairs forming a stiff, short, vertical fringe at the margin of the cup; disc scarlet-red, concave, exposed even when dried. Pigment diffusing, turning purple-violet then colorless when placed in 3% KOH. Hairs to 125 µm x 2.5-4.0 µm, generally much shorter, cylindrical with hemispherical or slightly tapered tip, hyaline, thin-walled, straight or slightly curved when dry, flexuous in aqueous solutions, densely roughened throughout their entire length with minute granules. Granules up to 0.3 µm long, slightly longer than broad, appearing perpendicular to the surface of the hair, hyaline, insoluable in 3% KOH. Ectal excipulum composed of short-celled textura prismatica, cells 4-10 by 3-6 µm, becoming textura angularis to globulosa in some portions of the cup, hyaline (after pigment decolorizes in KOH), with walls up to 1 µm thick. Asci cylindrical with a slightly tapered base, (35-) 43-70(-80) by 3.5-6.0(-8) µm and hemispherical apex with a small but distinct pore plug staining as a tapered cylinder in IKI with KOH pretreatment, no croziers present. Spores 10-18(-22) by 2.0-3.0 µm, non-septate, hyaline, smooth, tapered toward both ends, slightly curved along the longitudinal axis, without distinctive inclusions. Paraphyses hyaline, narrowly lanceolate, 2-3 µm at the widest point about 1/3 below the tip, tapered to a rounded apex ca 1 µm broad, exceeding the asci in the hymenium by up to 20 µm, septate in the lower portion only.

HOST - Only known from dead pinnae on partially living fronds of *Gleichenia* (=*Dicranopteris*)

RANGE - Known only from Brasil, Peru and Puerto Rico.

ETYMOLOGY - After the collector Ernst Heinrich Ule, a German born naturalist who spent most of his career in Brasil. (Stevenson, 1971).

PREVIOUSLY PUBLISHED ILLUSTRATIONS - None.

SPECIMENS EXAMINED - Brasil: A.S. Costa, 6.IX.36, as White Herbarium 3439 and CUP 27983, Porto de embarque Ubatuba, S. Paulo, determined by H.H. Whetzel and W.L. White, on pinnae of fern which appears to be *Gleichenia* (FH). Peru: E. Ule, Oct. 1902, as Herbarium Brasiliense 3310, Cerro de Cumbaso, on *Gleichenia dichotoma* (FH). Puerto Rico: H.H. Whetzel, Kern & Toro P.R. Fungi 2683, CUP 14742, July 18, 1924. Finca Maria, Yauco. Holotype of *D. dicranopteridis* Seaver & Whetzel (CUP).

DISCUSSION - *D. ulei* is the most commonly collected member of a group of Dasyscyphi with bright red hymenia and pink appearing hairs. It is apparently found only on dead portions of living fronds of *Gleichenia*. This kind of association with living plants is also found in the unrelated temperate species *D. gaultheriae* (Ellis & Everh.) Sacc. which occurs on grey spots of *Gaultheria shallon*.

Variation in spore length among the known collections is from 10 to 22 µm, but since they are all on the same host and the size does not seem to correlate with any other characters, all will be treated as the same species including the type collection of *D. dicranopteridis* Seaver & Whetzel.

A related and apparently unnamed species commonly occurs on palm fronds.

2. *Dasyscyphus chermisinus* Cash, J. Wash. Acad. Sci. 48: 256. 1958. Fig. 2.

HOLOTYPE - E.J.H. Corner 1225, December 19, 1948, Corcorvado Rio de Janeiro, Brasil, on *Alsophila* petioles. (BPI).

Apothecia macroscopically identical to *D. ulei* and with the same pigment change in KOH. Hairs also the same. Ectal excipulum composed of hyaline, indistinct, long-celled textura prismatica with light straw colored irregular cells on the surface. Asci 40-45 x 3.5-5.0 µm, hyaline,

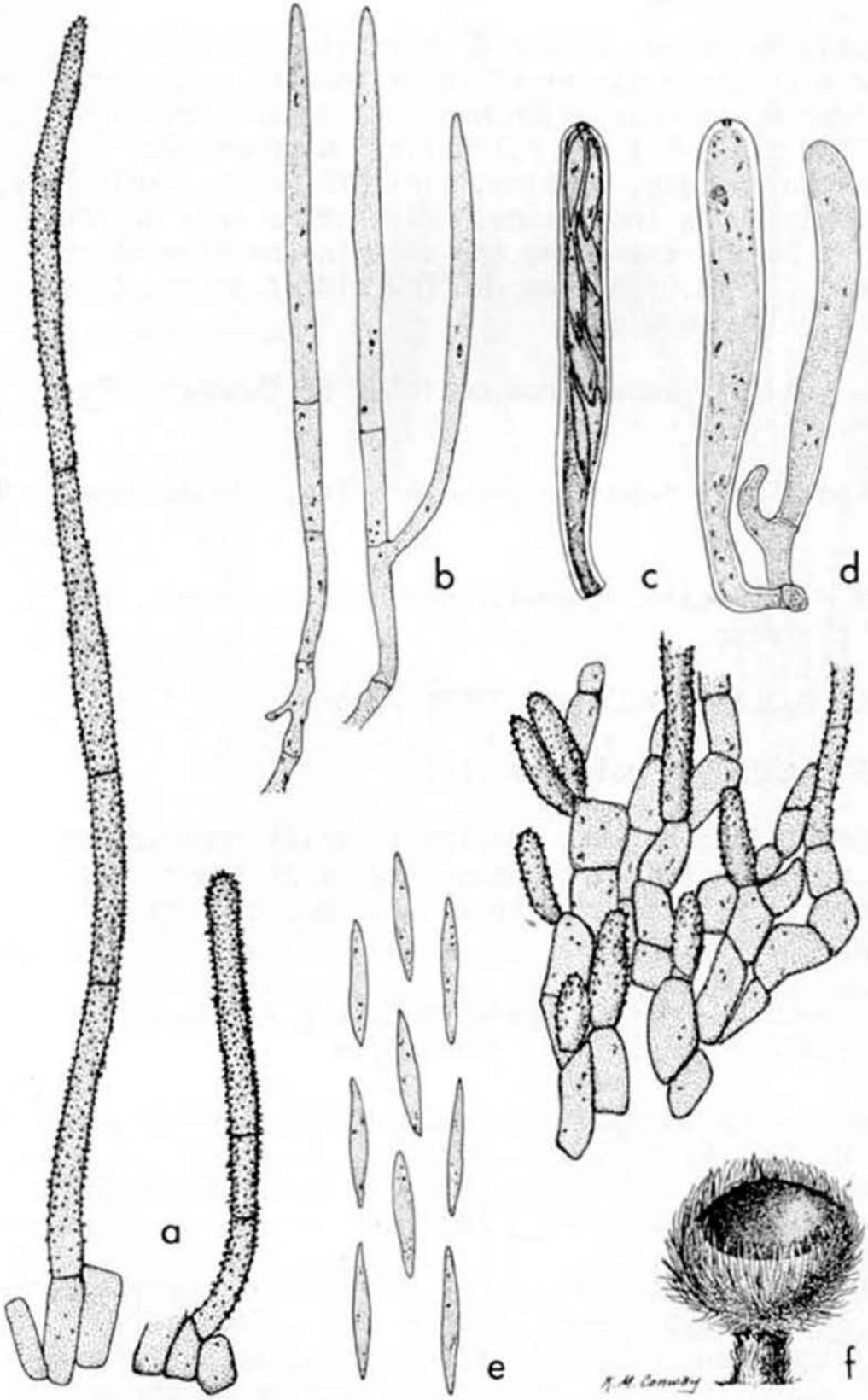


Fig. 1. *Dasyscyphus ulei*, a. hairs, b. paraphyses, c. asci, e. spores, d. surface view of ectal exciple, f. apothecium. From White #3310. a-e 1320X, f. approx. 30X.

cylindrical, 8-spored, with a J+ pore plug visible unstained with phase microscopy as a tapered cylinder, tapered toward the base which has no apparent crozier. Spores 18-30 x 0.8-1.1 µm, cylindrical with bipolar symmetry, non-septate, hyaline, flexible, often geniculate, without conspicuous inclusions. Paraphyses very narrowly lanceolate, barely exceeding the asci in the hymenial arrangement, 1.2-2.0 µm diam. at the widest point, tips rounded, 0.5-1.0 µm wide.

HOST - As yet only known from petioles of the large fern *Alsophila*.

RANGE - Known only from the type locality, Rio de Janeiro, Brasil.

ETYMOLOGY - From Latin Chermisino = Blood-colored, the color of the disc.

PREVIOUSLY PUBLISHED ILLUSTRATIONS - None.

SPECIMENS EXAMINED - Holotype (BPI).

DISCUSSION - Although this species is still represented by only one collection, it appears to be distinct. It has an obvious relationship to *D. ulei* but differs in spore shape and substrate.

3. *Dasyscyphus fimbriifer* (Berk. & Curt.) Sacc., Syll. Fung. 8:452. 1889. var. *fimbriifer*

≡*Peziza (Dasyscyphae) fimbriifer* Berk. & Curt., J. Linn. Soc. Bot. 10:377. 1868.
≡*Atractobolus fimbriifer* (Berk. & Curt.) O. Kuntze, Revis. Gen. Pl. 3:445. 1898.

TYPE - Charles Wright 654. Cuba, December. Holotype: Herb. Berkeley (K); Isotype: Herb. Curtis (FH). The Farlow Herbarium specimen also bears the designation "B&C Fungi Cub. 681" which is merely the species number in the publication. Both the holotype and isotype collections contain only a few immature or damaged apothecia.

Apothecia up to 0.6 mm in diam., stipitate, superficial, wine glass-shaped, light cream-colored, covered with long, bright white hairs without lumps of colored,

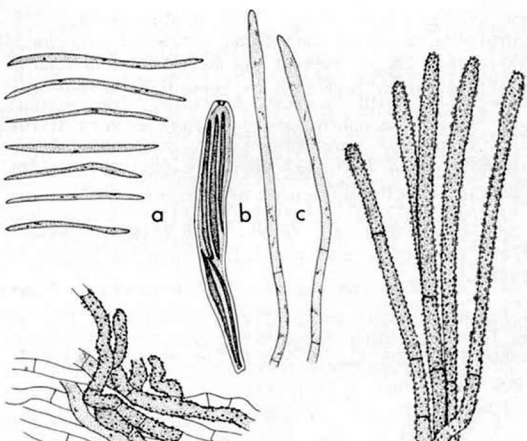


Fig. 2. *Dasyscyphus chermisinus*, a. spores, b. asci., c. paraphyses, d. hairs, e. surface view of exciple. From the holotype 1370X.

resinous matter; disc cream-color, exposed when moist, covered by hairs when dry; opening when rehydrated; hairs of different lengths, the longest to 350 x 4-6 µm, often tapered to 3-4 µm toward the apex and base, hyaline, thin-walled but rigid, septate at 12-30 µm intervals, ornamented on the surface with rod-shaped granules up to 0.5 µm in height and slightly less in diam. The granules appear to be slightly slanted toward the apex of the hairs; shorter hairs are similar, but usually cylindrical. Asci 60-85 x 6-8 µm, cylindrical, with hemispherical to conical apices and tapered bases, 8-spored, with obvious pore and tapered, J+ plug 1.5 µm long, 1.0 µm wide at the top, visible with phase optics as a tapered tube, croziers not observed, arising from a subhymenium of textura intricata. Spores (13-)15-28(-32) x 2.0-3.0(-3.7) µm, fusiform with rounded

tips about 1 µm broad, and with nearly bipolar symmetry, non-septate, or rarely 1 or 3 septate, often with refractile inclusions almost filling the cell, often slightly geniculate at one or both ends or curved along the longitudinal axis, hyaline, biseriate in the ascus. Paraphyses filiform, 5-10 µm longer than asci at maturity, 1.5-2.0 µm wide, but narrowing slightly at the base and apex; sometimes branched near the base, hyaline, septate in the lower portion. Ectal excipulum of textura porrecta; cell lumen visible; cell walls faintly visible with phase contrast optics; cells mostly 7-15 x 3.0-4.5 µm, becoming larger and forming texture prismatica near the margin of old apothecia.

HOST - Found primarily on the fleshy portions of the fronds of tree ferns and other large members of the Cyatheaceae, also known from *Gleichenia*, and reported from bamboo (Dennis, 1960).

RANGE - Common in Venezuela and Colombia, known from Cuba, Ecuador, and Jamaica. Probably extensive throughout the higher elevations of its hosts' ranges in the New World Tropics, but not yet reported from the Old World Tropics.

ETYMOLOGY - *fimbriifer* = bearing a fringed border. From the Latin *fimbria*, a fringed border.

PREVIOUSLY PUBLISHED ILLUSTRATIONS - Dennis, Kew Bull. 9:310, fig. 20. 1950.

SPECIMENS EXAMINED - Cuba: Wright, 654, December, sometime between 1856 and 1866, no location given "on stems of ferns." Portions of this type material deposited in the Curtis Herbarium at (FH) and the Berkeley Herbarium at (K). Venezuela: Dumont - VE 2062, K.P. Dumont, J.H. Haines, G.J. Samuels, 13. VII. 1971, 19 km above Maracay on Maracay Choroní road, Parq. Nac. Henry Pittier, Edo Aragua (NYS) on rachis of unidentified tree fern. Dumont - VE 2117, 2129, 2138 (NYS) same data and location but on spiney fern rachis. Dumont - VE 2861, K.P. Dumont, G.J. Samuels and L. Borjas, 24. VII. 1971, ca 4 km inside San Javier del Valle resort, 7 km NE of Mérida, Edo Mérida, on fern rachis (NY); Dumont - VE 5021, K.P. Dumont, G.J. Samuels, G. Morillo and J. Farfan, 13. III. 1972, trail from Los Pocitos through La Roma to Río Grande Arriba, Edo Sucre, on fern rachis (NY). Jamaica: CUP-MJ 156, R.P. Korf et al.,

9.I. 1971, along Lady's Mile Trail to just south of Woodcutter's Gap, vicinity of Newcastle, border of St. Andrew and Portland Parishes, on rachis of *Gleichenia* sp. (CUP); CUP-MJ 301, R.P. Korf et al., between Woodcutter's Gap and ruins of Major Wallin's House, vicinity of Newcastle, Portland Parish, on rachis of *Gleichenia* (CUP): CUP-MJ 341, R.P. Korf et al., 11.I. 1971, near Dick's Pond, west of Hardwar Gap, near Holywell Recreation Area, St. Andrew Parish, elev. 2800-3000 ft., on *Gleichenia* rhizome (CUP); CUP-MJ 584, R.P. Korf et al., 17.I. 1971, trail from Whitfield Hall to Portland Gap, to Blue Mt., border of St. Thomas and Portland Parishes, on rachis of *Cyathea* (CUP). Colombia: Dumont-CO 155, 192, 207, 221, K.P. Dumont, J.H. Haines, J.M. Idrobo and L.F. Velásquez, 29.V. 1974, EL Bosque de Las Mercedes, Bojaca, Dpto. Cundinamarca, on rachis of tree fern, (NY); Dumont - CO 307, K.P. Dumont, J.H. Haines, and J.M. Idrobo, 1.VII. 1974, Alto de San Miquel, road between Sibate and Fusagasuga, Dpto. Cundinamarca, on rachis of fern (NYS); Dumont - CO 979, 980, 994, K.P. Dumont, J.H. Haines, J.M. Idrobo and L.F. Velásquez, 10.VII. 1974, vicinity km 15 from Fomeque, road between Calera and Fomeque, Dpto. Cundinamarca, on rachis of Cyatheaceae (NYS); Dumont - CO 2737, 2748, 2752, K.P. Dumont, P. Buriticá, J.L. Luteyn and L.A. Molina, 15.I. 1976, ca 23 mi. from Altamira on the Altamira-Florencia Road, Dpto. Huila, elev. ca 7400 ft., on fern rachis (NY). Ecuador: Dumont - EC 1467, K.P. Dumont, S.E. Carpenter and P. Buriticá, 24.VII. 1975, ca 2 km from Puyo, on the Ambato-Puyo Road, Prov. Pastaza, elev. ca 4,000 ft., on fern rachis (NY).

D. fimbriifer is one of the earliest names applied to the tropical fern inhabiting Hyaloscyphaceae. It appears to be a part of a small complex of taxa which are indistinguishable macroscopically and in their excipular and hair characteristics, but differ in spore characters. As material from different geographical regions and different seasons is examined, the separation of those taxa as species becomes less clear. It is proposed here to treat these taxa as varieties of *D. fimbriifer*.

With a dissecting microscope or good field lens, *D. fimbriifer*, including all of its varieties, is distinguished by its long white to pale yellow hairs which point away from the substrate to partially obscure its cream-colored hymenium. *D. varians* differs in having shorter, buff-yellow hairs with lumps of amber to ruby-colored matter.

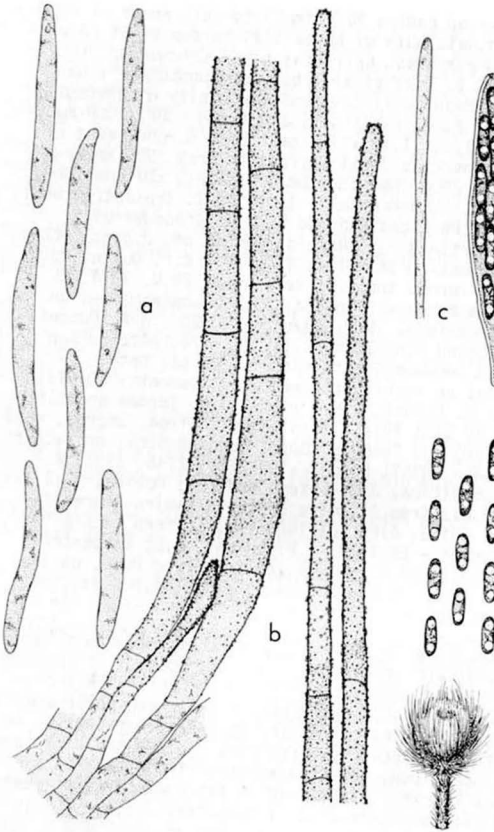


Fig. 3. *Dasyscyphus fimbriifer*, a. spores of var. *fimbriifer*, b-f. holotype of var. *singerianus*, b. hairs, c. paraphysis, d. ascus, e. spores, f. apothecium a-e, 1350X, f. much larger than natural size.

A number of collections from high elevations in Colombia and Venezuela have 0- to 1- septate spores 14-20 x 3-3.5 µm, long hyaline hairs characteristic of *D. fimbriifer* and short yellow hairs with colored matter at the tips characteristic of *D. varians*. Since the spore differences are small and placing too much emphasis on water soluable matter probably unwise, a new variety is unwarrented. These specimens are: Colombia, Dumont - CO 352B, K.P. Dumont, J.H. Haines and J.M. Idrobo, 1.VII. 1974, Quebrada Aquas Blancas, road between Sibate and Fusagasuga, Dpto. Cundinamarca, on petiole of tree fern (NYS); Dumont - CO 457, K.P Dumont, J.H. Haines and J.M. Idrobo, 2VII. 1979, Páramo de Choachí, road between Bogotá and Choachí, Dpto. Cundinamarca, on rachis of unidentified fern (NYS). Venezuela: Dumont - VE 2570, 2591, K.P. Dumont, J.H. Haines, G.J. Samuels, S. Silverborg, and L. Borjas, 20. VII. 1971, ca 63 km from Mérida, Univ. Los Andes Forest Reserve, La Carbonera, Edo. Mérida, on tree fern (NYS); Dumont - VE 2886, 2904. K.P. Dumont, G.J. Samuels and L. Borjas, 24.VII. 1971, ca 4 km inside San Javier del Valle resort, 7 km NE of Mérida, Edo. Mérida. on tree fern (NYS).

4. *Dasyscyphus fimbriifer* var. SINGERIANUS (Dennis) Haines, Comb. et stat. nov. Fig. 3, e-f

Basionym - *Dasyscyphus singerianus* Dennis, Kew Bull. 13: 465. 1958.

HOLOTYPE - R. Singer, B602, 28.I. 1956, Cataratas San Juan, Prov. Nor-Yungas, Dpto. LaPaz, Bolivia, altitude ca 2400 m, "on dead petioles and especially thorns of *Dicksonia* and other tree ferns" (K).

Apothecia, hairs and ectal exciple indistinguishable from the typical variety. Asci. 35-50 x 3.6-4.8 µm, pore plug visible with phase optics, blued with Melzer's solution, not subtended by a crozier. Spores 6-12 x 1.5-2.0 µm, non-septate, cylindrical, with rounded tips, not curved in the longitudinal axis, symmetry bipolar, usually with a large vacuole at each end. Paraphyses 1.8-2.0 µm at the widest point, which is 5-15 µm below the tip, exceeding the asci by 5-15 µm.

HOSTS - Usually on tree ferns and large members of the Cyatheaceae. One collection, EC - 1404, on a palm species

is included here.

RANGE - Throughout the andean range from Venezuela to Bolivia and Jamaica. It is probably common wherever the hosts occur, and coincident with the range of the typical variety.

ETYMOLOGY - *singerianus* for the eminent mycologist Rolf Singer, the collector of the type specimen.

PREVIOUSLY PUBLISHED ILLUSTRATIONS - Dennis Kew Bull. 13: 466. 1958. Fig. 7.

SPECIMENS EXAMINED - Bolivia: (see holotype). Colombia: Dumont - CO 1087, K.P. Dumont, J.M. Idrobo and L.F. Velásquez, 13.VII. 1974, near km post 20 from Cali on road between Cali and Buenaventura, Dpto. Valle, on petiole of Cyatheaceae (NYS); Dumont - CO 2230, K.P. Dumont, P. Buriticá and J.L. Luteyn, 7.I. 1976, vicinity of km post 18 from Bogotá, on the Bogotá-Villavicencia Road via Cáqueza, Dpto. Cundinamarca, elev. ca 10,200 ft. on fern rachis (NYS); Dumont - CO 2693, K.P. Dumont, P. Buriticá, J.L. Luteyn and L.A. Molina, 15.I. 1976, ca 20 mi. from Altamira on the Altamira-Florencia Road, Dpto. Huila, elev. ca 6,500 ft. on large fern rachis (NY); Dumont - CO 2975, K.P. Dumont, P. Buriticá, J.L. Luteyn and L.A. Molina 18,I. 1976, ca 32 mi. from Florencia, on the Florencia-El Doncello Road, Intendencia Caqueta, elev. ca 4,800 ft., on small fern rachis (NY). Ecuador: Dumont - EC 1404, K.P. Dumont, S.E. Carpenter and P. Buritica, 24.VII. 1975, ca 73 km from Ambato, on the Ambato-Puyo Road, border between Tungurahua and Pastaza Provinces, elev. ca 4,800 ft., on unidentified palm frond (NY). Jamaica: CUP-MJ-290, R.P. Korf, J.R. Dixon, K.P. Dumont, R.W. Erb, D.H. Pfister, D.R. Reynolds, A.Y. Rossman and G.W. Samuels, 11.I. 1971, on trail between Woodcutter's Gap and ruins of Major Wallin's House, vicinity of Newcastle, Portland Parish, on rachis of *Cyathea* sp. (CUP). Peru: Dumont - PE 409, K.P. Dumont, S.E. Carpenter, M.A. Sherwood & P. Buriticá, 2.VII. 1976, vicinity km post 450 from Lima on the Huanuco, elev. 8,500 ft., on fern rachis (NY). Venezuela: Dumont - VE 2123, VE 2142, K.P. Dumont, J.H. Haines and G.J. Samuels, 13.III. 1971, ca 19 km above Maracay, on Maracay-Choroní Rd., Parq. Nac. Henry Pittier, Edo. Aragua on rachis of tree fern (NYS); Dumont VE 3132, 26.VII. 1971, K.P. Dumont, G.J. Samuels

and L. Borjas, ravine ca 76 km from Barrancas, on Mérida-Barinas Rd., Edo. Barinas, on large unidentified fern (NYS).

DISCUSSION - *Dasyscyphus singerianus* was originally described as having 1-septate spores, but on reexamination of the type specimen with phase contrast microscopy after mounted for 24 hrs. in 3% KOH to loosen and expand the cell wall material no septum was observed. Most spores, however, have a prominant refractive vacuole at each end which compresses the cell contents into the center which under low magnifications could be mistaken for a septum. Without the character of spore septation, it is only a matter of spore size which separates it from *D. fimbriifer*. Although the spore size difference is considerable, an intermediate series of collections has been examined. Colombia: Dumont - CO 350, K.P. Dumont, J.H. Haines and J.M. Idrobo, 1.VII. 1974, Quebrada Aguas Blancas, road between Sibate and Fusagasuga, Dpto. Cundinamarca (NYS); Dumont - CO 1481, K.P. Dumont, J.H. Haines, J.M. Idrobo and L.F. Velásquez, 16.VII. 1974, Western slope of Cordillera Occidental, road between El Tambo and Veinte de Julio, Dpto. Cauca, on rachis of tree fern (NYS). Mexico: CUP-ME 244, K.P. Dumont, 15.VIII. 1967, 3-4 mi. N of junction to Simojoval, on road from Tuxtual Gutierrez to Villahermosa, Chiapas, on tree fern (? *Cyathea* sp.) (CUP), (NYS). Venezuela: Dumont - VE 2878, K.P. Dumont, G.J. Samuels and L. Borjas, 24.VII. 1971, ca 4 km inside San Javier del Valle resort, 7 km NE of Mérida, Edo. Mérida, on fern rachis (NY). These specimens have spores 9-12 µm long and usually contain more than two refractive vacuoles. The following collections have spores ranging from 12-16 µm in length and complete the connection between *D. fimbriifer* var. *fimbriifer* and *D. fimbriifer* var. *singerianus*: Dumont - CO 2708, K.P. Dumont, P. Buriticá, J.L. Luteyn and L.A. Molina 15.I. 1976, ca 20 mi. from Altamira on the Altamira-Florencia Road, Dpto. Huila, elev. ca 6,500 ft., on fern rachis (NYS). Dumont - CO 2749, K.P. Dumont, P. Buriticá, J.L. Luteyn and L.A. Molina, 15.I. 1976, ca 23 mi. from Altamira on the Altamira-Florencia Road, Dpto. Huila, elev. ca 7,400 ft. on fern rachis (NY).

5. *Dasyscyphus BREVISPORUS* (Otani) Haines, comb. et stat. nov. Fig. 4.

≡*Dasyscyphus fimbriifer* var. *brevisporus* Otani, (as *D. fimbriiferus* var. *brevisporus*). Reports of the Cryptogams in Papua, New Guinea (Tokyo), p. 31, 1975.

HOLOTYPE - Y. Otani, No. 10659, TNS-F-50005, 18.I. 1974, Mt. Albert Edward, Woitape, Central District, New Guinea, on fern rachis (TNS).

Apothecia solitary or scattered on the substrate, goblet shaped, to 1.5 mm in diam., stipitate, stip to 0.8 mm long, excipulum light buff, completely covered with very long, upward oriented, stiff, bright white, dry-appearing hairs to 0.6 mm long; no conspicuous adhering particles visible under a dissecting microscope; disc buff-yellow, completely obscured by the hairs when dry; no color change when placed in 3% KOH. Hairs to 600 x 3.0-3.5 µm, tapered to 1.8-2.2 µm at the apices, septate, hyaline, thin-walled toward the apex, up to 0.9 µm thick near the base, covered with small, discrete, rod-like particles to 1.0 µm long, slightly longer than broad, appearing capitate in optical section, perpendicular to the hair wall in longer hairs, appearing slightly slanted toward the apex in shorter hairs; a few long hairs bearing a small amount of hyaline resinous matter near their tips and visible only with a compound microscope; a few short, rough, thin-walled, flexuous hairs intermixed with the longer ones. Ectal exciple composed of distinct, thin-walled, hyaline textura prismatica, the individual cells 15-30 x 4-8 µm, becoming smaller toward the stipe. Asci 60-71 x 5.5-7.0 µm, 8-spored, cylindrical with a hemispherical apex and tapered base, j+ pore clearly visible with phase contrast optics, appearing as a tapered cylinder about 1.0 µm in diam. in optical cross section of stained material. Spores 10-13 x 1.8-2.7 µm, non-septate, hyaline, smooth, nearly cylindrical, slightly curved, with rounded tips, usually without conspicuous vacuoles or other inclusions. Paraphyses cylindrical or very slightly enlarged in the upper third, 1.8-2.5 µm in diam. at the widest point, slightly tapered above to a blunt apex, hyaline, smooth, without adhering particles, septate in the lower two-thirds only, exceeding the asci by up to 10 µm in the hymenium.

HOST - On pinnae and rachises of large ferns. The portion of the type examined by the author was a portion of fern rachis about 3.0 mm in diam.

RANGE - Know only from type collection from New Guinea.

ETYMOLOGY - *Brevisporus* - short-spored, referring to its

having shorter spores than the type variety of *D. fimbriifer*.

PREVIOUSLY PUBLISHED ILLUSTRATIONS - Otani, Yoshio. Reports on the Cryptogams in Papua New Guinea published by the Party 1973-74, of "The Botanical Expedition to Papua New Guinea," The National Science Museum, Tokyo; fig. 15 f-j, Pl. 2H, p. 33, March, 1975.

SPECIMENS EXAMINED - A portion of the type was examined by the author (see holotype). There is a discrepancy in the locality information between the description and the packet for Otani No. 10659. The type packet gives the location as "Mt. Albert Edward" and the description as "Keglsugl." No attempt was made to resolve the difference.

DISCUSSION - This taxon is related to *D. fimbriifer* as concluded by Otani (1975). The granulation of the hairs, the substrate, the characters of the excipulum asci and paraphyses are similar to *D. fimbriifer* var. *fimbriifer*, and the spore size range is small enough to be included in *D. fimbriifer* var. *singerianus*. However, the very long hairs, robust apothecia, the different overall appearance and range are sufficient to allow it to stand as a separate species.

6. *Dasyscyphus varians* Rehm, Hedwigia 39:94. 1900 var. *Varians*. Fig. 5, a-e.

=*Lachnum gleicheniae* Cash, Mycologia 30:105. 1938.
≡*Lachnella gleicheniae* (Cash) Seaver, N. Amer. Cup-fungi (inoperculates) p. 266. 1951.
=*Dasyscyphus flavidulus* Rehm, Ann. Mycol. 7:542. 1909.

Isotype - E. Ule #758. Brasil, holotype in herb. Rehm (S) and lectotype in herb. Sydow (S).

Apothecia scattered on substrate, often spreading over large areas, goblet-shaped or funnel-shaped, to 0.6 mm in diam. and to 0.8 mm high, stipitate, pale buff, completely covered with short, pale buff to lemon-yellow hairs with conspicuous lumps of amorphous, water-soluable matter at the tips; lumps amber to dark ruby red, up to 0.1 mm in diam., dissolving but not changing color with 3% KOH; disc cream to ochre, usually obscured by marginal hairs when dry and exposed in mature apothecia when moist.

Hairs cylindrical to 100 µm long with a slightly tapered base and a hemispherical apex, generally 40-70 x 2.8-5.0 µm, thin-walled, pale straw-yellow with transmitted light, septate, roughened with hyaline, rod-shaped granules similar to those of *D. fimbrifer* and which appear to be slightly inclined towards the apex in some hairs. Ectal excipulum composed of short-celled, thin-to thick-walled, hyaline textura prismatica becoming textura angularis in some portions of the cup. Asci 40-52 x 3.8-5.1 µm, 8-spored, cylindrical with a tapered base and hemispherical apex, with a small but distinct J+ pore plug visible as a tapered cylinder in optical cross-section, croziers not observed at the base. Spores 6-11 x 1.5-2.2 µm, eliptical, tips rounded, slightly more tapered in the basal portion, hyaline, smooth, often with 2 conspicuous refractive inclusions, slightly curved along the longitudinal axis. Paraphyses hyaline, narrowly lanceolate or cylindrical with a tapered apex, septate only in the lower portion, 1.5-2.6 µm at the widest point, exceeding the asci by 1.0 µm in the hymenial arrangement.

HOSTS - On rachises of members of the Cyatheaceae, Gleicheniaceae and Dicksoniaceae including *Cyathea dealbata, Gleicheinia pectinata* and *Dicksonia squarrosa*. Also known from *Papuapteris linearis*.

RANGE - Found in northern and western South America, the Caribbean, Hawaii, New Guinea and New Zealand. It is probably found throughout the upper elevations of the range of the larger Cyatheaceae and otherlarge tropical ferns. It is not yet known from the African continent.

ETYMOLOGY - Varians = varying. Probably referring to the apparent color changes explained in the discussion.

PREVIOUSLY PUBLISHED ILLUSTRATIONS - Dennis Kew Bull. 9: 312. Fig. 22; Otani, Reports on the Cryptogams in Papua New Guinea p. 29. Fig. 14, a-d; Cash, Mycologia 30:99. Fig. 2 (as *Lachnum gleicheniae*); Dennis, Kew Bull. 9:311 (as *Dasyscypha flavidula*).

SPECIMENS EXAMINED - Colombia: Dumont - CO 158, K.P. Dumont, J.H. Haines, J.M. Idrobo and L.F. Velásquez, 29. VI. 1974, El Bosque de Las Mercedes, Bojaca, Dpto. Cundinamarca, on fern rachis (NYS); Dumont - CO 308, K.P. Dumont, J.H. Haines and J.M. Idrobo, 1.VII. 1974, Alto de

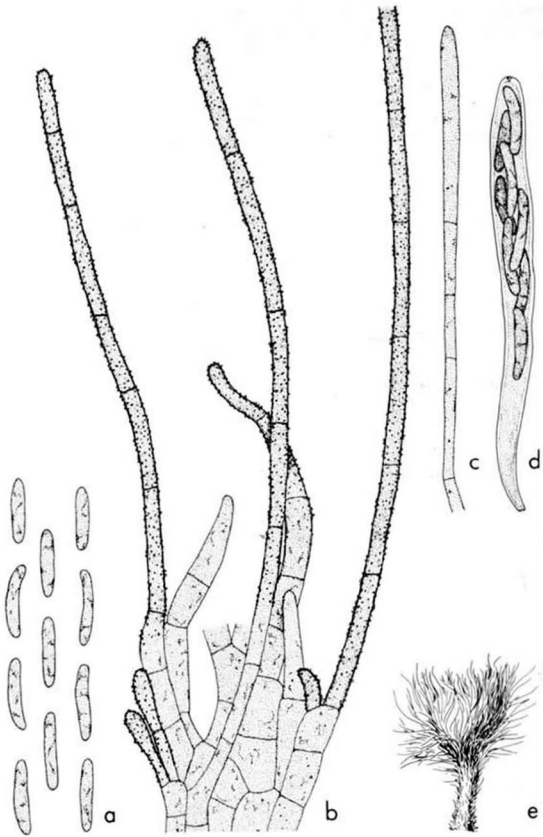


Fig. 4. *Dasyscyphus brevisporus*, type specimen, a. spores, b. ectal excipulum with hairs, c. paraphysis, d. ascus, e. apothecium. a-d. 1350X, e. much larger than natural size.

San Miguel, road between Sibate and Fusagasuga, Dpto. Cundinamarca, on fern petiole (NYS); Dumont - CO 358, K.P. Dumont, J.H. Haines and J.M. Idrobo, 1.VII. 1974, Quebrada Aguas Blancas, road between Sibate and Fusagasuga, Dpto. Cundinamarca, on fern rachis (NY); Dumont - CO 554, K.P. Dumont, J.H. Haines, L.F. Velásquez and R. Fonnegra, 5.VII. 1974, Buenos Aires, Providencia, Anorí, Río Anori, Dpto. Antioquia. on tree fern petiole (NYS); Dumont - CO 870, K.P. Dumont, J.H. Haines, L.F. Velásquez and R. Fonnegra, 6.VII. 1974, Popales, Providencca, Anori, above Rio La Tirana, Dpto. Autioquia, on tree fern rachis (NYS); Dumont - CO 1184, K.P. Dumont, J.M. Idrobo and L.F. Velásquez, 13.VII. 1974, vicinity km 20 from Cali, road between Cali and Buenaventura, Dpto. Valle, on petiole of Cyatheaceae (NYS); Dumont - CO 1486, K.P. Dumont, J.H. Haines, J.M. Idrobo and L.F. Velasquez, 16.VII. 1974, Western slope of Cordillera Occidental, road between El Tambo and Viente de Julio, Dpto. Cauca, on rachis of tree fern (NYS); Dumont - CO 2297, K.P. Dumont, P. Buriticá and J.L. Luteyn, 7.I. 1976, ca 14 mi. from Villavicencio on the Villavicencio-San Martin Rod., Dpto. Huila elev. ca 2,600 ft., on fern rachis (NY); Dumont - CO 2887, 2925, 2929, K.P. Dumont, P. Buriticá, J.L. Luteyn and L.H. Molina, 17.I. 1976, a 13 mi. from Florencia on the Florencia-El Doncello Road, Intendencia Caquetá. elev. ca 1,200 ft. on fern frond (NY). Ecuador: Dumont - EC 340, K.P. Dumont, S.E. Carpenter and P. Buriticá, 17.VII. 1975, ca 75 km SW of Chillogallo, on the old road from Quito to Santo Domingo, Prov. Pichincha. elev. ca 5,600 ft., on fern rachis (NY); Dumont - EC 1371, 1395, 1400, K.P. Dumont, S.E. Carpenter and P. Buriticá, 24.VII. 1975, ca 73 km from Ambato, on the Ambato-Puyo Road, border between Tungurahua and Pastaza Provinces, elev. ca 4,800 ft., on fern rachis (NY); Dumont - EC 1797, 1801, K.P. Dumont, S.E. Carpter and P. Buriticá, 31.VII. 1975. ca 21 km from Zanora, on the Zamora-Yanaza Road, Prov. Zamora, elev. ca 3,000 ft., on fern rachis (NY); Dumont - EC 1896, 1910, 1913, K.P. Dumont, S.E. Carpenter and P. Buriticá, 1.VIII. 1975, ca 12 km from Zamora, on the Zamora-Loja Road, Prov. Zamora, elev. ca 5,000 ft., on fern rachis (NY); Dumont - EC 1927, 1935, K.P. Dumont, S.E. Carpenter and P. Buriticá, 1.VIII. 1975, ca 22 km from Zamora, on the Zamora-Loja Road, Prov. Zamora, elev. ca 5,800 ft., on fern rachis (NY); Dumont - EC 2001, 2024, K.P. Dumont, S.E. Carpenter and P. Buriticá, 3.VIII. 1975, ca 5 km from Limón (General Plaza Gutierez), on the Limón-Mendez Road, Prov. Morona

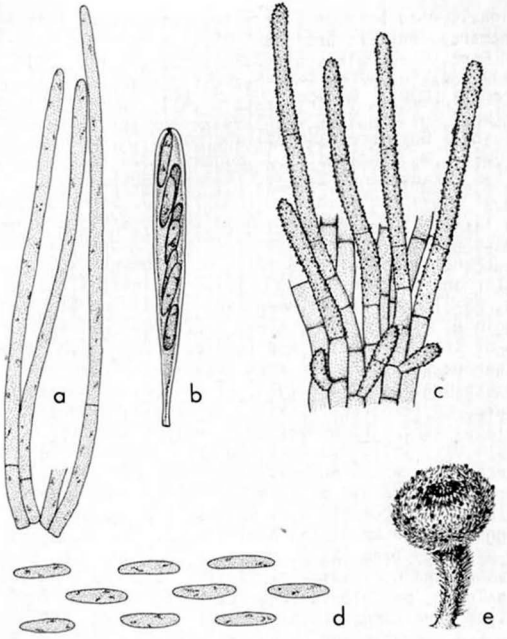


Fig. 5. *Dasyscyphus varians*. From VE 2878, a. paraphyses, b. ascus, c. exciple with hairs, d. spores, e. apothecium, a-d. 1370X, e. much larger than natural size.

Santiago, elev. ca 4,000 ft., on tree fern petiole (NY). Hawaii: Otto Degener, No. 2810, Otto Degener and Henry Wiebke, 12.IV. 1928, South of Hanaliioliio, Molokai, T.H. "on stipes of endemic *Dicranopteris*" as holotype of *Lachnum gleicheniae* Cash (BPI); C.L. Shear and N.E. Stevens 580, 28.XII. 1927, Olinda Pipe Line, Maui, on tree fern rachis, as *Lachnum gleicheiae* Cash (BPI); C.L. Shear and N.E. Stevens, 582, 17.II. 1928, above Waimea,

Oahu, on rachis of *Gleichenia* sp. as *Lachnum gleicheniae* Cash (BPI). Jamaica: R.P. Korf et al., CUP-MJ 110, 8.I. 1971. Traveller's rest. Silver Hill Gap, on the border of Portland and St. Andrew Parish, elev. 3,000-3,250 ft. on fern rachis (CUP). Mexico: CUP, ME 244, K.P. Dumont, 15. VIII. 1967, 3-4 mi. N of Junction to Simojovel, on road from Tuxtula Gutierrez and Villahermosa, Chiapas, on tree fern (CUP). New Zealand: S.J. Hughes #1328 (DAOM 162333) 4.IX. 1963, Kauaeranga Valley, Thames, Auckland Dist., on rachis of *Dicksonia squarrosa* (DAOM); G.J. Samuels, PDD 31947, 7.VIII. 1973, Walker's Bush Track, Waitake Ranges, Waitemata County, Auckland, on rachis of *Cyathea dealbata* (PDD). Panama: Dumont - PA 1578, K.P. Dumont, S.E. Carpenter and S.A. Mori, 30 VI. 1975, Vicinity Altos de Pacora, 26-31 km N of Pan American Highway, on old road to Mandinga, Prov. Panama, elev. ca 2,100-2,200 ft. on rachis of tree fern (NY); Puerto Rico: F.J. Seaver and C.E. Chardon #546 (The New York Botanical Garden West Indian Exploration #1811) 1923, El Yunque, as *Dasyscypha flavidula?* on fern rachis (NY). Venezuela: Dumont - VE 1245, 1257, 1286, K.P. Dumont, J.H. Haines and G.J. Samuels 4.VII. 1971, 2-3 km along trail behind hotel, up Mt. Guacamaya, Rancho Grande, Parq. Nac. Henry Pittier, Edo. Aragua, on rachis of tree fern (NYS); Dumont - VE 1524, 1529, K.P. Dumont, J.H. Haines, G.J. Samuels and G.S. Bunting. In mountains N of Nirgua, Edo. Yuracuy, on rachis of large fern (NYS); Dumont - VE 2203, K.P. Dumont, J.H. Haines and G.J. Samuels, 14.VII. 1971. ca 7 km from Colonia Tovar, on Colonia Tovar-La Victoria Road, Edo Aragua, on fern rachis (NYS); Dumont - VE 2878, K.P. Dumont, G.J. Samuels and L. Borjas, 24.VII. 1971, ca 4 km inside San Javier del Valle resort, 7 km NE of Mérida, Edo. Mérida, on fern rachis (NY).

DISCUSSION - *D. varians* var. *varians* is the most common and widespread discomycete inhabiting the decaying remains of tropical ferns. It is related to *D. fimbriifer* and *D. brevisporus* in the slightly elongated hair granulations which often appear to be very slightly inclined toward the hair tips and in the exciple of rather distinct textura prismatica. It is distinguished from all other taxa of Hyaloscyphaceae by the combination of hair and spore size and the presence of yellow to dark red pigments on the hairs.

The aspect of this taxon which has caused confusion

in its identification is the pigmentation associated with the hairs. One of the distinctions drawn here by the author between *D. fimbriifer* and *D. varians* is that the former has hyaline hairs and the latter a pale straw pigment located in the walls of the hair. In addition, a water-soluable lemon-yellow pigment is located on or in hairs of young apothecia which progressively darkens and concentrates into large lumps of matter 20-50 µm. These lumps are light amber on lemon-yellow hairs at first and darken to deep garnet red on light buff-white hairs with age. The pigment may be absent altogether in water soaked specimens. These color shifts can cause an array of differently colored apothecia growing together on the same piece of substrate. A second confusing aspect of *D. varians* is the continuum of spore sizes. *D. varians* var. *varians* and *D. varians* var. *pteridophyllus* represent modes in the spore size continuum and intermediate spore sizes can be found.

It is possible that *D. varians* published by Rehm in 1900 is a later synonym of *D. tubiformis* P. Hennings & E. Nyman, Monsunia 1:32, 1899 but a number of inquiries did not locate the Hennings type, so for the time being, *D. tubiformis* remains unexamined. *D. cyatheicola* P. Hennings, Hedwigia 41:25. 1902 is perhaps also a later synonym, but no type was located for it either.

7. *Dasyscyphus varians* var. PTERIDOPYLLUS (Rodw.) Haines, comb. et stat. nov.
   Basionym - *Dasyscypha pteriodophylla* Rodway, Pap. & Proc. Roy. Soc. Tasmania 1920:158, 1921.

TYPE COLLECTION - L. Rodway, October 1920, National Park (Tasmanian?), on stipe of dead *Dicksonia antarctica*. (HO). No specimen is mentioned in the place of original publication, but this specimen is clearly marked "type."

Apothecia, hairs, asci, paraphyses, excipulum and disc indistinguishable from those of the typical variety of *D. varians*. Spores 11-17 x 1.0-1.9 µm, straight, with bipolar symmetry, fusiform, tapered to sharply acute apices, rarely 1-septate, sometimes with 2 or 4 refractive vacuoles.

HOSTS - Known from species of Cyatheaceae, *Cyathea dealbata*, Dicksoniaceae, *Dicksonia antarctica* and

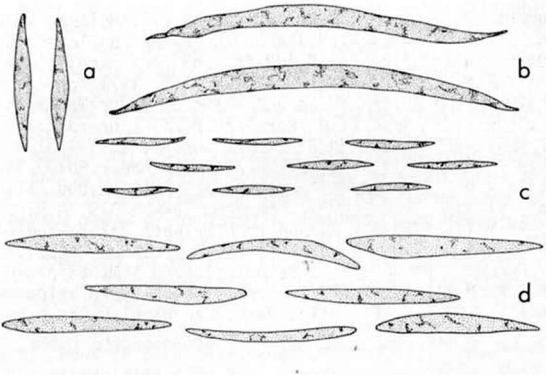


Fig. 6. Spores, a. from lectotype of *Dasyscypha javanica*, b. from Penzig and Saccardo #26 *D. oncospermatis* var. *macrospora*, c. from holotype of *D. varians* var. *pteridophyllus*, d. from holotype of *D. oncospermatis* var. *oncospermatis*, all 1370X.

Gleicheniaceae, *Gleichenia* sp.

RANGE - Colombia, Jamaica, Mexico, Panama, Peru, Puerto Rico, New Guinea, New Zealand, Tasmania and Venezuela. Perhaps throughout the range of large tropical ferns and coincident with the range of the type variety.

ETYMOLOGY - Pteridophyllus = fern leaves.

PREVIOUSLY PUBLISHED ILLUSTRATIONS - Dennis, Kew Bull. 13: 329. 1958. Fig. 8; Otani, Reports on the Cryptogams of Papua, New Guinea 1975:27, Fig. 13 e-i. 1975.

SPECIMENS EXAMINED - Colombia: Dumont - CO 393, K.P. Dumont, J.H. Haines and J.M. Idrobo, 1.VII. 1974, Quebrada Aguas Blancas, road between Sibate and Fusagasuga, Dpto. Cundinamarca on fern petiole (NYS); Dumont - CO 1514, K.P. Dumont, J.H. Haines, J.M. Idrobo and L.F. Velásquez, 16.VII. 1974, Western slope of Cordillera Occidental road between El Tambo and viente de Julio, Dpto. Cauca, on rachis of tree fern (NYS); Dumont - CO 2746, 2751,

K.P. Dumont, P. Buriticá, J.L. Luteyn and L.A. Molina, 15. I. 1976, ca 23 mi. from Altamira on the Altamira-Florencia Road, Dpto. Huila. elev. ca 7,400 ft., on fern rachis (NY). Jamaica: CUP-MJ 280, R.P. Korf et al., 11.I. 1971, on trail between Woodcutter's Gap and ruins of Major Wallin's House, vicinity of Newcastle, Portland Parish, on rachis of *Gleichenia* (CUP); CUP-MJ 336, R.P. Korf et al., 11.I. 1971, Near Dick's Pond, west of Hardwar Gap, near Holywell Recreation Area, St. Andrew Parish, elev. 2,800-3,000 ft., on rachis of *Gleichenia* (CUP). Mexico: CUP-ME 319, K.P. Dumont, 25.VIII. 1967, km 141 on road between Oaxaca and Valle National, Oaxaca, on tree fern, *Cyathea* sp.? (CUP). Panama: Dumont - PA 263, K.P. Dumont, S.E. & S.M. Carpenter and S.A. Mori, 14.VI. 1975, from base of Cerro Pilón to summit, 5 km NE of El Valle, Prov. Cocles elev. ca 2,200-3,000 ft., on tree fern petiole (NY); Dumont - PA 337, K.P. Dumont, S.E. & S.M. Carpenter and S.A. Mori, 14.VI. 1975, vicinity of La Mesa, 2.5 km N of El Valle, Prov. Cocle, elev. ca 2,100 ft., on fern rachis (NY); Dumont - PA 1571, K.P. Dumont, S.E. Carpenter and S.A. Mori, 30.VI. 1975, vicinity Altos de Pecora, 26-31 km N of Pan American Highway, on old road to Mandinga, Prov. Panama, elev. ca 2,100-3,000 ft., on petiole of fern (NY). Peru: Dumont - PE 412, 444, K.P. Dumont, S.E. Carpenter, M.A. Sherwood and P. Buriticá, 2.VII. 1976, vicinity km post 450, from Lima on the Huanuco-Tingo María Rd., Dpto. Huanuco elev. 8,500 ft., on fern rachis (NY). Dumont - PE 1725, K.P. Dumont, S.E. Carpenter, M.A. Sherwood & P. Buriticá, 19.VII. 1976, along the Cuzco-Pilcopata-Paucartambo Rd., at a point ca 135 km from the intersection of the Cuzco-Puno Rd., Dpto. Cuzco., on fern rachis (NY). Puerto Rico: Haines - PR 11, 15, J.H. Haines, R.P. Korf, et al., 5.VI. 1970, El Toro Trail, El Yunque Luquillo Experimental Forest, elev. ca 700 m, on *Alsophylla* rachis (NYS); Haines - PR 14, J.H. Haines, R.P. Korf, et al., 8.VII. 1970, Rt. 191 & 930, El Yungue, Luquillo Experimental Forest, elev. 700 m, on *Gleichenica pectinata* rachis (NYS); Haines - PR 17, J.H. Haines, R.P. Korf, et al., 8.VI. 1970, Rt. 930, El Yunque, Luquillo Experimental Forest, elev. ca 675 m, on rachis of *Cyathea dryopteriodes* (NYS); Haines PR - 19, J.H. Haines, R.P. Korf, et al., 8.VI. 1970, Rts. 191 & 930, El Yunque, Luquillo Experimental Forest, elev. ca 675 m, on rachis of *Alsophila borinquena* (NYS). New Zealand: PDD 19348 (=DAOM 75775), J.M. Dingley, 28.VIII. 1954, Whitianga, Auckland Prov., on *Cyathea medullaris* Swartz, (DAOM), PDD 31944 (=JHH 2808), G.J. Samuels, 8.VII. 1973, Walker's

Bush Track, Waitakere Ranges, Waitemata County, Auckland Prov., on rachis of *Cyathea dealbata* (NYS, PDD). Tasmania: (see type) Venezuela: Dumont - VE 2206, K.P. Dumont, J.H. Haines and G.J. Samuels, 14.VII. 1971, ca 7 km from Colonia Tovar, on Colonia Tovar-La Victoria road, Edo. Aragua, on fern rachis (NYS); Dumont - VE 2568, K.P. Dumont, J.H. Haines, G.J. Samuels, S. Silverborg and L. Borjas, 20.VII. 1971, ca 63 km W of Mérida, Univ. Los Andes Forest Reserve, La carbonera, Edo. Mérida, on rachis of tree fern (NYS).

DISCUSSION - Since a large number of collections were examined, intergradations were found between those that match the type of *D. pteridophyllus* and those fitting the description of *D. varians*. The two taxa are not retained as separate species and *D. pteridophyllus*, the more recent of the two names is reduced to a variety. There are several names described earlier than *D. pteridophyllus* which if types could be located may prove to be the same species. These are *D. tubiformis* (see under *D. varians*), *D. javanica* var. *citrinula* Penz. & Sacc. 1901, and *D. merrillii* Sydow 1913.

8. *Dasyscyphus oncospermatis* (Berk. & Br.) var. *oncospermatis* Sacc., Syll., Fung. 8:465. 1889. (as *Dasyscypha oncospermatis*)

≡*Peziza oncospermatis* Berk. & Br., J. Linn. Soc. Bot. 14:105. 1975.
≡*Aranea oncospermatis* (Berk. & Br.)Petch, Ann. Roy. Bot. Gard. Peradiniya 6:164. 1917.
≡*Atractobolus oncospermatis* (Berk. & Br.) O. Kuntze, Revis. Gen. Pl. 3(2):446. 1898.
=*Dasyscypha lanariceps* (Cke. & Phill.) Sacc., Syll. Fung. 8:465, 1889.
≡*Peziza lanariceps* Cke. & Phill., Grevillea 8:62. 1879.
≡*Atractobolus lanariceps* (Cke. & Phill.) O. Kuntze. Revis. Gen. Pl. 3:446. 1898.
=*Dasyscypha javanica* Penz. & Sacc., Malpighia 15:209. 1901. (not to be confused with *Arenaea javanica* Penz. & Sacc., *Erinella javanica* Henn. & Nym. nor *Erinella javensis* Höhn.)
=*Dasyscypha cyatheae* Rehm, Leafl. Philipp. Bot. 6:2280. 1914.

HOLOTYPE - Thwaits, Ceylon #435, Habgalla (sic), Dec. 1867,

ex herb C.E. Broome (K).

Apothecia scattered on substrate, often spreading over large areas, with convoluted margins or branched stipes with as many as a dozen cups on a single stipe, up to 1.0 mm across in multiple structures, single apothecia smaller, infundibulaform covered with short, straight, buff-yellow hairs capped with lumps of light red to deep garnet-colored resinous-appearing matter; disc concealed by hairs when dried. Hairs cylindrical with hemispherical tips and slightly tapered bases, straight, septate, straw-colored with transmitted light, 3.0-4.6 by up to 100 µm long, generally 40-70 µm, with walls up to 0.7 µm thick, roughened with granules as in *D. varians*. Ectal excipulum composed of small-celled, hyaline to buff textura prismatica. Asci 52-80 x 4.0-7.0 µm, 8-spored, cylindrical with a tapered base and hemispherical apex with a distinct J+ pore plug visible as a tapered cylinder in optical cross section. Spores (17-) 18-28(-31) x (1.5-) 2.0-3.0 (-3.5) µm, straight, hyaline, non-septate or rarely 1- or 3-septate, fusiform with distinctly pointed tips, usually with refractive vacuoles ranging from very tiny inclusions to almost filling the spore. Paraphyses filiform, very slightly tapered at the immediate apex, hyaline, 1.2-1.7 µm wide, slightly longer than the asci, septate and often branched in the lower portion.

HOST - Known from large ferns of the Cyatheaceae; *Hemitilia, Alsophila, Cyathea*. It is also known from *Rhipogonum* (Liliaceae), but the report from *Oncosperma* is questionable.

RANGE - Known from Ceylon, Australia, Java and the Philippines.

ETYMOLOGY - *Oncospermatis* from *Oncosperma*, a genus of Palms.

PREVIOUSLY PUBLISHED ILLUSTRATIONS - Penzig & Saccardo, Icones Fungorum Javanicorum, Tab. L, fig. 3 as *D. javanica*; Dennis, Kew Bull. 17:356, fig. 50.

SPECIMENS EXAMINED - Ceylon: (type; see above for information) Sydow, Fungi exotici exsiccati #227, Jan. 1914, Hatgala, Ceylon, T. Petch, on rachis of *Hemitiliae walkerae* (DAOM) (CUP). Australia: Berggren #363,

Melbourne 1974-1975, on *Rhipogonum*, (type of *Peziza lanariceps*) ex herb. CKE (K). Java: Penzig #20, XI. 1897, Tjibodas, on rachis of *Alsophia*, as *D. javanica* ex herb. Saccardo (PAD). Philippine Islands: C.F. Baker #2727, 31.I. 1914, Mt. Makiling, Los Baños, on rachis of *Cyathea candata*, holotype of *D. cyatheae*, ex herb. Rehm (S); C.F. Baker, Fungi Malayana #23, I. 1914, Mt. Makiling, ex herb. Sydow (S), (NY).

DISCUSSION - *Dasyscyphus oncospermatis* is closely related to *D. varians* in having similar hairs, colored exudates and exciple. It differs by having longer spores and asci and by having a branched stipe in some collections. It has not been resolved whether this species occurs in South America. Although some collections have been made there which have spore sizes in the range of *D. oncospermatis*, the branched character of the stipe has not been found.

There is some confusion over host identification which results in a fern-inhabiting species having the specific epithet "*oncospermatis*" which is derived from the palm *Oncosperma*. The type specimen does appear to be on a segment of fern stipe as was stated by Petch (Dennis, 1963).

Even though *Dasyscyphus javanica* is reduced to synonomy under *D. oncospermatis*, it is necessary to choose a lectotype for it from among the three collections mentioned by Penzig & Saccardo in the original description. I hereby choose collection #20 from PAD as lectotype. It is a small but completely recognizable collection.

9. *Dasyscyphus oncospermatis* var. *MACROSPORUS* (Penz. & Sacc.) Haines, comb. et stat. nov.

≡*Arenaea macrospora* Penz. & Sacc. Malpighia 15:211. 1901.

TYPE - According to the original description the type (implicit holotype because it is the only specimen mentioned) is "in petiolis putridis Palmarum, Tjibodas, 8.II. 1897 (16)."

Apothecia, hairs and excipulum indistinguishable from the type variety of *D. oncospermatis*. Asci

cylindrical, or clavate, 8-spored, 90-110 x 12-14 µm, thick-walled walls up to 1.5 µm thick, definite large J+ pore plug. Spores 36-67 x 2.5-3.5 µm, fusiform, with bipolar symetry and a very fine, hair-like appendage 1-2.5 µm long at each end, curved along the longitudinal axis, non-septate, usually without refractive contents. Paraphyses filiform 1.1-1.5 µm wide, sometimes enlarged slightly at the apex, septate, without pigments or conspicuous inclusions.

HOST - Although the type description states that *Dasyscyphus oncospermatis* was collected on palm petioles, collection #20 from Saccardo's herbarium in Padua which was collected at the same place and date is on remnants of a fern petiole as the piece of substrate in the packet has fern pinnae attached to it.

RANGE - Known only from two collections made in Java.

PREVIOUSLY PUBLISHED ILLUSTRATIONS - Penzig & Saccardo, Icones Fungorum Javanicorum Tab. LI, fig. 4. 1904.

SPECIMENS EXAMINED - 8.II (no year given) Tjibodas Java, #23 ex herb. Saccardo (PAD). This is the only collection under this name at Padua. It bears the same data as the type description but a different collection number.

DISCUSSION - Since collection #23 from Saccardo's herbarium fits the type description and illustration well, it will be included here as representative of this taxon. There are only spore size and shape and minor differences in paraphysis shape to separate it from *D. oncospermatis* var. *oncospermatis*.

ACKNOWLEDGMENTS

I am deeply indebted to Dr. Kent P. Dumont, his National Science Foundation grant #GB2893, The Flora Neotropica Project, the New York State Museum/Science Service, Dr. Richard P. Korf and the many kind people of Venezuela, Colombia and Puerto Rico who made it possible for me to collect and examine tropical discomycetes, to Dr. Korf for reading and making constructive comments on the manuscript and to the curators and directors of the following herbaria who searched for and made available

type specimens: K, S, B, C, TNS, BPI, CUP, MICH, FH, TAA, HO, DAOM, NY, PAD.

I particularly wish to thank Dr. Danial E. Stuntz who had nothing to do with this paper, but had everything to do with instilling in me an interest in mycology which is the reason this was written.

All of the "Dumont-" specimens at NYS are duplicates of collections deposited at NY and a major herbarium in the country of origin.

BIOLIOGRAPHY

Bϕhler, H.C. 1974. Taxonomical studies on some Norwegian Helotiales (Ascomycetes) on fern remains. Norw. J. Bot. 21:79-100.

Dennis, R.W.G. 1954. Some inoperculate discomycetes of tropical America. Kew Bull. 9:289-348.

Dennis, R.W.G. 1960. Fungi Venezuelani. III. Kew Bull. 14:418-458.

Dennis, R.W.G. 1963. A redisposition of some fungi ascribed to the Hyaloscyphaceae. Kew Bull. 17:319-378.

Holm, L. and K. Holm. 1978. Some pteridicolous Ascomycetes Bot. Not. 131:97-116.

Otani, Y. 1975. Some discomycetes collected in Papua New Guinea, in Otani, Y. (Compiler) Reports on the cryptogams in Papua, New Guinea. The Party of 1973-1974, of "The Botanical Expedition to Papua New Guinea," The National Science Museum, Tokyo. pp. 5-37.

Stevenson, J.A. 1971. An account of fungus exsiccati containing material from the Americas. Beih. Nova Hedwigia 36:i-vii, 1-563.

MYCOTAXON

Vol. XI, No. 1, pp. 217-229 April-June 1980

PARMELIELLA DUPLOMARGINATA, A NEW LICHEN FROM NEW ZEALAND

AINO HENNSEN

Fachbereich Biologie der Universität Marburg

D-3550 Marburg/Lahn, Germany

AND

PETER W. JAMES

British Museum (Natural History), London SW7 5BD,

United Kingdom

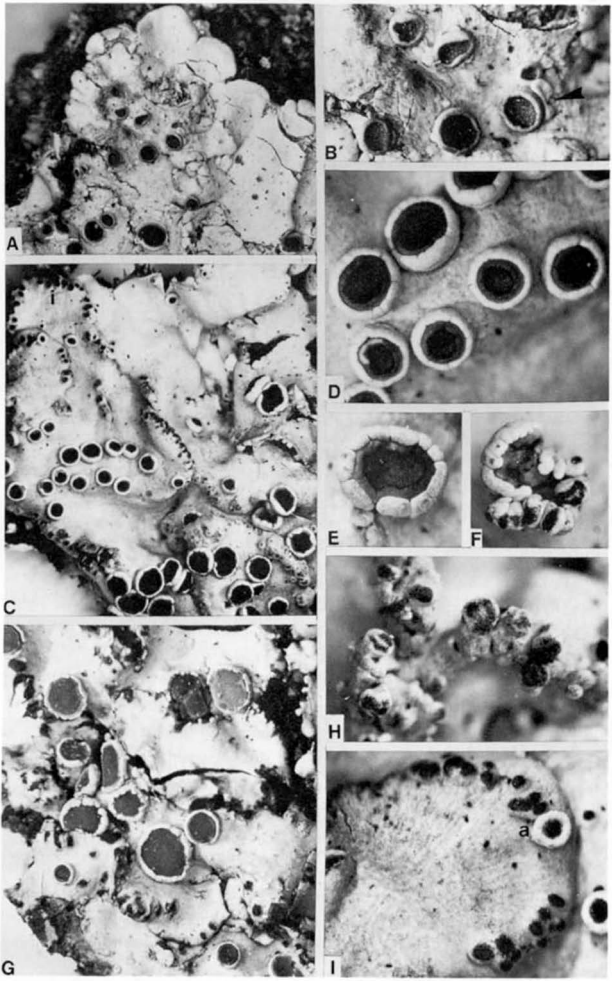
SUMMARY

The new species *Parmeliella duplomarginata* P.James et Henssen is characterized by the formation of a double apothecial margin comprising both an excipulum proprium and a margo thallinus, by the periclinal arrangement of the thallus hyphae, and by having a species of *Scytonema* as its phycobiont. The close relationship to *Parmeliella gayana* is discussed.

INTRODUCTION

In 1969 one of us (A.H.) described an unusual ontogenetic development of the apothecia of an undescribed *Parmeliella* species from New Zealand (Henssen 1969, also see Henssen & Jahns 1973, as "*Parmeliella coronata*"). This species is characterized by the formation of a conspicuous double apothecial margin comprising a well developed excipulum proprium surrounded by an equally distinct margo thallinus. Although a secondary development of a thalline margin is a common feature of the Pannariaceae (Henssen 1969, Keuck 1977) its form is unusual in the new species as the margo thallinus is developed some distance from the differentiating excipulum proprium (Fig. 2, 3A,B).

Subsequently we have been able to examine more collections of our new species finding that the margo thallinus may occasionally be only partly developed or sometimes ab-


A
B'
C
i
D
E
F
G
H
I
a

sent (Fig. 1 A,B).

The specific ephithet *duplomarginata* has been selected for the new species as it draws attention to the unusual form of the apothecial margin.

In morphology and anatomy *P.duplomarginata* closely resembles *P.gayana*. The thallus anatomy of both species is superficially like that of certain species of *Coccocarpia* but a comparative study of the ascocarp ontogeny of this family with that of the Pannariaceae indicates that such similarities that exist can only be considered as evidence of convergence (cf. also Keuck 1977).

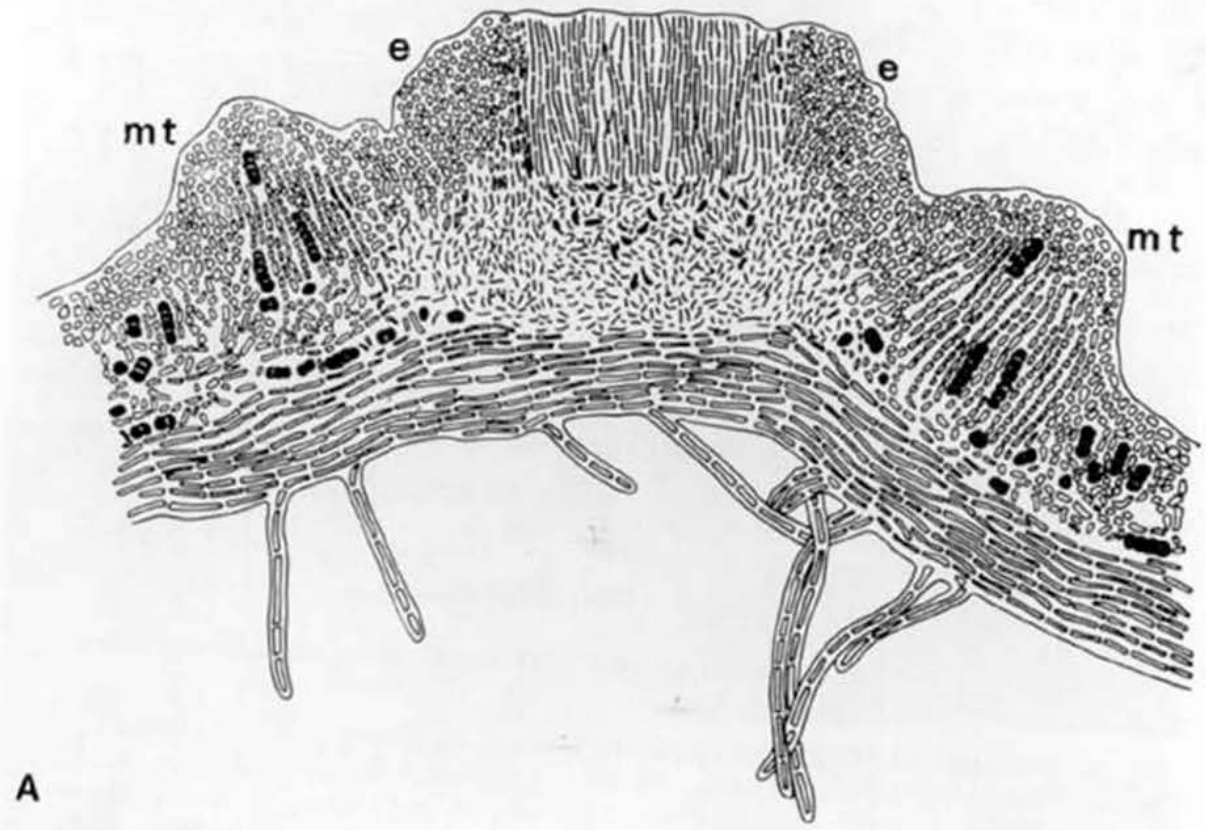
MATERIAL AND METHODS

Material. The abbreviations of herbaria follow those given in *Index Herbariorum*.

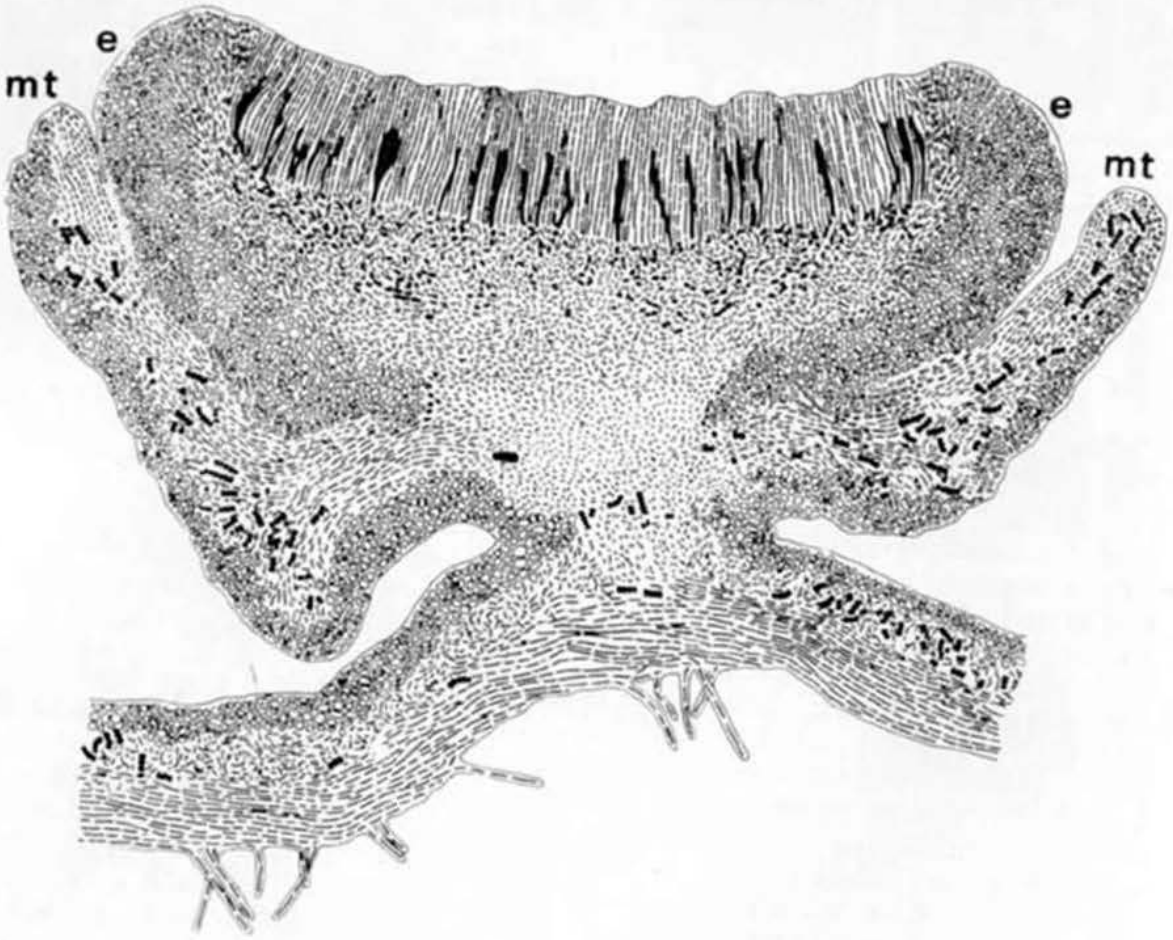
Parmeliella duplomarginata: see below: - *P. gayana*: (Mont.) Müll. Arg. Chile, prov. Arique, 1851 Lechler no. 641 (MB). - *P.plumbea* (Lightf.) Vain: British Isles, Scotland, Inverness Co., Dorlin, 1964 Henssen no. 17484d (MB).- Portugal, Azores, Pico, 1978, Henssen no. 26050b (MB); São Miguel, Furnas, 1977, Henssen no. 25511a (MB). *Psoroma* n.sp. Auckland Islands, Auckland Island, Ranui Cove, Observation Point Plateau. 1962, James no. 694A (BM); between Meggs Hill and Ranui Cove, 1962 James no. 755A (BM); - Rose Island, Grey Duck Creek, on *Fuchsia ecorticata*, 1963 James no. 993C (BM). - New Zealand, South Island, Hunter Valley, Boil the Billy Creek, on *Nothofagus*, 1963 James no. 1393B (BM).

Morphology. Samples were sectioned by freezing microtome and the sections mounted in lactophenol cotton-blue. Measurements of spores and anatomical structures were made

Fig. 1. Habit photographs of *Parmeliella duplomarginata* (A,B, James 1402; C-F,H,I holotype; G, Murray 4048). A, marginal part of the thallus with apothecia with a simple margin (x 6); B, apothecia surrounded by an excipulum proprium only at higher magnification (x 13.5; an area of secondarily developed thalline margin is indicated by an arrow); C, part of the thallus with numerous apothecia and aggregated pycnidia (x 4.5); D, young apothecia with urceolate discs and double margins (x 15); E, large apothecium with a double margin (x 15); F, apothecium with pycnidia in the margo thallinus (x 15); G, central part of the thallus (x 6); H, aggregated "stalked" pycnidia (x 15). I, finely striated lobe bearing numerous pycnidia and a young apothecium (x 15).



A



B

from permanent preparations; measurements of gross morphology on air-dried specimens. For studying the ascus structure KI, solution was added directly to the squash preparation or after pretreatment with 10% KOH.

Chemistry. Crude lichen extracts were chromotographed in solvent systems A,B and C of Culberson (1972).

TAXONOMIC PART

Parmeliella duplomarginata P.James et Henssen, sp. nov. Fig. 1-4.

Diagnosis. Thallus rosulatus, usque ad 10 cm latus, plus minusve adpressus, caeruleo-griseus, subtus pallidus vel nigricans, rhizinis villoso-vestitus. Lobi usque ad 1 cm lati, in margine radiati et subtiliter striati. Hyphae horizontaliter ordinatae. Apothecia laminalia, usque ad 1.7 mm lata, excipulo proprio et margine thallode circumdata. Sporae 8nae, eseptatae, incolores, ellipsoideae vel subglobosae, (10-)12-16 x (7-)8-11µm. Pycnidia saepe submarginalia aggregata, 0.25 - 0.5 mm lata. Conidiophora ramosa et brevicellularia, conidia lateralia et terminalia formantia. Conidia bacilliformia, 3-5 x 0.5-1µm. Alga at genus *Scytonema* pertinens.

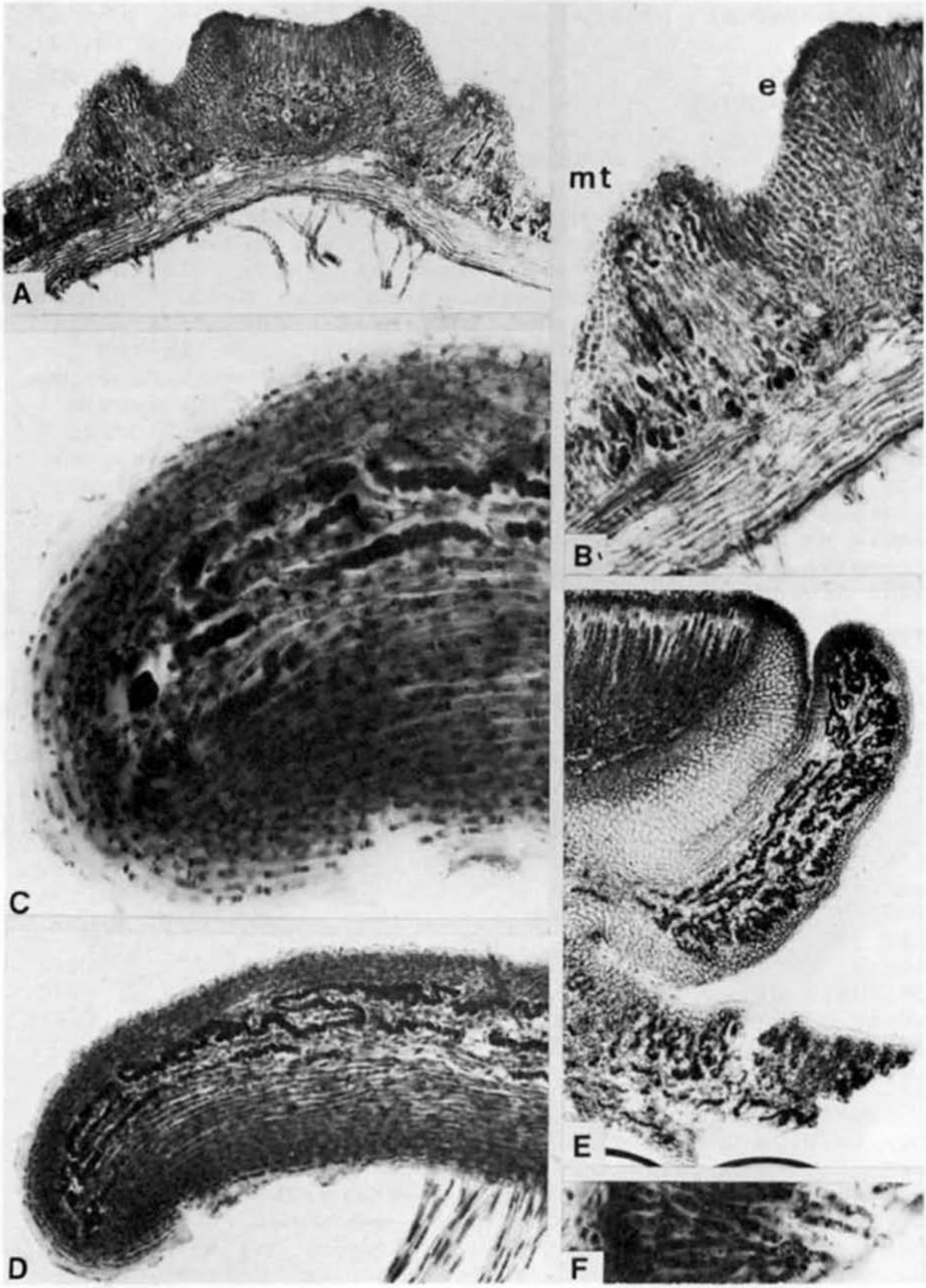
Chemistry: no substances of taxonomic value were detected.

Typus: New Zealand, North Island, Volcanic Plateau Bot. Distr., Rotoiti Bush, S.E. of Lake Rotoehu, in crown of fallen rimu in rimu-tawa-forest, 1929, G. Einar & Greta Du Rietz no. 3117 (Holotypus: UPSV; isotypi: BM, MB).

Further specimens examined: New Zealand, North Island Volcanic Plateau Bot. Distr., Ruapehu, above Whakapapa Huts, on a big shrub of *Olearia nummularifolia* on a *Danthonia* tussock plain between the uppermost tongues of *Nothofagus cliffortioides* forest, 1927, G. Einar & Greta Du Rietz no. 3180 (BM, UPSV); - South Island, Southland, Fiord Co., Secretary Island, on shrub at 1000 m, 1959, Murray no. 4048 (BM,CHR); Wilmot Pass, on shrub in a swamp at 500 m, 1959, Murray no. 3928 (BM); Otago, Vincent Co., above Lake Hawea, Hunter Valley, Lake Creek, on isolated *Nothofagus*, 1963, James no. 1402 (BM).

Thallus, rosette-shaped, up to 10 cm diam, pale-grey to blue-grey, attached by a thick felted mass of pale or bluish rhizoidal hyphae and "rhizoptae" (sensu Hannemann 1973). Lobes up to 1 cm broad, distinct and radiating towards the marginal part, contiguous and over-

Fig. 2. Development of the double margin in *Parmeliella duplomarginata*. A, young apothecium, B, mature fruitbody. - e excipulum proprium, mt margo thallinus (reproduced from Henssen & Jahns 1973).


A
e
mt
B
C
E
D
F

lapping for most of their length within the inner parts of the thallus, margins often secondarily notched or indented often forming secondary lobuli and corrugations in the older parts of the thallus (Fig. 1C,G). Upper surface undulate, young lobes faintly striate at the margins (Fig.1I).

Thallus sections 130-190µm thick, covered by a thin gelatinous or necrotic layer. Hyphae basically in a periclinal arrangement throughout the thallus, forming a primitive upper cortex, 20-30µm high composed of 4-5 rows of cells with cuboidal or shortly rectangular cells, in size 6-10 x 5-7 µm, walls uniformly thick. Algal zone c.50-70µm, with loosely interwoven medullary hyphae surrounding the filaments of the *Scytonema* phycobiont, algal filaments 9-12µm broad with intercalary heterocysts. Medullary hyphae gradually compacted towards the lower surface of the thallus were they form a layer of c.5-8 markedly adglutinated hyphae with thickened longitudinal walls, cells 12-25µm long, becoming shorter where they develop into rhizoidal hyphae. Rhizoidal hyphae c.5-8µm thick, thick-walled (Fig. 3D,4C), united to form rhizoptae towards the thallus centre.

Apothecia scattered or more frequently contiguous, up to 1.7 mm diam, becoming markedly sessile. Disc flesh-coloured to dark-brown, concave or lateron plane, surrounded by an excipulum proprium, c.0.1 mm thick, and usually an additional thalline margin, up to 1.5 mm thick (Fig.1C-E). Hymenium 90-115µm tall, upper part of the hymenial gelatine brown. Subhymenium inverted cone-shaped, 180-200µm high, extending downwards into a tall stipe, up to 220µm in height, which originates from medullary hyphae and forms an internal supporting tissue between the inner edge of the excipulum proprium. Hyphae in the supporting tissue and stipe densely interwoven, hyphal walls gelatinized (Fig.4D, E). Excipulum proprium c.100µm thick, composed of radiating hyphae. Margo thallinus 120-150µm thick, corticate on both, the inner and outer face (Fig. 3E,4D), lower cortex at the base up 70µm thick. In old apothecia thalline margin partly touching or firmly interconnected with the proper margin. Asci cylindrical, 80-100 x 10-15µm amyloid, wall thickened at the apex. Spores 8 per ascus, colourless, simple ellipsoid or subglobose, (10-)12-16 x (7-)8-11µm, wall thick, surface rugose. Paraphyses simple or occasionally branched in the upper part, c.2µm thick, short celled at the tips.

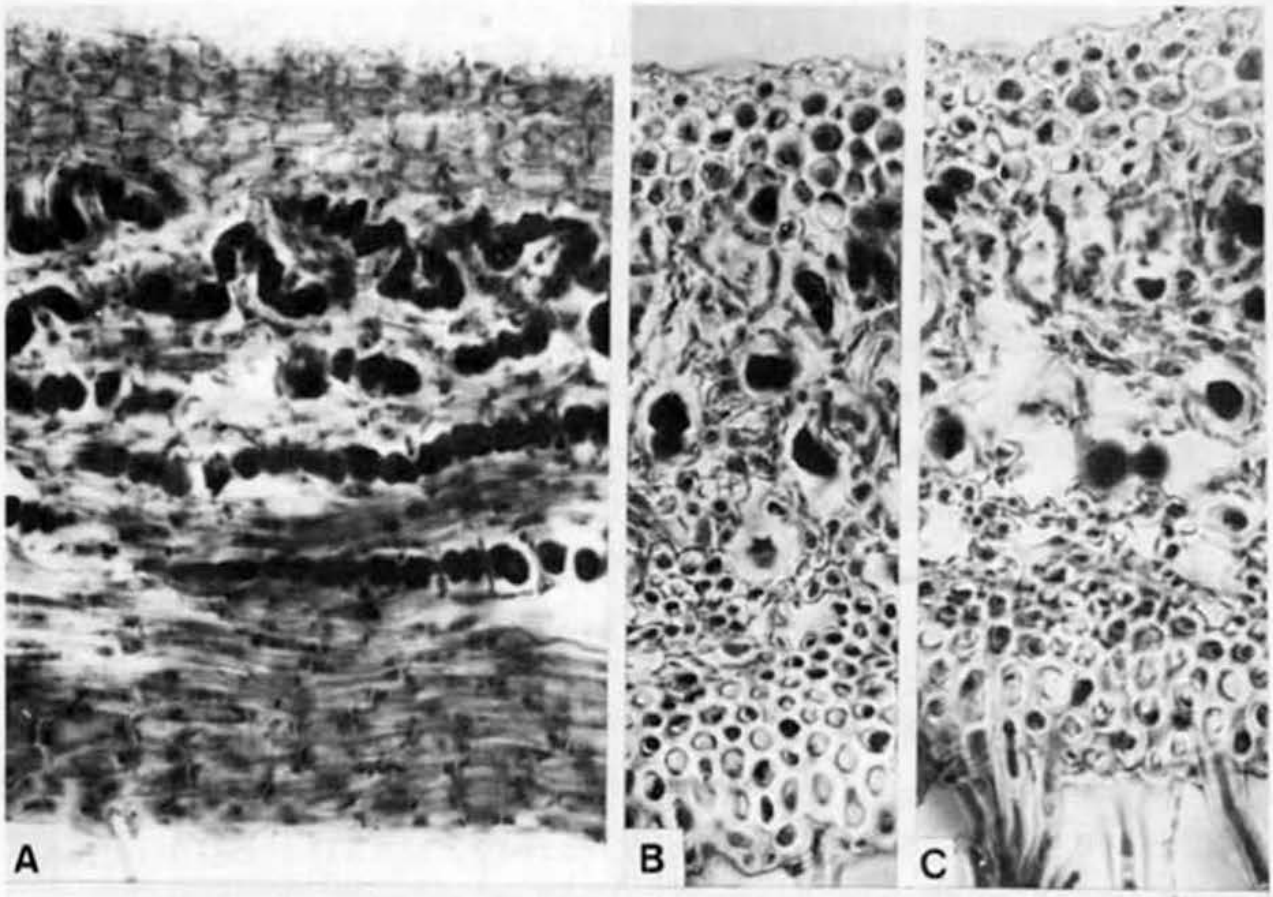
Fig. 3. Anatomy of *Parmeliella duplomarginata* (A,B, James 894A; C-F, holotype). A, young apothecium with the margo thallinus developing at some distance from the excipulum proprium (x 100); B, part of the same stage at a higher magnification (x 200); e excipulum proprium, mt margo thallinus); C-D, l.s. of lobe tip (x 500 and x 200), the filaments of *Scytonema* are incorporated in the layers of periclinally arranged thalline hyphae; E, part of an apothecium with double margin (x 100); F, conidiophores and conidia (x 500). (A, reproduced from Henssen 1969).

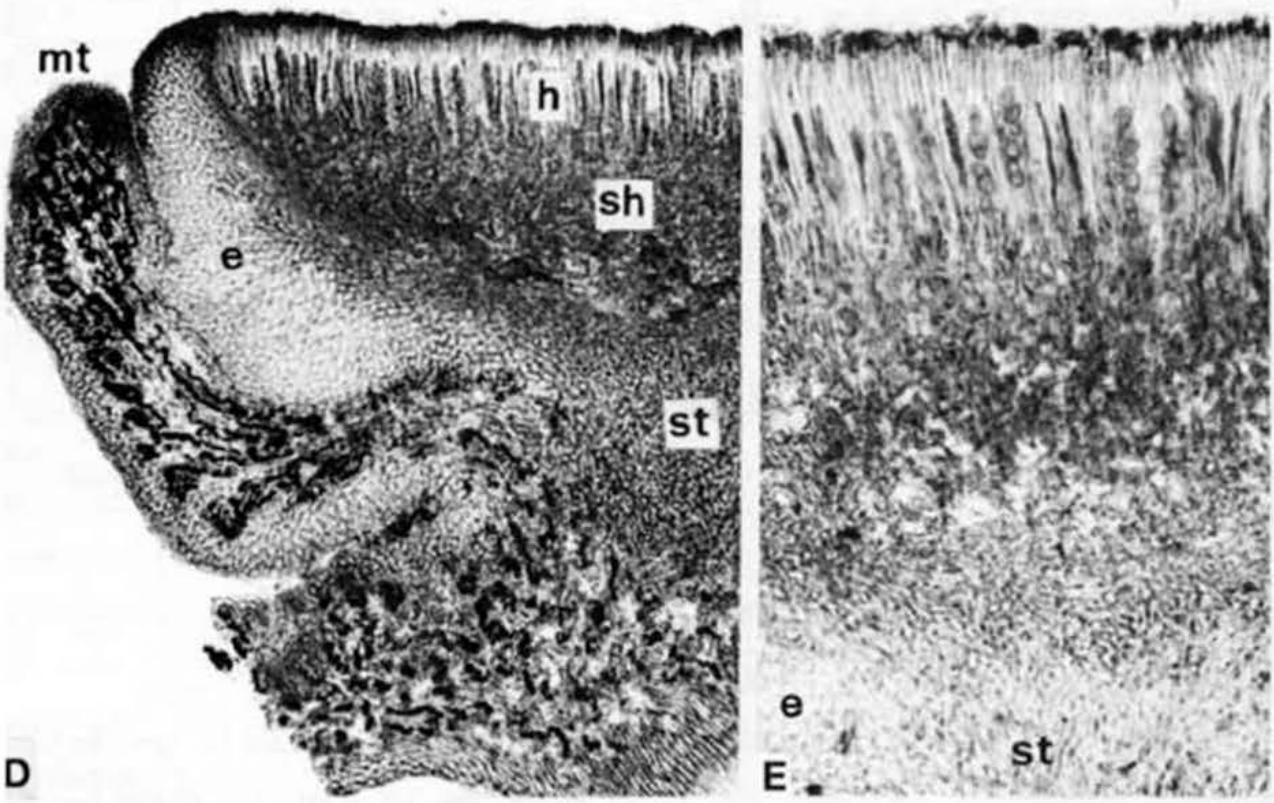
Pycnidia contiguous, mainly along the margins and ridges of the lobes (Fig. 1C,G), occasionally even in the margo thallinus of old apothecia (Fig. 1F), 0.25-0.5 mm diam, elevated in an outgrowth of the thallus finally becoming more or less stalked (Fig. 1F,H,I). Conidiophores branched and short-celled, conidia formed laterally and terminally (Fig. 3F). Conidia rod-shaped, 3-5 x 0.5-1µm.

The new species is somewhat variable. With regard to colour of the upper surface specimens range from pale blue-grey to pale olive and older parts of the thallus sometimes become partly blackened. In exposed, sunny sites, the thallus can be partly indigo-blue. In form the placoid-lobate habit is usually characteristic but in exposed situations the lobes often become elongated and tend to lack the development of secondary lobes towards the centre of the thallus characteristic for specimens of more sheltered habitats. Likewise in open situations the densely rhizinose undersurface is generally more intensely pigmented and often conspicuously blue-black, while in sheltered habitats the underside may be entirely pale or cream-coloured.

Most species seen are well fruited; the disc may be very pale orange-brown, but is more often dark brown in plants in exposed sites. The degree of development of the margo thallinus is very variable; in some specimens only part of the fruits have a fully developed thalline margin and in such cases only some uneven and irregular upgrowths surrounding part of the apothecium may be present (Fig. 1B, arrow); rarely, no margo thallinus is developed at all (Fig. 1A,B). When well developed, the thalline margin forms a supplementary, more or less crenulate surround for the otherwise lecideine apothecium so that only the upper part

Fig. 4. Anatomy in *Parmeliella duplomarginata*. A, l.s. of thallus with primitive upper and lower cortex, the latter composed of aggregated medullary hyphae (x 500); B-C, t.s. of thallus (x 500); D, marginal part of a large apothecium, the stipe composed of densely interwoven hyphae forming a supporting tissue (x 100); E, central part of a similar stage (x 500). - e, excipulum proprium; mt margo thallinus; h, hymenium; sh, subhymenium; st, supporting tissue.


A
B
C


mt
h
sh
e
st
D
e
st
E

of the pale brown proper margin of the fruit is exposed (Fig. 1D,E). Occasionally the entire proper margin may be obscured by the thalline margin (Fig. 1G). Initially the margo thallinus arises at some distance around the developing excipulum proprium (Fig. 2A,3A,B). In later stages of development the basal parts of proper and thalline margin are more or less intimately connected (Fig. 3E,4D).

The formation of a supporting tissue by medullary hyphae connecting the inner edge of the excipulum proprium corresponds to similar structures described for species of the *Parmeliella pycnophora*-group and *Erioderma* (Keuck 1977).

In *Parmeliella duplomarginata* the hymenial gelatine stains blue in iodine solution. The slimy outer part of the ascus wall is directly positive but the thickened apex only colours after pretreatment with KOH solution. The reaction in the apex is variable: in young asci an amyloid plug may be observed; in mature asci an inner closed or perforated amyloid cap, or more rarely, a faint coloration of the whole apex may be demonstrated. Similar variations were noted in a comparative study of the asci in *P.gayana* and *P.plumbea*. An inner amyloid cap perforated by a pore has previously been observed in *P.plumbea* by Keuck (1977), p.105), while Jørgensen (1978,p.90) describes an amyloid plug. In one of the specimens of *P.plumbea* studied by us (Henssen no. 17484d) the entire apex stained bluish in most of the asci. Variation of this kind in the iodine reaction has recently been discussed by Nannfeldt (1976) and is considered to be related to the age of the ascus and the mode of iodine treatment.

Ecology and distribution. *Parmeliella duplomarginata* is widely distributed in New Zealand; it has also been collected from most islands of the Auckland Islands as well as from Campbell Island. It is a species of rather open situations, often at the edge of *Nothofagus* forests especially on the eastern side of the main mountain ranges of New Zealand. It occurs on a wide range of phorophytes from

sea level to 1000 m and often grows with *Menegazzia* species, especially *M. pertransita*, in the crowns of mature trees; it has also been collected from rocks. In the Auckland Islands it often occurs on twigs and branches of *Myrsine divaricate-Coprosma foetidissima*-scrub in lowland or coastal areas, often with *Pseudocyphellaria aurata*, *P. intricata*, *Parmeliella amphibola*, *P.pycnophora*.

Systematic position. In its thallus and habit *Parmeliella duplomarginata* resembles other lobate-placoid species of the family, for example *P.plumbea* and *P.gayana*, species belonging to that group of the genus in which the lower medullary hyphae are horizontally extended (Keuck 1977). With regard to these species a true close relationship obviously exists between *P.gayana* and *P.duplomarginata*. In both species the hyphae are basically periclinally arranged throughout the thallus, a feature which is especially distinctive in the tips of the lobes (Fig. 3C,D, 4A-C), the phycobiont is a *Scytonema* species, and the rhizinose felt on the undersurface is composed of rather distinct rhizoidal hyphae and rhizoptae. In contrast, the hyphae in *P.plumbea* only are strictly periclinally arranged in the lower part of the thallus being anticlinally ordered towards the upper surface where they form a cortex of isodiametric cells; this particular arrangement can be recognized already in the tips of young lobes in *P.plumbea*. In *P.plumbea*, furthermore, the phycobiont is *Nostoc*, and the thallus lower side is covered by a thick felt of intertwined rhizoidal hyphae and rhizoptae designated as erioastrum (Hannemann 1973) or hypothallus (Jørgensen 1978) respectively. *P.gayana* and *P.duplomarginata* correspond also in the anatomical structure of the apothecium: In both species the inner edges of the excipulum are connected by a supporting tissue formed by medullary hyphae, a character shared with species of the *Parmeliella pycnophora*-group and *Erioderma*. *P.duplomarginata* principally differs from *P.gayana* in possessing an additional thalline margin

which surrounds the excipulum proprium. A similar development of a double margin occurs in certain other species of the *Pannaria-Parmeliella-Psoroma*-complex as, for example, in *Parmeliella periptera* and *Pannaria immixta*. In so far as these species have been examined, there appears to be no close relationship to *Parmeliella duplomarginata*. This suggests that the formation of a double margin in these species is the result of convergent evolution in several systematic groups in this generic complex. The systematic position of the entire group needs further careful study and the formulation of new concepts (cf. Jørgensen 1978). In connection with this observation it is of interest to mention that one of the species with a double margin, as yet undescribed, from the Auckland Islands (James 694A), is obviously closely related to certain squamulose species of *Psoroma* in spite of having blue-green alga as its phycobiont. In our estimation the use of the phycobiont as a means of generic delimitation has been overestimated in the *Pannaria-Parmeliella-Psoroma-Psoromaria*-complex.

Although there may be justification for the separation of *Parmeliella gayana* and *P.duplomarginata* as a separate genus, at the present time we feel that the knowledge of the three genera is still too fragmentary to effect this separation.

ACKNOWLEDGEMENTS

These studies were partly supported by a grant of the Deutsche Forschungsgemeinschaft given to one of us (A.H.). We are indebted to Bernd Renner to check the presence of lichen substances in the new species and to Mrs. Traute for technical help.

REFERENCES

Culberson, C.F. 1972. Improved conditions and new data for the identification of lichen products by a standardized thin layer chromatographic method. J. Chromatogr. 72; 113-125.

Hannemann, B. 1973. Anhangsorgane der Flechten, ihre Strukturen und ihre systematische Verteilung. J. Cramer, Bibliotheca Lichenologica vol. 1, Vaduz.

Henssen, A. 1969. Die Entstehung des Thallusrandes bei den Pannariaceen (Lichenes) mit einer generellen Diskussion über die Entwicklung lecanoriner und biatoriner Flechtenapothecien. Ber. Dtsch. Bot. Ges. 82: 235-248.

Henssen, A. and Jahns, H.M. 1973 ("1974"). Lichenes, eine Einführung in die Flechtenkunde. Stuttgart: Thieme.

Jørgensen, P.M. 1978. The lichen family Pannariaceae in Europe. Opera Botanica no. 45, Lund.

Keuck, G. 1977. Ontogenetisch-systematische Studie über Erioderma im Vergleich mit anderen cyanophilen Flechtengattungen. J. Cramer, Bibliotheca Lichenologica vol. 6, Vaduz.

Nannfeldt, J.A. 1976. Iodine reactions in ascus plugs and their taxonomic significance. Trans. Br. mycol. Soc.67: 283-287.

MYCOTAXON

Vol. XI, No. 1, pp. 230-232 April-June 1980

ARUALIS CAROLINENSIS KATZ, GEN. ET SP. NOV.

BARRY KATZ

Department of Botany, University of North Carolina
Chapel Hill, North Carolina 27514

ABSTRACT

The new genus and species *Arualis carolinensis* is described from *Pinus taeda* L. needles in North Carolina.

INTRODUCTION

During an investigation of the microfungi associated with loblolly pine (*Pinus taeda* L.) needles, several new and interesting fungi were isolated. Among them, a new imperfect state of a basidiomycete was discovered, which is described below as a new genus.

TAXONOMIC PART

Arualis Katz, gen. nov.
Deuteromycotina, Hyphomycetes

Coloniae tarde crescentes, leves, compactae, ochroleuco-brunneae, hyphis aereis sparsis. Hyphae zygodesmatibus praeditae, leviter tunicatae. Aleuroconidia a parte superiore zygodesmatum singillatim orta; cellulae conidiogenae interdum in ramis brevibus erectis congregatae. Conidia hyalina, levia, cylindrica, basi truncata, 1-2 cellularia, tenuiter tunicata.

Species typica: *Arualis carolinensis*

Colonies slow-growing, appearing flat and compact, tan-brown, with sparse aerial hyphae. Hyphae bearing clamp connections, smooth-walled. Aleuroconidia originating from distal ends of clamps, one per clamp; conidiogenous cells

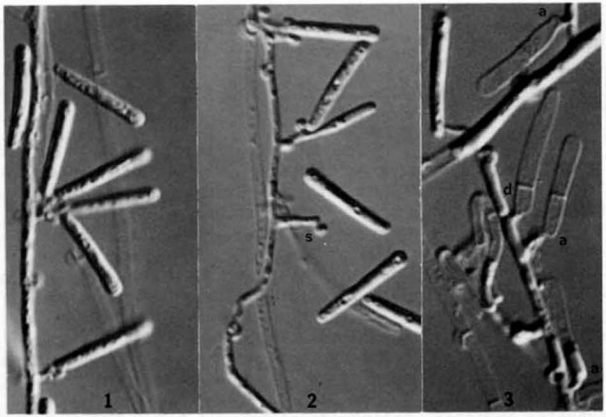
may be clustered on short perpendicular branches. Conidia hyaline, smooth, cylindric, with truncate bases, 1-2 celled, thin-walled.

Arualis carolinensis Katz. sp. nov.

Coloniae in agaro cum malto composito satae sub calore 20-23° die quinto decimo diametrum 17-19 mm attinentes, leves, compactae, brunneae (colore brunneo martio sensu Ridgway), margine hyalino, hyphis aereis sparsis. Hyphae immersae compactae, leves, zygodesmatibus praeditae, ad 2 µm crassae, cellulis vulgo 18-30 µm inter zygodesmata longis, nonnumquam a septis adventitiis subdivisis. Hyphae aereae angulis acutis vel rectis ramosae, plerumque 18-30 µm inter zygodesmata longae, a septis adventitiis subdivisae, hyalinae, leves, raro fertiles. Loci conidiogeni singulares, in parte superiore zygodesmatum, zygodesmatibus conidiogenis nonnumquam in ramis hypharum brevibus congregatis. Conidia quidem aleuroconidia, hyalina, levia, tenuiter tunicata, cylindrica, 1.5 - 2.5 X 8 - 13 µm, 1-2-cellularia, cicatricibus basalibus truncatis ornata. Sub calore 37°C nullus auctus.

On decomposing needles of *Pinus taeda* L., North America. Collection from *P. taeda* stand, Saxapahaw, Alamance county, North Carolina, April 22, 1977, by B. Katz. Holotypus: BAK #39. The name *Arualis* was invented for the genus. Its gender is feminine.

Colonies on malt agar at 20-23°C attaining a diameter of 17-19 mm in 14 days, flat and compact, mars brown (Ridgway), margin hyaline, aerial hyphae sparse. Submerged hyphae compact, smooth, bearing clamp connections, up to 2 µm wide, cells usually 18-30 µm between clamp connections, adventitious septa sometimes dividing these cells. Aerial hyphae acutely to perpendicularly branched, usually 18-30 µm between clamps, with adventitious septa, hyaline, smooth, infrequently fertile. Conidiogenous loci on distal ends of clamps, one per clamp, conidiogenous clamps sometimes clustered on short hyphal branches. Conidia are aleuroconidia, hyaline, smooth, thin-walled, cylindrical, 1.5 - 2.5 X 8-13 µm 1-2 celled, with truncate basal scars. Growth absent at 37°C.



Figures 1-3. 1. Hyphae with clamp connections, aleuroconidia developing from a solitary clamp and from a cluster of clamps. 2. Clamp connection after conidium has seceded (s). 3. Four conidia anastomosed to original mycelium. Three have germinated at edge of attachment scar (a) - in one, the cytoplasm remains in one cell. The fourth has germinated from the end distal to the attachment scar (d). 1,250X.

DISCUSSION

This fungus has a unique asexual state characterized by solitary, 1-2 celled aleuroconidia borne on the distal end of clamp connections (figures 1 and 2). When the conidia secede they leave conspicuous scars on the clamp connections (figure 2). Germinating conidia produce hyphae and will readily anastomose with the original mycelium (figure 3).

ACKNOWLEDGEMENT

The author gratefully acknowledges the advice and translation of the diagnoses by Dr. D. P. Rogers.

MYCOTAXON

Vol. XI, No. 1, pp. 233-240 April-June 1980

RHYTISMATACEAE ON SALAL LEAVES

RICHARD S. HUNT

Environment Canada
Canadian Forestry Service
Pacific Forest Research Centre
Victoria, B.C. V8Z 1M5
Canada

SUMMARY

Four Rhytismataceous fungi occur on leaves of salal (Gaultheria shallon Pursh). One, Lophodermium schweinitzii, had been reported as both L. schweinitzii and L. exaridum. A second species, Hypoderma gaultheriae sp. nov., had been reported as Lophodermium sp. The third and fourth, Coccomyces tumidus and C. dentatus had been reported as C. coronatus.

Gaultheria shallon, salal, is an ericaceous shrub that occurs in forested coastal areas from California northward to Alaska. It is used by florists and in British Columbia (B.C.), it has an annual retail value of $1-3 million. Rhytismataceae (Korf 1973) reported on leaves of this host are Lophodermium exaridum (Cke. & Pk.) Sacc. from California (Anonymous 1960), L. schweinitzii M. Wils. & Robertson from Oregon and Washington, Coccomyces coronatus (Fr.) Karst. from Washington (Shaw 1973), and Lophodermium sp. from B.C. (Lowe 1977). There are two collections in the herbarium of the Pacific Forest Research Centre (DAVFP) of the latter and although a recent collection on G. shallon from B.C. superficially resembled these (Figs. 1 and 2), it bore long stalked asci, typical for the genus Hypoderma. To clarify the identification of this new fungus and the reported Lophodermium sp., specimens of L. exaridum on G. shallon and Kalmia angustifolia L. were examined from the

herbarium of the University of California (UC). Specimens of L. schweinitzii on G. shallon reported by Shaw (1973), could not be located.

Morphologically, specimens of L. exaridum on K. angustifolia fit Tehon's (1935) description of the fungus species. However, specimens identified as L. exaridum on G. shallon are clearly different (e.g. hysterothecia and asci almost twice as large in the specimen on G. shallon) from both the specimens on K. angustifolia and Tehon's (1935) description. Also, this fungus is not a Hypoderma sp., but clearly fits the description (Wilson and Robertson 1949) for the reported (Shaw 1973) L. schweinitzii (Fig. 3). Of the described Hypoderma spp., the one on salal is most similar to H. virgultorum DC. (=H. rubi (Pers.) de Not.), but has smaller hysterothecia, wider spores and aseptate paraphyses. The Hypoderma on salal is described below as a new species.

Hypoderma gaultheriae sp. nov. (Figs. 1, 2, 5-8). Teleomorpha: Hysterotheciis conspersis hypophyllis, subcuticularibus intra folii necromaculas, ellipticis, atronitidis, 700-1100 x 350-500 um latis, 230-325 um altis; labiis atronitidis, 100-150 um latis, incrassatis elevatisque supra hysterothecias cum aperturis longitudinalibus; tectis plectenchymatis, fuscis, cum crassae parietis cellulis, 10-20 um altis, continuis contiguisque cum basilari pseudoparenchyma, ipsa fusca, cum crassae parietis cellulis, 25-35 um altis; periphysibus non vidis; hymenio albo in aperta hysterothecia, usque ad 200 um alto; ascis clavatis, attenuiter pedicellatis longatis, (52)95-115(137) x (8.5) 9.5-10.5(12.5) um, octoascosporis; paraphysibus simplicibus, filiformibus, nonnunquam apicis afflatis, 95-150 x 1-2 um; ascosporis brevis, fusiformibus, strictis vel curvatis apice late vel anguste sphaerica, saepe cum medio pseudoseptato a media vacuola formatibus 19-26 x (2.5)3.5-6.5 um; vaginis mucosis ascosporarum circumvolutis, 1.0-1.5 um.

Anamorpha: Pycnidiis atronitidis dispositis pariter quam hysterotheciis, 100-150 um. Conidiophoris simplicibus, 14-16 x 1.0-1.5 um. Conidiis holoblastis, hyalinis, ellipsoideis, 1.0 x 3.0 um.

Holotypus: DAVFP 22097, in Gaultheria shallon Pursh.

Teleomorph: Hysterothecia scattered within necrotic leaf spots, elliptical, shining black, 700-1100 x 350-500 um, hypophyllous, subcuticular, 230-325 um thick; labia shining black, 100-150 um wide, thickened and elevated above the hysterothecium, opening with a longitudinal slit to expose the whitish hymenium, periphyses not seen; basal pseudoparenchyma 25-35 um thick; hymenium hyaline, up to 200 um thick; epidermis dark brown, thick walled plectenchyma continuous and intergrading with the basal pseudoparenchyma, 10-20 um thick; asci clavate, tapering to a long fine stipe, (52)95-115(137) x (8.5)9.5-10.5(12.5) um, 8-spored; paraphyses simple, numerous, flexuous filaments sometimes with swollen tips or sometimes uncinate, 95-150 x 1-2 um; ascospores short, fusiform, straight or curved, tips broadly or narrowly rounded, 19-26 x (2.5)3.5-6.5 um with a 1-1.5 um gelatinous sheath, frequently with a medial pseudoseptum, formed by a central vacuole.
Anamorph: Pycnidia scattered within necrotic leaf spots and produced before hysterothecia appear; shiny black, 100-150 um, hypophyllous, subcuticular. Conidiophores long and straight, 14-16 x 1.0-1.5 um. Conidia holoblastic, hyaline, ellipsoid, up to 1.0 x 3.0 um.

Collections examined: C.S. Wood & R.S. Hunt, Copper Canyon Road at Trans Canada Highway, Chemainus, B.C., 26.IV.1978. DAVFP 22097 (Type). J.E. Bier, Lake Cowichan, B.C., V.1941. DAVFP 2089. W.G. Ziller, Lake Cowichan, B.C., 7.VI.1949. DAVFP 4651. 16.VII.1957. DAVFP 22158. Youbou, B.C., 8.VI.1949. DAVFP 4611. R.S. Hunt, Lake Cowichan, B.C., 21.VIII.1979. DAVFP 22096. Sooke, B.C., 25.V.1979. DAVFP 22098. Cumberland, B.C., 6.VII.1979. DAVFP 22099. Port Renfrew, B.C., 28.IX.1977. DAVFP 21555. C.S. Wood & W. Nijholt, Caycuse, B.C., 3.IV.1979. DAVFP 22105. J.A. Calder & K.T. MacKay, Heriot Bay, Quadra Is., B.C., 5.V.1951. DAOM 172767. J.A. Calder, D.B.O. Savile & R.L. Taylor, Masset, Q.C.I., B.C., 3.V.1957. DAOM 172768. Moresby Logging Camp, Q.C.I., B.C., 30.V.1957. DAOM 172769. Langara Is., Q.C.I., B.C., 15.VII.1957. DAOM 172771. J.A. Calder & R.L. Taylor, White Creek Muskeg, Q.C.I., B.C., 7.V.1964. DAOM 172770. K. Egger, Tlell, Q.C.I., B.C., 17.VI.1979. DAOM 172534.

Legends to Figures

FIG. 1. Hysterothecium and pycnidia of a Lophodermium sp. reported on Gaultheria shallon from B.C.

FIG. 2. Hysterothecium and pycnidia of Hypoderma gaultheriae on Gaultheria shallon.

FIG. 3. Hysterothecium of Lophodermium schweinitzii on Gaultheria shallon from California.

FIG. 4. Polygon shaped hysterothecium of Coccomyces dentatus on Gaultheria shallon.

FIG. 5. Cross-section of Hypoderma gaultheriae showing the hymenium in the dark hysterothecium. X176.

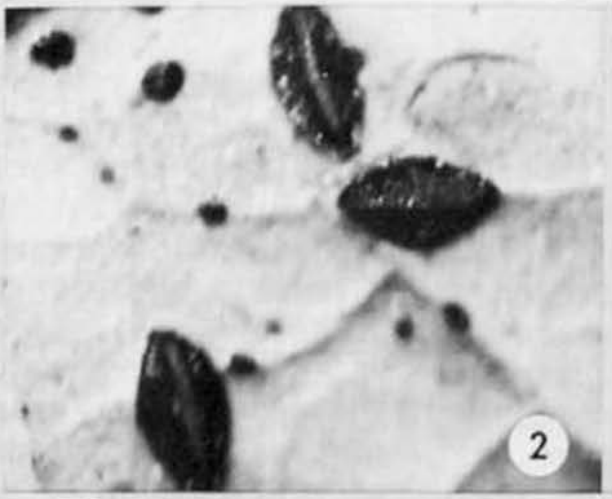
FIG. 6. Long stalked asci and flexuous paraphyses of Hypoderma gaultheriae. X396.

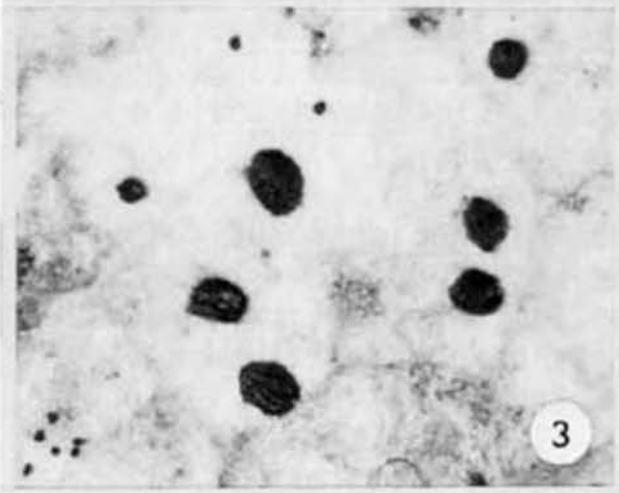
FIG. 7. Ascospores of Hypoderma gaultheriae showing the pseudoseptum. X396.

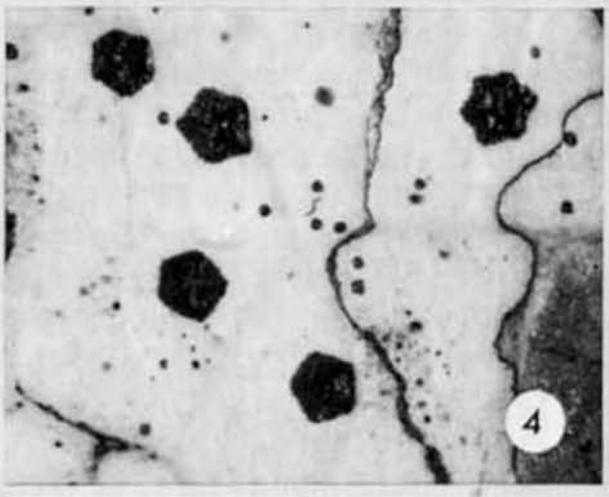
FIG. 8. Cross-section of a pycnidium of Hypoderma gaultheriae. X396.

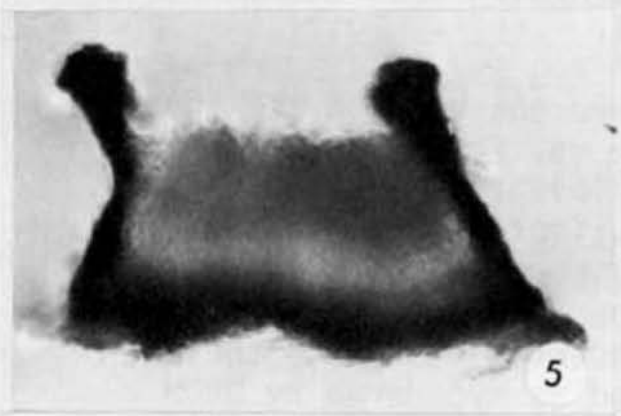
Attempts to germinate Hypoderma gaultheriae ascospores from air-dried collections were unsuccessful. However, similar cultures were consistently obtained from hysterothecia tissue, pycnidia and blackened veins from the Chemainus and Sooke collections. The fungus grew slowly on potato dextrose agar, between 5-25°C with an optimum at 21°C, where a 9-cm petri plate was covered in 35 days. Initially, most mycelium was appressed to the agar and was beige colored. Gradually, the centre of the colony became brown with white floccose hyphae above and beige colony margins. Later, the floccose mycelium became slightly beige with a white margin. On the reverse side, the culture was beige with scattered darker areas. Irregular shaped sclerotia eventually developed in the darker areas. Hyaline to light brown hyphae were 1(2) um wide, straight or twisted and predominantly branched at right angles. Brown hyphae were 5-12 um wide and branched

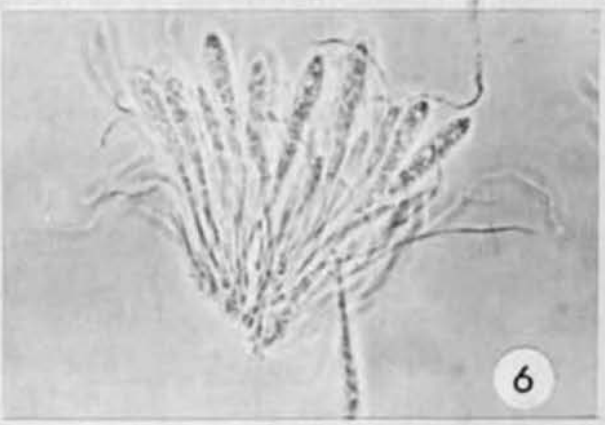

1

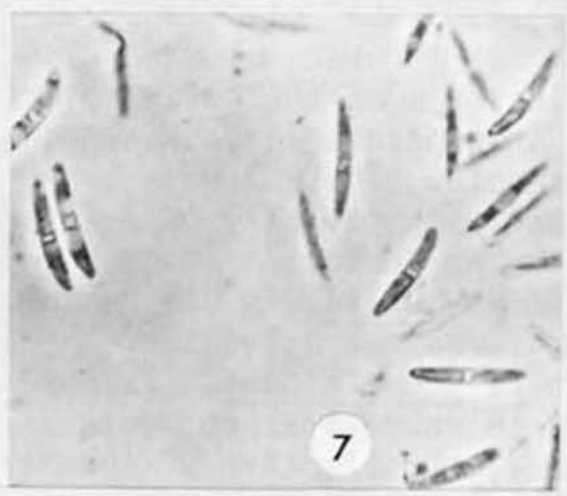

2

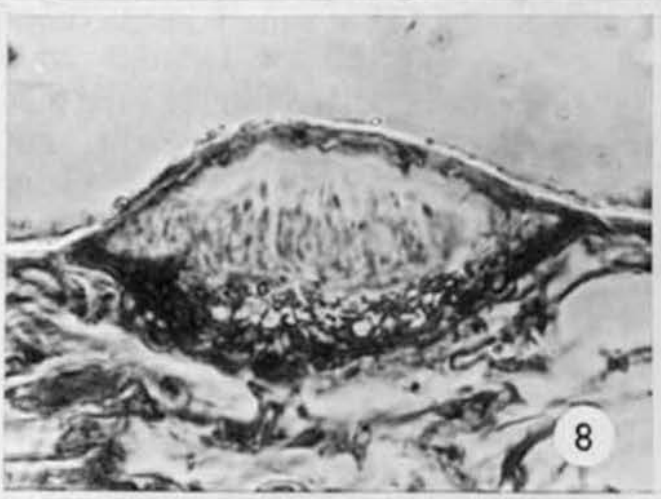

3


4


5


6


7


8

irregularly. Cross walls were frequent at irregular intervals. No fructifications were observed at room temperature in plates kept for 6 months.

The necrotic lesions associated with H. gaultheriae are on green leaves, and have an associated anamorph, whereas L. schweinitzii lesions are on dead leaves, and apparently lack an anamorph. Lesions of H. gaultheriae commonly had masses of dark plectenchymatous tissue within some host veins so that the veins on the top and bottom of the leaves were blackened. A few blackened veins were observed once in association with L. schweinitzii. The shape of H. gaultheriae's hysterothecia tended to be more narrowly ellipsoid (Fig. 1), whereas L. schweinitzii's tended to be broadly ellipsoid (Fig. 3).

Hypoderma gaultheriae can be recognized readily in the field by the following signs and symptoms: a) generally large lesions on green leaves, b) black veins within the lesions, c) subcuticular pycnidia, d) narrowly ellipsoid shiny black hysterothecia, and e) infection of a small radiating patch of plants. In many instances, it appears to be secondary to leaf mining moths or Valdensinia heterodoxa Peyronel.

Neither asci nor spores were observed in the two specimens labelled Lophodermium sp. from G. shallon in herbarium DAVFP (nos. 4611 and 4651). However, they are on green leaves, and have subcuticular pycnidia associated with more narrowly ellipsoid hysterothecia (Fig. 1) and some blackened veins. These characteristics place the fungi into H. gaultheriae. Recently, parts of these collections have been identified as Hypoderma by DAOM taxonomists (Shoemaker pers. comm.).

Mixed in with two of the collections of the L. schweinitzii from California, but in separate lesions, are a few distinct Coccomyces hysterothecia. These are irregular trapezoids or polygons and open radially by 3-7 slits (Fig. 4). The ascospores are non-septate. Among a collection of unidentified fungi on G. shallon in DAVFP, two additional collections of this fungus were located. There was also an association with L. schweinitzii. This Coccomyces sp. lacks the ellipsoid to round hysterothecia and multiseptate spores (Dennis 1978), distinctive of the reported (Shaw 1973) C. coronatus on G. shallon.

Shaw (1973) regards C. dentatus (Kunze & Schum. [sic]) Sacc. as a synonym of C. coronatus whereas Sherwood (1979) treats them separately, as does Dennis (1978). Specimens at DAVFP fit the description for C. dentatus (Rehm 1896), except that the asci and ascospores are considerably larger. Specimens of the reported C. coronatus were obtained to clarify their identification and compare them to DAVFP specimens. None of these Coccomyces were on the same leaves as L. schweinitzii. Two of these specimens could be identified as C. coronatus; however, Sherwood (1979) has shown that many specimens identified as C. coronatus should be called C. tumidus (Fr.) de Not., as should the specimens on salal (Sherwood pers. comm.). Two specimens appeared to be conspecific with the B.C. and California specimens, and measurements of the asci and ascospores bridged the range given for C. dentatus (Rehm 1896). Sherwood (pers. comm.) has identified C. dentatus on salal leaves, and I believe the specimens I examined fit an expanded concept of the species. Measurements on salal of C. dentatus asci are 56-139 x 8.8-12.6 and ascospores 44-69(84) x 1.6-2.5 um.

In the field, C. dentatus on salal is readily distinguished from C. tumidus by its polygon-shaped apothecia whereas C. tumidus has round to ellipsoid apothecia.

The known Rhytismataceous fungi on G. shallon leaves are Lophodermium schweinitzii, Hypoderma gaultheriae, Coccomyces tumidus and C. dentatus.

Acknowledgements

I wish to thank Drs. I. Tavares, R.A. Shoemaker and C.G. Shaw for loaning specimens and making helpful observations, and Dr. M.A. Sherwood for taxonomic comments.

Literature Cited

Anonymous. 1960. Index of plant diseases in the United States. U.S. Dep. Ag. Handb. 165, 531 p.

Dennis, R.W.G. 1978. British Ascomycetes. J. Cramer, Vaduz, Germany. 585 p.

Korf, R.P. 1973. Discomycetes and tuberales. In The Fungi IVA Ed. by G.C. Ainsworth, F.K. Sparrow and

A.S. Sussman. Academic Press, New York. pp. 249-319.

Lowe, D.P. 1977. Check list and host index of bacteria, fungi and mistletoes of British Columbia. Can. For. Serv., Victoria. BC-X-32, 540 p.

Rehm, H. 1896. Ascomyceten: Hysteriaceen und Discomyceten. Rab. Krypt.-Fl. von Deutschland, Osterreich und der Schweiz I. 3: 78-79.

Shaw, C.G. 1973. Host fungus index for the Pacific Northwest. I. Hosts. Wash. Ag. Exp. Sta. Bull. 765, 121 p.

Sherwood, M.A. 1979. Phacidiales exsiccati decades I-III. Mycotaxon X: 241-245.

Tehon, L.R. 1935. A monographic rearrangement of Lophodermium. II. Biol. Monographs 13(4): 1-151.

Wilson, M. and N.F. Robertson. 1949. The biology, culture, morphology, and relationships of Lophodermium vagulum sp. nov; the cause of a disease of Chinese rhododendrons. Trans. Roy. Soc. of Edinburgh 61: 517-539.

MYCOTAXON

Vol. XI, No. 1, pp. 241-249 April-June 1980

THE ACANTHOCYTE, A UNIQUE CELL TYPE IN STROPHARIA (AGARICALES)

David F. Farr

Mycology Laboratory, Plant Protection Institute
Agricultural Research, Science and Education Administration
U. S. Department of Agriculture
Beltsville Agricultural Research Center
Beltsville, Maryland 20705

INTRODUCTION

In the course of culturing species of the agaric genus Stropharia (Fr.) Quél., I observed an unusual cell type on the vegetative mycelium which I have named the acanthocyte. This paper discusses the morphology and development of this cell type in pure culture and its occurrence and distribution among Stropharia species in herbarium specimens.

MATERIALS AND METHODS

Cultures. Acanthocytes are found on both monocaryotic and dicaryotic mycelium. The growth and development of acanthocytes were observed on a medium composed of 1.5% malt extract and 1.5% agar in 60- or 110-mm petri dishes. In some cases 3-mm square pieces of sterilized dialysis tubing were placed over the agar surface. After it was overgrown by mycelium, the tubing was removed and the adhering mycelium examined microscopically. Early developmental stages were more easily photographed if they were first stained in phloxine (1% in H_2O).

For SEM observation, 1- to 2-cm segments of agar containing the fungal mycelium were removed from petri dishes and placed in vials containing fixative (2% paraformaldehyde and 3% glutaraldehyde in a 0.1 M sodium phosphate buffer, pH 7.2). After 2 hours of fixation, specimens were dehydrated in an alcohol series and critical point dried from liquid carbon dioxide. Agar segments with fungal hyphae exposed were mounted on stubs

and coated with gold-palladium in a Hummer II sputtering device. Coated specimens were viewed in a Hitachi HHS-2R scanning electron microscope.

Herbarium Specimens. A small amount of vegetative mycelium and associated substrate was removed from the base of the stipe and placed on a microscope slide. A drop of 1% potassium hydroxide was added before adding a cover slip.

MORPHOLOGY AND DEVELOPMENT IN CULTURE

Initial attempts to observe the development of the acanthocyte in situ via specialized growth chambers met with little success. Therefore the developmental sequence presented is a composite picture derived from observing several cultures at different times in their growth.

Figures 1-27 outline the development of the acanthocytes. These cells develop only above or on the agar surface. The formation of a short lateral branch more or less at right angles to the parent mycelium is the first sign of the differentiation of an acanthocyte. The apex of this side branch produces several short branches. (Figs. 1-5). At this point a cross wall has generally been formed which delimits the side branch from the parent mycelium. In dicaryotic cultures this cross wall will be associated with a clamp connection. Traces of a crystalline material now become apparent as a thin deposit along the outer wall (Figs. 6-9, 27). Initial deposition generally occurs in a more or less uniform layer. Later deposition, however, is more irregular with the formation of discrete crystals over the outside of the cell (Figs. 10-16, 22-25). These crystals may be so abundant that the apex of the cell appears surrounded by a small clump of "rocks." The apical branches can be completely hidden by the crystalline deposition.

At this point the branches elongate becoming thin cylindrical projections (Figs. 11-16). As the branches grow crystalline material is deposited along the outer walls (Figs. 22, 23, 25, 26). This results in an initially thick, smooth deposit that gradually narrows to an acute apex just beyond the tip of the branch. Discrete crystals are not generally formed along the branches. Deposition around the branches is not uniform so that one side often has a thicker layer of crystalline material than the other (Figs. 22, 25, 26). The width of an

acanthocyte, the distance between the tips of the two most distant arms, varies from 50 to 125 µm.

The end result is the formation of "spiny" cells (Figs. 17-21, 24, 26) scattered over the surface of the mycelium in the agar dish. For this reason the term acanthocyte is being used to refer to these structures. The foregoing description was based on cultures of Stropharia rugosoannulata Farlow (DF2575). In addition acanthocytes have been seen in cultures of S. ambigua (Pk.) Zeller, S. hornemannii (Fr. ex Fr.) Lundell & Nannf., S. coronilla (Bull. ex Fr.) Quél., and S. hardii Atk.

While the above discussion outlines the most common developmental pattern, there is variation at some stages. This is reflected in the morphology of the mature cell. The major deviation involves the degree and type of branching that occurs at the apex of the short lateral branch. Generally the branching is restricted to the apex. But in some cases branches may be formed along the length of the lateral branch (Fig. 5). Occasionally cells may form only two or three branches (Fig. 19). In both cases the mature structure has a more open morphology. The amount of crystal formation at the apex of the lateral branch also varies (compare Fig. 18 with Fig. 21). Finally the long thin branches forming the "arms" of the acanthocytes sometimes branch. These secondary branches generally do not develop beyond a short projection and are eventually covered by the crystalline deposition. This results in the formation of short channels in the crystalline layer (Figs. 13, 17, 19).

These cells are found on both dicaryotic and monocaryotic cultures. All 39 monocaryons from two collections of S. rugosoannulata (DF2777, DF2778) formed acanthocytes. Preliminary work utilizing energy dispersive X-ray analysis in conjunction with SEM indicates that the crystalline material is composed primarily of calcium.

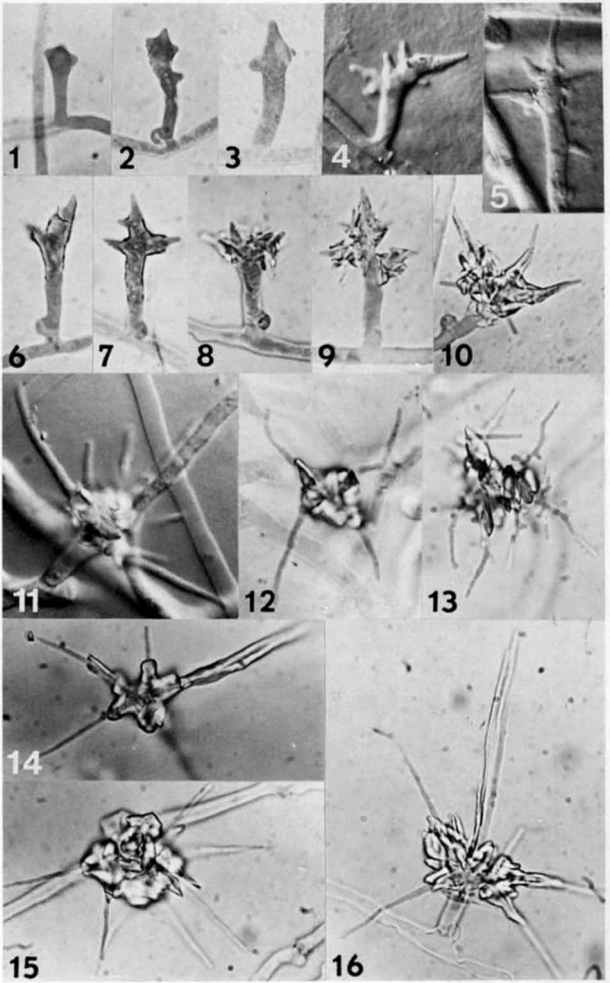
ACANTHOCYTES IN HERBARIUM SPECIMENS

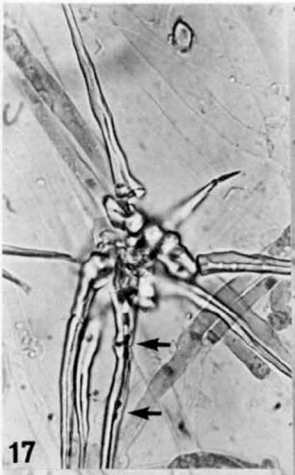
Upon encountering acanthocytes in culture I naturally became interested in which species they might be found. The occurrence of acanthocytes on vegetative mycelia in cultures suggested their possible presence on the vegetative mycelium in the natural substrate. Although herbarium specimens frequently contain large amounts of substrate, fossicking around in the substrate

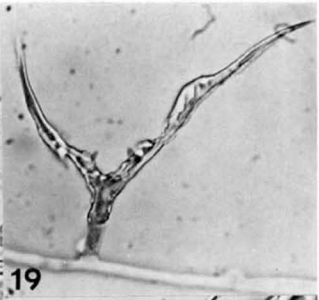
Figs. 1-16. Stages in the development of acanthocytes. Figs. 1-5. Early stages showing the short lateral branch and the initial apical branching. (1-3. Stained in phloxine, X 1000; 4-5. not stained, photographed with interference contrast optics, X 1200.) Figs. 6-10. Initial deposition of crystalline material, stained in phloxine, X 1000. Figs. 11-16. Elongation of the apical branches. Note short side branches in Fig. 13 and thin layer of crystalline material deposited on longest arm in Fig. 16. (12-16. stained in phloxine; 11. interference contrast; 11-12. X 1400; 13-16. X 1000).

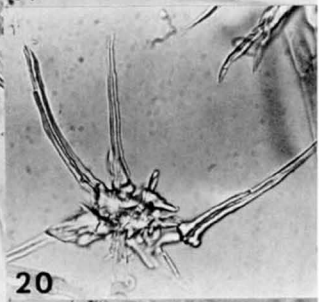
Figs. 17-21. Mature acanthocytes from agar cultures. Fig. 17. The lower arm shows the small channels which result from the formation of small secondary branches as in Fig. 13; X 1100. Fig. 18. The branches have an acute tip and are easily broken from the main body; X 1300. Fig. 19. An acanthocyte with only two branches and a reduced amount of crystalline deposition over the apex of the lateral branch; X 1000. Fig. 20. A side view of a typical acanthocyte; X 1000. Fig. 21. A mature acanthocyte with well developed arms but lacking the heavy deposit of crystals seen in Fig. 18.

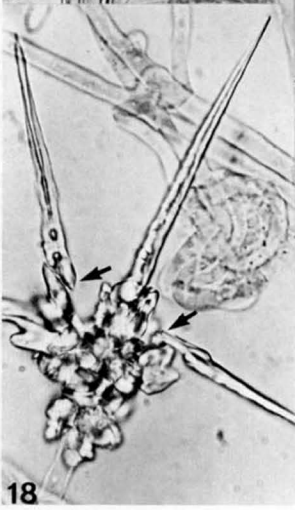
Figs. 22-27. SEM photographs of various stages of acanthocyte formation in agar culture. Figs. 22-23. Early stages before elongation of the branches. (22. X 4600; 23. X 3700.) Fig. 24. Mature acanthocyte with discrete crystals over the apex. Figs. 25-26. Uneven deposition of crystalline material along elongating branches. (25. X 4800; 26. X 2200.) Fig. 27. Early stage of development with a more or less even distribution of crystalline material over the surface; X 4600.

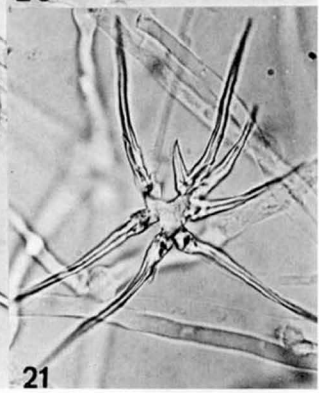

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16

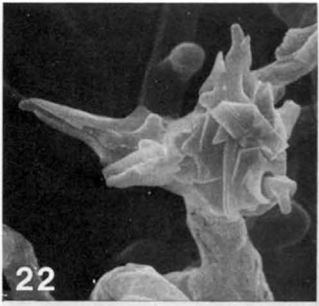

17


19

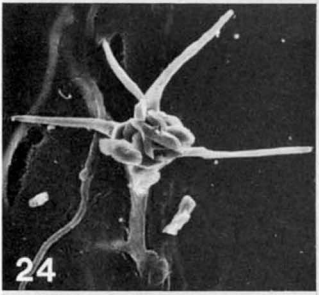

20

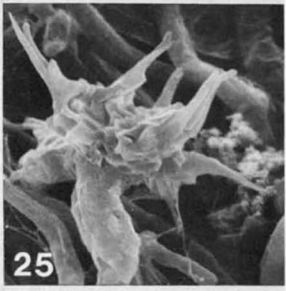

18

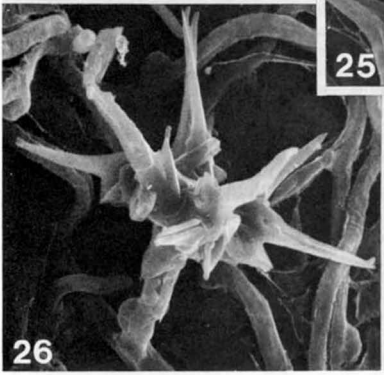

21

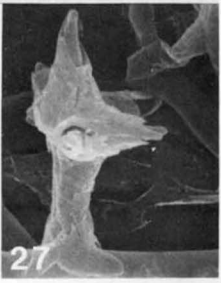

22


23


24


25


26


27

would be difficult and contamination from the mycelium of other fungi could be a problem. However, the base of the stipe was a potential site for locating acanthocytes because the vegetative mycelium associated with the basidiocarp could be distinguished with certainty. Subsequent examination of stipe bases of herbarium specimens revealed acanthocytes on the vegetative mycelium. The appearance of the acanthocytes in herbarium specimens is similar to those on mycelium in culture. They ranged in size from 20-140 µm with most falling in the range of 50-100 µm.

Some general comments are necessary concerning the location and determination of the presence of acanthocytes. They are almost exclusively located on the vegetative mycelium. Thus, to observe them, examination of a small amount of substrate is generally required. This may seem to be a deterrent to locating these structures in herbarium specimens. However, I have found very few specimens that lacked adequate amounts of substrate to make a reliable determination. While a positive determination depends on the use of a compound microscope, acanthocytes can with experience be observed directly on the herbarium specimen with a dissecting microscope.

Acanthocytes are only infrequently encountered on hyphae of the basidiocarp. In one basidiocarp of S. rugosoannulata I found a few scattered acanthocytes on gill tissue. A similar situation in Stropharia sp. has been reported by A. H. Smith (pers. comm.). The base of the stipe occasionally produces acanthocytes but generally there is a sharp demarcation between the acanthocyte producing vegetative cells and the compact tissue of the stipe which lacks acanthocytes.

The use of herbarium specimens for a survey of this type is fraught with a significant difficulty. Primarily the problem is one of having to depend upon the identifications provided by various mycologists who may have not had a sufficient understanding of the species involved. Because of this, reliable statements regarding the occurrence of acanthocytes can be made for only those species that are easily recognized and whose species concepts have not undergone extensive revision over the years. Those species whose identifications are reasonably certain and which have been found to produce acanthocytes are Stropharia aeruginosa (W. Curtis ex Fr.) Quêl., S. ambigua (Pk.) Zeller, S. coronilla (Bull. ex Fr.) Quêl., S. cyanea (Bolt. ex Secr.) Tuomikoski, S. hardii Atk., S.

hornemannii (Fr. ex Fr.) Lundell & Nannf., S. kauffmanii A. H. Sm., S. rugosoannulata Farlow, S. subsquamulosa A. H. Sm. & Mitchell.

How often are these cells found in a particular species? All 28 collections of S. rugosoannulata from several localities in the U.S. were found to produce acanthocytes. Similarly all 94 collections examined of S. ambigua from the western U.S. and Canada had acanthocytes. All collections examined of the other species listed above were found to have acanthocytes if a sufficient amount of substrate was present. The consistent occurrence of these structures in a given species suggests they have taxonomic value. The question of whether the character is important at the generic, subgeneric or specific level is currently being investigated. Preliminary studies have shown that acanthocytes are not found in some common species of Psilocybe and Nematoloma.

SUMMARY

A striking cell type has been observed in Stropharia species. This cell, formed as a short branch of the vegetative mycelium, initially develops several short branches at its apex. A thick crystalline deposit is laid down over the surface of the cell giving the cell at maturity a spiny appearance. Therefore these cells have been designated acanthocytes. Acanthocytes are a consistent feature of the vegetative mycelium in herbarium specimens and mycelium of monocaryotic and dikaryotic cultures in the genus Stropharia.

MYCOTAXON

Vol. XI, No. 1, pp. 250-254 April-June 1980

CONTRIBUTION TO THE LICHEN FLORA OF URUGUAY XIV. NEW OR ADDITIONAL RECORDS FROM CENTRAL URUGUAY.

HECTOR S. OSORIO.

Departamento de Botánica.
Museo Nacional de Historia Natural.
Casilla de Correo 399.
Montevideo, URUGUAY.

SUMMARY. Thirty-nine lichen species collected in Central Uruguay are enumerated. Heterodermia flabellata, Parmelina muelleri and Rinodina homobola are added to the known flora of Uruguay.

This paper is based on a study of some small collections of lichens gathered in the central region of Uruguay. Although many of the species reported here have been collected from other localities, our scant knowledge of the lichen flora from this region has encouraged the author to publish the results obtained.

Except the samples collected by the author and deposited in his private herbarium, all materials cited here are kept in the Herbarium, Museo Nacional de Historia Natural, Montevideo (MVM).

Acarospora boliviana Magn.
DURAZNO: La Paloma-Est. Km 319 Road, 18 km N from La Paloma, on sandstone at roadside, Osorio 7025. Formerly this species was known from three localities in South Uruguay.

A. lorentzii (Müll.Arg.) Hue.
FLORIDA: Arroyo Sauce de Mansavillagra and Hwy. 41, on stones, Osorio 7039.

Anthracothecium goniostomum Müll. Arg.
FLORIDA: Río Santa Lucía, Estancia Los Cerros, on bark, Izaguirre (MVM 17.430).

Buellia subisabellina Sahlbr.
FLORES: Hwy. 3, km 164, trunk of Casuarina at roadside, Osorio 6338.

Caloplaca cinnabarina (Ach.) Zahlbr.
DURAZNO: La Paloma-Est. Km 319 Road, 18 km N from La Paloma, on sandstone at roadside, Osorio 7018.

FLORIDA: Arroyo Sauce de Mansavillagra and Hwy. 41, on stones, Osorio 7036; Arroyo Casupá, on granitic stones, Del Puerto (MVM 17.545).

C. crocea (Kremp.) Haf. & Poelt.
FLORIDA: Arroyo Sauce de Mansavillagr and Hwy. 41, on Salix, Osorio 7048.
TACUAREMBO: Arroyo Malo, Once Cerros, 20 km SE from Curtina, on bark, Mones (MVM 17.631).

Candelaria concolor (Dicks.) Stein.
FLORES: Arroyo Grande, Paso del Puerto, on Celtis tala, Osorio 3576.
FLORIDA: Arroyo Sauce de Mansavillagra and Hwy. 41, on Salix, Osorio 7043.
TACUAREMBO: Paso de los Toros, on bark, Gortari (MVM 17.307).

C. fibrosa (Fr.) Müll. Arg.
FLORES: Arroyo Grande, Paso del Puerto, on shrubs' branches, Osorio 3578.

Collema glaucophthalmum Nyl. var. implicatum (Nyl.) Degel.
FLORIDA: Arroyo Sauce de Mansavillagra and Hwy. 41, on Salix, Osorio 7050.

Diploschistes actinostomus (Pers.) Zahlbr.
DURAZNO: La Paloma-Est. Km 319 Road, 18 km N from La Paloma, on sandstone at roadside, Osorio 7016. This species has been previously reported from the adjacent department of Tacuarembó (Magnusson 1950).

D. ochraceus (Anzi) Stein.
DURAZNO: La Paloma-Est. Km 319 Road, 18 km N from La Paloma, on sandstone, Osorio 7017.

Dirinaria applanata (Fée) Awas.
FLORIDA: La Cruz, on bark, Lorier (MVM 17.911).

Haematomma montevidense (Räs.) Follm. & Rud.
DURAZNO: La Paloma-Est. Km 319 Road, 18 km N from La Paloma, on sandstone at roadside, Osorio 7024.

Heterodermia diademata (Tayl.) Awas.
TACUAREMBO: Arroyo Malo, Once Cerros, 20 km SE from Curtina, on bark, Mones (MVM 17.628).

H. flabellata (Fée) Awas.
FLORIDA: Arroyo Sauce de Mansavillagra and Hwy. 41, on Salix, Osorio 7049. New to Uruguay.

Hypotrachyna pluriformis (Nyl.) Hale
FLORIDA: La Cruz, on bark, Lorier (MVM 17.913). In Uruguay this species was previously known in two localities, both in its central region, too. (Hale 1975).

Lecanora fusca Müll. Arg.
FLORIDA: Arroyo Casupá, on granitic stones, Del Puerto (MVM

17.544); Arroyo Sauce de Mansavillagra and Hwy. 41, on stones, Osorio 7032.
DURAZNO: La Paloma-Est. Km 319 Road, 18 km N from La Paloma, on sandstone at roadside, Osorio 7023.

Lecidea oreinodes (Koerb.) Web. & Hertel
DURAZNO: La Paloma-Est. Km 319 Road, 18 km N from La Paloma, on sandstone at roadside, Osorio 7021.a. In Uruguay this species was only known from the department of Montevideo from material collected in the last century (Müller Arg. 1888, as Lecidea angolensis).

L. russula Ach.
DURAZNO: La Paloma-Est. Km 319 Road, 18 km N from La Paloma, on sandstone at roadside, Osorio 7020.
FLORIDA: Arroyo Casupá, on granitic stones, Del Puerto (MVM 17.550).

Leptogium austroamericanum (Malme) Dodge.
TACUAREMBO: Arroyo Malo, Once Cerros, 20 km SE from Curtina, on bark, Mones (MVM 17.632).

Ochrolechia subpallescens Vers.
FLORES: Hwy. 3, km 164, on Casuarina at roadside, Osorio 6340.

Parmelia canaliculata Lynge.
FLORES: Arroyo Grande, Paso del Puerto, on Celtis tala, Osorio 3573.
FLORIDA: Río Santa Lucía, Estancia Los Cerros, on bark, Izaguirre (MVM 17.428).

Parmelina lindamanii (Lynge) Hale
TACUAREMBO: Tambores, Pozo Hondo, on bark, San Martín (MVM 17.400).

P. muelleri (Vain.) Hale
TACUAREMBO: Tambores, Pozo Hondo, on bark, San Martín (MVM 17.401). New to Uruguay. The present discovery extends significatively its distribution in South America. Until this report Tucumán in Argentina (Hale 1976) and Guarapuava in the Brazilian state of Paraná (Osorio 1977), were the most southern collections known.

P. pilosa (Stizb.) Hale
FLORIDA: Arroyo Sauce de Mansavillagra and Hwy. 41, on Salix, Osorio 7044.
TACUAREMBO: Arroyo Malo, Once Cerros, 20 km SE from Curtina, on trees, Mones (MVM 17.629).

Parmotrema eciliatum (Nyl.) Hale
TACUAREMBO: Tambores, Pozo Hondo, on bark, San Martín (MVM 17.399). It was cited before for the department of Montevideo (Müller Arg. 1888) and San José (Osorio 1979), both in South Uruguay.

P. reticulatum (Tayl.) Choisy.
FLORIDA: La Cruz, on bark, Lorier (MVM 17.912).

Phaeographina arechavaletae Müll. Arg.
FLORES: Arroyo Grande, Paso del Puerto, on shrubs' branches, Osorio 3579.

Physciopsis syncolla (Tuck.) Poelt.
FLORES: Arroyo Grande, Paso del Puerto, on bark, Osorio 3574.

Pseudoparmelia exornata (Zahlbr.) Hale
RIO NEGRO: Río Negro, Palmar de Mujica, on bark, Boretto (MVM 17.916).

Ps. papillosa (Lynge ex Gyeln.) Hale
FLORIDA: Arroyo Casupá, on granitic stones, Del Puerto (MVM 17.548).

Pyxine subcinerea Stirt.
FLORIDA: La Cruz, on bark, Lorier (MVM 17.910).

Ramalina celastri (Spreng.) Krog & Swinsc.
FLORES: Hwy. 3, km 164, trunk of Casuarina at roadside, Osorio 6336.
FLORIDA: Arroyo Sauce de Mansavillagra and Hwy. 41, wooden fence post at roadside, Osorio 7040; Río Santa Lucía, Estancia Los Cerros, on bark, Izaguirre (MVM 17.429); La Cruz, on bark, Lorier (MVM 17.914).
RIO NEGRO: Río Negro, Palmar de Mujica, on shrubs, Boretto (MVM 17.917).
TACUAREMBO: Arroyo Malo, Once Cerros, 20 km SE from Curtina, on trees, Mones (MVM 17.630).

R. prolifera Tayl.
FLORIDA: Río Santa Lucía, Estancia Los Cerros, on shrubs, Izaguirre (MVM 17.432).

Rinodina homobola (Nyl.) Vain.
FLORES: Arroyo Grande, Paso del Puerto, on wooden fence post, Osorio 3577. New to Uruguay.

Teloschistes chrysophthalmus (L.) Th. Fr. var. cinereus Müll. Arg.
FLORES: Arroyo Grande, Paso del Puerto, on Celtis tala, Osorio 3575; Hwy. 3, km 164, on Casuarina at roadside, Osorio 6339.
FLORIDA: La Cruz, on bark, Lorier (MVM 17.915).

T. cymbalifer (Mey. & Flot.) Müll. Arg.
FLORIDA: Río Santa Lucía, Estancia Los Cerros, on shrubs, Izaguirre (MVM 17.431).

T. exilis (Michx.) Vain.
TACUAREMBO: Arroyo Malo, Once Cerros, 20 km SE from Curtina, on trees, Mones (MVM 17.627).

Usnea dichroa Mot. var. spinulosa Mot.
FLORES: Hwy. 3, km 164, on wooden fence post at roadside, Osorio 6344.
RIO NEGRO: Río Negro, Palmar de Mujica, on shrubs, Boretto (MVM 17.918).
TACUAREMBO: Arroyo Malo, Once Cerros, 20 km SE from Curtina, on trees, Mones (MVM 17.624); Tambores, Pozo Hondo, on bark, San Martín (MVM 17.402). This species has been cited recently from two localities in SW Uruguay (Osorio 1979 & 1980). With the new localities cited here this species would seem to be widely distributed in the whole country.

LITERATURE CITED.

HALE, M.E., Jr. 1975. A revision of the lichen genus Hypotrachyna (Parmeliaceae) in tropical America. Smiths. Contr. Bot. 25: 1-73.
---- ---- 1976. A monograph of the lichen genus Parmelina Hale (Parmeliaceae). Smiths. Contr. Bot. 33: 1-60.
MAGNUSSON, A.H. 1950. Lichens from Uruguay. Medd. Göteborgs Bot. Trädg. 18: 213-237.
MÜLLER ARGAU. J. 1888. Lichenes montevidenses. Rev. Mycol. 10 (37): 1-5.
OSORIO, H. S. 1977. Contribution to the lichen flora of Brazil. II. Lichens from Guarapuava, Parana State. Dusenia 10(2): 101-102.
---- ---- 1979. Contribution to the lichen flora of Uruguay XI. Lichens from Arazatí, San José Department. The Bryologist 82: 472-473.
---- ---- 1980. Contribution to the lichen flora of Uruguay XIII. Lichens from Sierra Mahoma, San José Department. Phytologia 45: 217-220.

MYCOTAXON

Vol. XI, No. 1, pp. 255-268 April-June 1980

SYNONYMIE DE ENTOMOPHTHORA VIRULENTA HALL ET DUNN ET DE CONIDIOBOLUS THROMBOIDES DRECHSLER

J.P. LATGE (1)

D.S. KING (2)

B. PAPIEROK (1)

(1) *Unité de Lutte Biologique contre les Insectes Institut Pasteur, 75015 Paris, France*

(2) *Mycology Department, American Type Culture Collection Rockville, MD 20852, Etats-Unis*

ABSTRACT

Morphological characters (measurements of primary conidia and zygospores, number of nuclei per conidium), biochemical characters (composition of fatty acids of neutral and polar lipids, electrophoretic patterns of isoenzymes) and pathogenic characters (virulence against Aphids) were used to compare *Entomophthora virulenta* HALL & DUNN and *Conidiobolus thromboides* DRECHSLER. The similarities between the two species are sufficient to demonstrate their synonymy.

INTRODUCTION

Décrite par HALL & DUNN en 1957 comme pathogène de l'Homoptère *Therioaphis trifolii* MON. (= *T. maculata* BUCKT.) *Entomophthora virulenta* est ainsi caractérisée:

"Conidies sphériques à pyriformes avec une papille basale, une paroi mince et un cytoplasme granuleux; longueur (base comprise) 20-32 µ, moyenne 26 µ; largeur 16-28 µ; moyenne 22 µ. Conidies secondaires similaires aux primaires. Conidiophores simples, formant une couverture légèrement brune à rougeâtre sur tout le corps de l'insecte. Corps hyphaux, courtes sections d'un hyphe, de forme irrégulière, souvent branchés ou tordus; 8-12 µ de largeur, 30-60 µ (ou plus) de longueur. Cystides rarement rencontrées. Spores durables généralement azygospores (quelques zygospores observées), sphériques (quelques unes irrégulières) avec une épispore épaisse, lisse et une à plusieurs vacuoles ou globules lipidiques volumineux dans un cytoplasme granuleux; diamètre 15-31 µ, moyenne

22 µ; pas de chlamydospores ou spores interstitielles.Hôte attaché au substrat par des rhizoïdes".

Depuis 1957, de nombreuses souches de *E. virulenta* ont pu être isolées dans différents pays à partir d'Homoptères, de Diptères ou de Lépidoptères (GUSTAFSSON, 1965;SOPER & BRYAN, 1974;HARTMANN & WASTI, 1976;REMAUDIERE et al., 1976). L'étude de ces souches a montré que la description de HALL & DUNN est entachée de 2 erreurs:

- les insectes tués par *E. virulenta* ne sont jamais attachés à la plante par des rhizoïdes (HUMBER et al., 1977)
- les spores durables de *E. virulenta* sont toujours des zygospores. GUSTAFSSON (1965) a déjà signalé la présence de zygospores chez *E. virulenta* mais le même auteur signalait aussi l'existence de rhizoïdes sur les cadavres. La formation exclusive de zygospores en tant que spores durables de *E. virulenta* a été confirmée par LATGE (1976). Cette étude a montré qu'il est difficile de discerner la nature des spores durables jeunes (surtout si elles sont formées sur le même hyphe) et peut expliquer l'interprétation de HALL & DUNN (1957) qui signalent la présence de quelques zygospores parmi une majorité d'azygospores.

E. virulenta, ainsi nouvellement défini, possède les 3 caractéristiques du genre *Conidiobolus* récemment révisé par KING (1976a,b): (1) existence de conidies primaires sphériques plurinucléées;(2) présence de zygospores;(3) croissance facile de type saprophytique. Cet auteur a d'ailleurs suggéré que plusieurs espèces d'*Entomophthora*, notamment *E. virulenta*, devraient être replacées à l'intérieur du genre *Conidiobolus*. GUSTAFSSON (1965) avait déjà noté que le mode de formation des zygospores de *E. virulenta* était similaire à celui d'espèces du genre *Conidiobolus*;cet auteur rapprochait d'ailleurs *E. virulenta* de *C. brefeldianus*. En réalité, *C. brefeldianus* se différencie très facilement de *E. virulenta* par son aptitude à produire des microconidies (COUCH, 1939;KING, 1976b). L'espèce de *Conidiobolus* dont la morphologie est la plus proche de *E. virulenta* semble *C. thromboides* (KING, 1976b;LATGE, 1976).

La mise en synonymie de 2 espèces d'Entomophthorales, notamment du genre *Conidiobolus*, sur les seules bases morphologiques est souvent difficile. Ainsi, une révision taxonomique récente de *Entomophthora obscura* HALL & DUNN (REMAUDIERE et al., 1979) montre qu'une extrême variabilité est constatée dans les mensurations des conidies et des azygospores de cette espèce. Des caractères biochimiques et pathologiques ont alors efficacement complété la définition de l'espèce fongique considérée.

TYRRELL (1967) a le premier suggéré l'utilisation des

profils d'acides gras des lipides totaux en vue de la différenciation des espèces d'Entomophthorales entre elles. L'étude des profils d'acides gras des lipides polaires et des lipides neutres s'est récemment révélée plus précise que celle des seuls lipides totaux (LATGE & DE BIEVRE, 1980). Par ailleurs, la considération des profils électrophorétiques d'isoenzymes tels que ceux de la leucine aminopeptidase, de la tetrazolium oxydase et de la phosphatase alcaline a permis une différenciation de certaines espèces du genre *Conidiobolus* en accord avec la séparation obtenue d'après les données morphologiques (KING, 1976c). Ainsi les deux critères biochimiques utilisables à ce jour dans l'étude taxonomique des Entomophthorales, sont la composition en acides gras des lipides polaires et neutres du champignon et les profils électrophorétiques d'isoenzymes. Le nombre de noyaux des conidies primaires (BATKO, 1964) et les exigences nutritionnelles (LATGE, 1975a,b;KING, 1976) peuvent être aussi utilisés dans la caractérisation des espèces d'Entomophthorales. La considération de certains éléments se rapportant à la pathogénie de la mycose et au développement du champignon dans l'hôte peut être également utile à la caractérisation d'une espèce d'Entomophthorales. Ainsi, la présence éventuelle et la forme des rhizoïdes attachant l'insecte au substrat ont été considérées depuis longtemps comme un critère taxonomique important chez les Entomophthorales (GUSTAFSSON, 1965). La recherche de cystides sur le cadavre, la mesure de la durée d'incubation de la maladie et de l'intensité de la sporulation ont pu mettre en évidence la variabilité existant à l'intérieur d'une espèce telle que *E. obscura* (REMAUDIERE et al., 1979;PAPIEROK & WILDING, 1980).

Ces résultats nous ont amenés à étudier l'éventuelle identité spécifique de *E. virulenta* et de *C. thromboides* en considérant non seulement les données morphologiques mais aussi des caractères biochimiques et pathologiques.

MATERIEL ET METHODES

I. Souches

Les références des souches utilisées sont précisées dans le tableau I. Il n'a pas été retrouvé d'exsiccata type de *E. virulenta* et de *C. thromboides*. Les souches types de *E. virulenta* et de *C. thromboides* ont respectivement les références ATCC 14270 et ATCC 12587. Nous désignons comme lectotype de *E. virulenta* les figures 12 et 14 de la description originale de HALL & DUNN (1957). La figure 2 de la description originale de DRECHSLER (1953) a été déjà dési-

gnée comme lectotype de *C. thromboides* par KING (1977);des exsiccata de culture de la souche type de *C. thromboides* ATCC 12587 contenant des conidies et des zygospores sont désignés comme néotypes de cette espèce et sont déposés à l'herbier du laboratoire de Cryptogamie du Muséum d'Histoire naturelle de Paris (PC).

TABLEAU I. Références d'isolement.

SOUCHES	SOURCE	PAYS	AUTEURS
E.VIRULENTA (ATCC 14270) = CBS 18360	Insecte: *Therioaphis trifolii*	Etats-Unis	HALL & DUNN (1957)
E.VIRULENTA (ATCC 36931)	Insecte: *Myzus persicae*	Etats-Unis	SOPER & BRYAN (1974)
C.THROMBOIDES (ATCC 12587) = CBS 15956	Feuille moisie	Etats-Unis	DRECHSLER (1953)
C.THROMBOIDES (ATCC 32194)	Champignon: *Craterellus cornucopioides*	Etats-Unis	KING,LAHN & JONG (1976)
C.STROMOIDEUS (ATCC 15430)	Insecte: associé à *E.muscae*	Inde	SRINIVASAN & THIRUMALACHAR (1962)
C.OSMODES (ATCC 38865)	Sol	France	COREMANS-PELSENEER (1977)

II. Observations

1. Conidies et zygospores

a. Mesures

Les conidies produites en boîtes de Petri à 21°C sur milieu PDA (2 % glucose) ATCC 336 sont montées sur lame dans l'eau. Pour chaque souche, 20 conidies sont mesurées. Les zygospores sont produites sur le même milieu PDA à 21°C à l'obscurité. Pour chaque souche, trois boîtes de Pétri sont ensemencées et 18 spores mesurées par boîte. Les spores sont mesurées dans le mélange bleu coton-lactophénol.

b. Nombre de noyaux

Les noyaux des conidies primaires sont colorés à l'hématoxyline ferrique d'après la méthode de LU (1967). Leur nombre est compté sur 20 conidies pour chaque souche.

c. Microscopie électronique

Les zygospores pour examen au microscope électronique à balayage sont produites sur un milieu gélosé à base de glucose (4 %) et d'extrait de levure (1 %). Elles sont deshydratées et soumises à la fixation au point critique avant métallisation à l'or-palladium. L'évolution de la morpholo-

gie des zygospores de *E. virulenta* au cours de leur vieillissement a été aussi suivie en culture liquide.

2. Croissance

La croissance des souches de *E. virulenta* et *C. thromboides* est notée sur un milieu PDA après 3 jours de croissance à 21°C à l'obscurité. L'inoculum est un cercle de 4 mm de diamètre.

3. Composition en acides gras des lipides neutres et polaires

Les souches sont cultivées pendant 24 h dans un milieu contenant 4 % de glucose, 1 % d'extrait de levure (DIFCO) et 1 % d'Antimousse Rhodorsil 426 R en fermenteur BIOLAFITTE de 2 litres (20°C, 700 tours par min., 30 l air/h). Le mycélium est récupéré par filtration, lavé 3 fois à l'eau distillée et stocké au congélateur. Les lipides neutres et lipides polaires des différentes souches sont extraits par le chloroforme et le méthanol, puis hydrolysés. Les esters méthyliques des acides gras ainsi libérés sont analysés par chromatographie en phase gazeuse et leur concentration est exprimée en % (LATGE & DE BIEVRE, 1980).

Les lipides neutres et polaires de *C. stromoideus* (espèce morphologiquement voisine de *C. thromboides*) et ceux de *C. osmodes* (espèce souvent isolée de pucerons mais morphologiquement différente de *C. thromboides* et de *C. stromoideus*) ont été aussi analysés. Ces 2 espèces sont comparées à *C. thromboides* et à *E. virulenta* du seul point de vue composition en acides gras.

4. Profils électrophorétiques

Les deux systèmes enzymatiques utilisés, l'alcool deshydrogénase (E.C. 1.1.1.1) et la leucine aminopeptidase (E.C. 3.4.11.1) sont étudiés d'après une modification de la technique de SHAW & PRASAD (1970). Chaque souche est cultivée dans 2 tubes de milieu gélosé ATCC 1005 (glucose 2 %, extrait de levure 0,5 %, peptone 1 %) pendant 4 jours; le mycélium total est récupéré et transféré dans une fiole d'Erlenmeyer de 250 ml avec 100 ml de milieu liquide ATCC 1005. Après 4 jours d'agitation à 200 tpm à 20°C, le mycélium est filtré, puis agité en tube pendant 7 minutes avec 10 g de billes de verre de 1 mm. L'homogénisat est absorbé sur papier filtre et soumis à une électrophorèse sur gel d'amidon à 13 % sous 250 V. Le tampon du gel contient 5,5 mM d'acide citrique associé à 8,8 mM de Tris Base (Sigma). Le tampon du réservoir est du borate de sodium 0,297 M. Les bandes des isoenzymes sont repérées par leur Rf.

5. Infection expérimentale de pucerons

L'action pathogène de la souche ATCC 36931 de *E. virulenta* et de la souche ATCC 12587 de *C. thromboides* a été recherchée vis-à-vis de l'Aphide *Acyrthosiphon pisum* HARRIS. La méthode d'estimation du pouvoir pathogène à l'égard des adultes ailés de cette espèce a été décrite récemment (PAPIEROK & WILDING, 1979); 4 fois 5 lots de 10 pucerons sont exposés au flux des conidies émises par des cultures durant respectivement 5,20,80 et 320 mn.

RESULTATS ET DISCUSSION

I. Observations morphologiques

Il n'existe pas de différence entre les moyennes des diamètres des spores et conidies de *E. virulenta* et de *C. thromboides*. Les mesures effectuées sur les 4 souches en culture sont identiques aux mensurations données dans les descriptions originales de HALL & DUNN et de DRECHSLER (Tableau 2). Les conidies secondaires sont de forme simi-

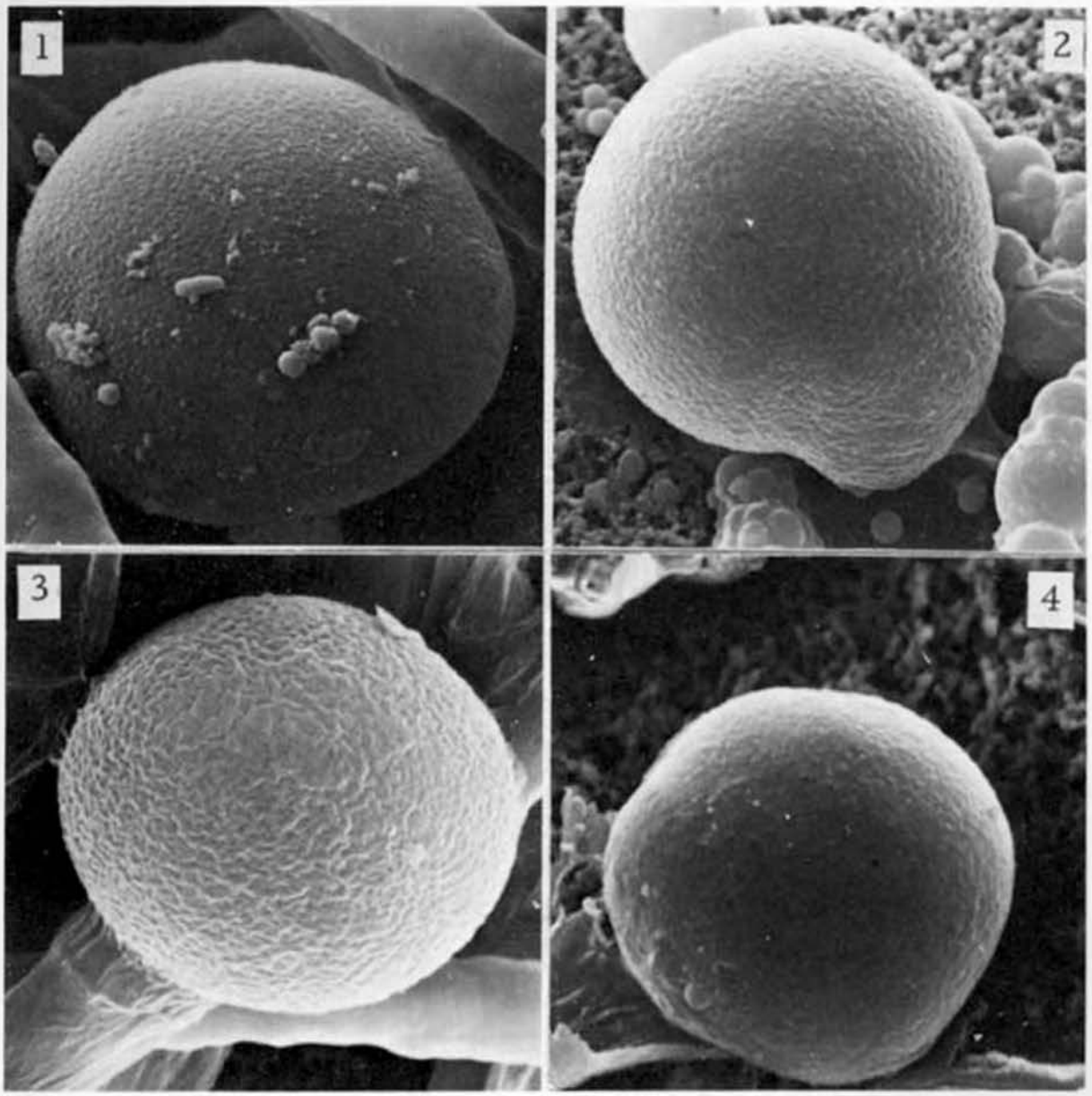
TABLEAU 2. Mesures en µm des conidies primaires et des zygospores de *Entomophthora virulenta* et de *Conidiobolus thromboides* selon les descriptions originales et à partir des souches de mycothèque.

SOUCHES	CONIDIES PRIMAIRES	
	Diamètre	Longueur
E. VIRULENTA		
desc.orig.	16(22)28(a)	20(26)32
ATCC 14270	20(24)30	24(28)35
ATCC 36931	21(23)25	26(28)30
C. THROMBOIDES		
desc.orig.	19(?)27	24(?)32
ATCC 12587	21(25)28	24(30)34
ATCC 32194	18(23)25	22(27)31

	ZYGOSPORES			
	Spore jeune		Spore mûre	
E. VIRULENTA	Diamètre	Paroi	Diamètre	Paroi
desc.orig.	?	?	15(22)31	?
ATCC 14270	24(27)32	0,6(1,2)2,2	20(24)31	3,3(4,1)5,5
ATCC 36931	22(25)30	0,6(1,9)4,4	15(24)28	3,3(4,6)6,1
C. THROMBOIDES				
desc.orig.	?	?	18(?)24	2,0(?)2,5
ATCC 12587	25(28)33	0,6(1,9)3,9	21(26)29	2,2(4,4)5,5
ATCC 32194	24(27)34	0,6(2,1)4,4	22(25)29	3,3(4,4)5,5

(a) les valeurs extrêmes des mensurations entourent la moyenne mentionnée entre parenthèses

laire aux conidies primaires. Les conidies primaires des 4 souches contiennent un nombre de noyaux identique compris entre 22 et 30 noyaux par conidie (26 en moyenne). Au microscope électronique à balayage, les zygospores de *E. virulenta* et de *C. thromboides* présentent la même fine ornementation. Celle-ci peut d'ailleurs légèrement varier en fonction des spores observées;cependant, la hauteur des crêtes reste toujours inférieure à 0,25 µm (Figs 1,2,3).



FIGS 1,2,3. Types d'ornementation observés indifféremment chez les zygospores de *E. virulenta* (souches ATCC 14270 et ATCC 36931) ou de *C. thromboides* (souches ATCC 12587 et ATCC 32194) produites en milieu solide. FIG. 4. Zygospore de *E. virulenta* (ATCC 36931), 10 jours après sa formation en milieu liquide.

La considération de l'âge des zygospores est très importante. Le diamètre des spores jeunes sans paroi épaisse est toujours plus grand que celui des spores mûres (Tableau 2). Par ailleurs, on remarque au microscope électronique à balayage que l'ornementation des zygospores s'estompe au cours du vieillissement de la zygospore dans le milieu liquide (Fig. 4).

Après 3 jours de culture, la croissance atteint 39 mm pour les 2 souches de *E. virulenta* et 49 et 46 mm respectivement pour les souches ATCC 12587 et 32194 de *C. thromboides*. La différence de vitesse de croissance entre les 2 souches n'est pas suffisante pour représenter une distinction interspécifique. En effet, des différences beaucoup plus grandes ont été notées au laboratoire entre les vitesses de croissance de souches appartenant à une même espèce telle *E. aphidis*, *E. obscura*, *E. sphaerosperma* ou *E. phalloides*.

II. Observations biochimiques

Les profils d'acides gras des lipides neutres de *C. thromboides* et *E. virulenta* sont identiques (Tableau 3).

TABLEAU 3. Composition en acides gras des lipides neutres de *Entomophthora virulenta*, *Conidiobolus thromboides*, *C. osmodes* et *C. stromoideus* (a).

	E.VIRULENTA		*C.THROMBOIDES*		*C.OSMODES*	*C.STROMOIDEUS*
	14270	36931	12587	32194	38865	15430
C12:0	-	-	-	-	6,9	-
C13:0	-	-	-	-	-	tr(b)
C14:0	10,2	9,3	9,3	7,6	12,3	10,7
C15:0						
C14:1	0,6	1,2	tr	0,8	tr	tr
C16:0	13,4	9,5	14,8	13,1	8,9	23,7
C16:1	22,2	22,9	22,4	19,4	8,2	12,6
C iso 17	0,7	1,1	0,6	0,7	-	-
C17:0	1,4	0,8	1,2	1,6	2,3	-
C18:0	1,6	1,4	1,8	2,0	2,4	8,9
C18:1	40,3	43,6	31,8	40,8	40,5	44,2
C18:2	1,1	2,8	1,9	1,3	1,8	tr
C18:3	tr	0,6	1,1	1,3	1,3	tr
X1	tr	tr	tr	tr	-	-
X2	1,3	0,6	1,1	tr	0,9	tr
C20:3	1,1	1,9	2,8	1,8	1,3	tr
C20:4	6,1	4,1	10,8	9,2	12,9	tr

(a) le numéro des souches est le numéro de collection ATCC
(b) tr:concentration inférieure à 0,5 %

Ils sont caractérisés par l'absence d'acides en C12:0 et C13:0, la présence en faible concentration de C17:0 et de C iso 17 et la forte teneur de C14:0, C16:0, C16:1, C18:1 et C20:4. Le rapport des teneurs C16:0/C16:1 est toujours inférieur à 1. *C. osmodes* se différencie facilement de ces souches par la présence d'une forte teneur en C12:0, l'absence de C iso 17 et des teneurs relativement faibles en C16:0 et C16:1. A la différence de *C. thromboides* et de *E. virulenta*, *C. stromoideus* contient peu de C20:4 et ne renferme pas de C17:0 ni de C iso 17. Par ailleurs, le rapport des concentrations de C16:0/C16:1 est toujours supérieur à 1.

Les profils d'acides gras des lipides polaires ressemblent à ceux des lipides neutres (Tableau 4). *C. thromboides* et *E. virulenta* ont encore des profils d'acides gras similaires avec de fortes concentrations en C16:0, C16:1, C18:1 et C20:4 (et un rapport C16:0/C16:1 inférieur à 1). Les lipides polaires de *C. osmodes* ne contiennent pas de C iso 17, ni de C18:0; cette espèce est riche en C20:4; le rapport C16:0/C16:1 est supérieur à 1. De même, les lipides polaires

TABLEAU 4. Composition en acides gras des lipides polaires de *Entomophthora virulenta*, *Conidiobolus thromboides*, *C. osmodes* et *C. stromoideus* (a).

	E.VIRULENTA		*C.THROMBOIDES*		*C.OSMODES*	*C.STROMOIDEUS*
	14270	36931	12587	32194	38865	15430
C12:0	-	tr(b)	-	tr	tr	-
C13:0	-	-	-	-	-	tr
C14:0	8,7	5,0	5,8	6,6	6,9	2,2
C15:0	0,6	tr	tr	0,7	1,5	tr
C14:1						
C16:0	15,1	10,5	13,5	13,3	7,1	14,4
C16:1	19,3	14,7	18,8	17,7	4,3	11,8
C iso 17	1,8	1,5	1,4	0,9	-	-
C17:0	2,3	0,7	3,1	2,5	0,7?	-
C18:0	0,9	1,3	0,8	1,0	-	1,3
C18:1	29,3	29,1	27,7	34,6	27,4	47,6
C18:2	1,3	4,0	2,0	1,6	4,5	2,4
C18:3	1,4	2,2	3,1	2,4	3,6	-
X1	0,8	0,8	tr	tr	-	-
X2	1,7	1,2	tr	tr	-	-
C20:3	1,0	1,7	2,9	1,8	2,0	4,5
C20:4	15,8	26,6	20,7	16,1	41,4	14,9

(a) le numéro des souches est le numéro de collection ATCC
(b) tr:concentration inférieure à 0,5 %

de *C. stromoideus* ne contiennent toujours pas de C17:0 et C iso 17 mais possèdent de fortes teneurs en C18:1 et un rapport C16:0/C16:1 supérieur à 1.

D'après les phénogrammes de KING (1976b), les 3 espèces de *Conidiobolus* morphologiquement voisines de *E. virulenta* sont *C. thromboides*, *C. stromoideus* et *C. megalotocus*. TYRRELL (1967, 1971) et TYRRELL & WEATHERSTON (1976) ont montré que la composition en acides gras de *C. megalotocus* est caractéristique des espèces à microconidies; bien que ne produisant pas de microconidies en culture, *C. megalotocus* a donc été regroupé avec des espèces telles que *C. brefeldianus* ou *C. coronatus* (KING, 1976b), cette espèce n'est donc pas considérée ici. Les présentes analyses d'acides gras des lipides neutres et polaires de *E. virulenta*, *C. thromboides* et *C. stromoideus* montrent que la composition des 2 premières espèces est similaire et différente de celle de *C. stromoideus*. Ce résultat rejoint les analyses de TYRRELL (1967) qui, sans avoir fait le rapprochement entre les deux espèces *E. virulenta* et *C. thromboides*, a cependant noté des compositions en acides gras des lipides totaux identiques pour les deux espèces.

Le tableau 5 montre les profils électrophorétiques des 2 enzymes testées chez les 4 souches de *C. thromboides* et *E. virulenta*. Bien que les résultats de l'alcool deshydrogénase soient variables, la considération de ces profils enzymatiques atteste l'existence de liens étroits entre ces 2 espèces.

TABLEAU 5. R_f de la leucine aminopeptidase et de l'alcool deshydrogénase de *Entomophthora virulenta* et de *Conidiobolus thromboides*.

SOUCHES	LEUCINE AMINOPEPTIDASE	ALCOOL DESHYDROGENASE
E. VIRULENTA		
ATCC 14270	0,85	0,86
		0,83
		0,74
		0,67
ATCC 36931	0,85	-
C. THROMBOIDES		
ATCC 12587	0,85	0,86
		0,83
ATCC 32194	0,85	-

III. Observations pathologiques

Les individus de *Acyrthosiphon pisum* sont également sensibles à *E. virulenta* et à *C. thromboides* (Tableau 6). Les concentrations létales 50 (CL 50) de *E. virulenta* (21,4

conidies/mm^2) et de *C. thromboides* (15,5 conidies/mm^2) sont du même ordre de grandeur. Dans les deux cas, la mortalité débute dès la fin du séjour des pucerons en atmosphère saturée, c'est-à-dire 29h 20' après le début de l'exposition aux conidies. Le développement du champignon a lieu post-mortem, il est limité à la tête et au thorax, l'abdomen prenant un aspect ratatiné. La présence de toxine a été démontrée chez *E. virulenta* (CLAYDON, 1978; CLAYDON & GROVE, 1978);un tel comportement in vivo du champignon est certainement dépendant de l'action de ces toxines. Il n'existe pas de rhizoïdes attachant les pucerons à la plante-hôte, ni de cystides sur les cadavres sporulant, contrairement à ce qu'affirment HALL & DUNN dans la description originale.

Ces résultats corroborent les observations de REMAUDIERE et al. (1976) qui ont récemment remis en question la pathogénicité de *E. virulenta*. En effet, la rareté de son isolement dans la nature (une dizaine de fois en une dizaine d'années de prospection), le manque de spécificité (*E. virulenta* a été isolé d'Homoptères, Diptères et Lépidoptères) et le faible envahissement mycélien du cadavre (alors que *E. virulenta* ne présente aucune exigence nutritionnelle particulière) laissent supposer que *E. virulenta* a une existence saprophytique du type *Conidiobolus* avec un comportement pathogène occasionnel ou opportuniste.

TABLEAU 6. Concentration létale 50 (CL 50) d'une souche de *Entomophthora virulenta* et d'une souche de *Conidiobolus thromboides* vis-à-vis de *Acyrthosiphon pisum*.

SOUCHES	CL 50 (a)	LIM.INT.CONF. (b)	χ^2 (c)	D.D.L. (d)	PENTE (e)	E.TYPE (f)
E.VIRULENTA (ATCC 36931)	21,4	16,2-28,5	29,6	18	1,61	0,25
C.THROMBOIDES (ATCC 12587)	15,5	11,3-19,7	25,3	18	1,90	0,27

(a) CL 50 exprimée en conidies/mm^2
(b) lim.int.conf.:limites de l'intervalle de confiance avec une probabilité de 95 %
(c) au point 5 %, χ^2 = 28,9 avec 18 degrés de liberté
(d) d.d.l.: degrés de liberté
(e) pente: pente de la droite de regression
(f) e.type: écart-type

CONCLUSION

La morphologie (conidies primaires et zygospores), la croissance, la biochimie (composition en acides gras des lipides neutres et polaires et profils électrophorétiques) et la pathologie de *E. virulenta* et *C. thromboides* sont identiques. Les éléments de ressemblance sont suffisamment nombreux pour affirmer que *E. virulenta* et *C. thromboides* sont conspécifiques. Sur la base de l'examen des souches authentiques dites "type" de ces deux espèces trouvées en parfaite correspondance avec les descriptions originales dont les illustrations sont désignées comme lectotypes, la synonymie de *C. thromboides* s'établit donc comme suit:

Conidiobolus thromboides DRECHSLER 1953
J. Wash. Acad. Sci., *43*, 29-43
= *Entomophthora virulenta* HALL & DUNN 1957 syn. nov.
≡ *Culicicola virulenta* (HALL & DUNN) BATKO 1964

Types de *C. thromboides*:
Lectotype:figure 2 de la description de DRECHSLER (1953) désigné par KING (1977);néotype:exsiccata contenant des conidies et spores provenant de cultures de la souche ATCC 12587 et de la souche ATCC 14270 déposés à l'herbier du Laboratoire de Cryptogamie du Muséum d'Histoire naturelle de Paris (PC).

Comme dans le cas de la reconsidération taxonomique de *Entomophthora obscura* HALL & DUNN (REMAUDIERE et al., 1979), nos résultats confirment l'intérêt de compléter la caractérisation morphologique d'une espèce de *Conidiobolus* ou de *Entomophthora* par une étude biochimique et pathologique. Le présent travail confirme que certaines espèces d'*Entomophthora* appartiennent au genre *Conidiobolus* et montre la nécessité d'une révision taxonomique de ce groupe fongique. Nos résultats montrent que 8 critères peuvent être au moins utilisés dans la taxonomie des Entomophthorales:(1) forme et taille des conidies primaires (2) forme et taille des zygospores (3) forme et taille des conidies secondaires (4) nombre de noyaux des conidies (5) exigences nutritionnelles (6) composition en acides gras des lipides neutres et polaires (7) profils électrophorétiques d'isoenzymes (8) comportement pathogène.

REFERENCES

BATKO, A. 1964. Some new combinations in the fungus family *Entomophthoraceae* (Phycomycètes). Bull. Acad. Sci. Polon. Sci., Ser. Sci. Biol., 12, 403-406.

CLAYDON, N. 1978. Insecticidal secondary metabolites from entomogenous fungi: *Entomophthora virulenta*. J. Invert. Pathol., 32 (sous presse).

CLAYDON, N.& J.F. GROVE. 1978. Metabolic products of *Entomophthora virulenta*. J.C.S. Perkins, I, 2, 171-173.

COUCH, J.N. 1939. A new *Conidiobolus* with sexual reproduction. Am. J. Bot., 26, 119-130.

DRECHSLER, C. 1953. Three new species of *Conidiobolus* isolated from leaf mold. J. Wash. Acad. Sci., 43, 29-43.

GUSTAFSSON, M. 1965. On species of the genus *Entomophthora* FRES. in Sweden. I. Classification and distribution. Landbrukoshögskolans Annal, 31, 103-212.

HALL, I.M. & P.H. DUNN. 1957. Entomophthoraceous fungi parasitic on the spotted alfalfa aphid. Hilgardia, 27, 159-181.

HARTMANN, G.C. & S.S. WASTI. 1976. Mycosis of the gypsy moth *Porthetria dispar* (L.) by *Entomophthora virulenta* HALL & DUNN with notes on its mammalian safety. Entomophaga, 21, 377-382.

HUMBER, R.A., R.S. SOPER, N. WILDING & G. REMAUDIERE. 1977. The identification of certain widely studied strains of *Entomophthora* pathogenic for aphids. Mycotaxon, 5, 307-310.

KING, D.S. 1976a. Systematics of *Conidiobolus* (Entomophthorales) using numerical taxonomy. I. Biology and cluster analysis. Can. J. Bot., 54, 45-56.

KING, D.S. 1976b. Systematics of *Conidiobolus* (Entomophthorales) using numerical taxonomy. II. Taxonomic considerations. Can. J. Bot., 54, 1285-1296.

KING, D.S. 1976c. Strain variation in *Conidiobolus*. Proceedings 1st Int. Coll. Invertebrate Pathology, Kingston, 277-281.

KING, D.S. 1977. Systematics of *Conidiobolus* (Entomophthorales) using numerical taxonomy. III. Descriptions of recognized species. Canad. J. Bot., 55, 718-729.

KING, D.S., E. LAHN & S.C. JONG. 1976. *Conidiobolus thromboides* isolated in Maryland. Mycologia, 68, 939-942.

LATGE, J.P. 1975a. Croissance et sporulation de six espèces d'Entomophthorales. I. Influence de diverses sources de carbone. Entomophaga, 20, 201-207.

LATGE, J.P. 1975b. Croissance et sporulation de six espèces d'Entomophthorales. II. Influence de diverses sources d'azote. Mycopathologia, 57, 53-57.

LATGE, J.P. 1976. Etude morphologique et cytologique de la formation de spores durables chez une espèce d'Entomophthorale. C.R. Acad. Sci. Paris, 282D, 605-608.

LATGE, J.P. & C. DE BIEVRE. 1980. Lipid composition of *Entomophthora obscura* HALL & DUNN. J. Gen. Microbiol. (sous presse).

LU, B.C. 1967. The course of meiosis and centriole behaviour during the ascus development of the Ascomycete *Gelasinospora calospora*. Chromosoma, 22, 210-226.

PAPIEROK, B. & N. WILDING. 1979. Mise en évidence d'une différence de sensibilité entre 2 clones du Puceron du Pois, *Acyrthosiphon pisum* HARR. (Homoptères *Aphididae*), exposés à 2 souches du champignon Phycomycète:*Entomophthora obscura* HALL & DUNN. C.R. Acad. Sci. Paris, 288D, 93-95.

PAPIEROK, B. & N. WILDING. 1980. Etude du comportement de plusieurs souches de *Entomophthora obscura* HALL & DUNN (Phycomycète *Entomophthoraceae*) vis-à-vis des pucerons *Acyrthosiphon pisum* HARR. et *Sitobion avenae*

F. (Homoptères *Aphididae*). Entomophaga (soumis pour publication).
REMAUDIERE, G., J.P. LATGE, B. PAPIEROK & J. COREMANS-PELSENEER. 1976. Sur le pouvoir pathogène de quatre espèces d'Entomophthorales occasionnellement isolées d'Aphides en France. C.R. Acad. Sci. Paris, 283D, 1065-1068.
REMAUDIERE, G. J.P. LATGE & B. PAPIEROK. 1979. Reconsidération taxonomique de *Entomophthora obscura* HALL & DUNN. Ann. Microbiol. (Inst. Pasteur), 130A, 151-162.
SHAW, C.R. & R. PRASAD. 1970. Starch gel electrophoresis of enzymes: A compilation of recipes. Biochem. Genet., 4, 297-320.
SOPER, R.S. & T.A. BRYAN. 1974. Mammalian safety of the aphid attacking fungus *Entomophthora thaxteriana*. Environ. Entomol., 3, 364-367.
SRINIVASAN, M.C. & M.J. THIRUMALACHAR. 1962. Studies on species of *Conidiobolus* from India. II. Sydowia Ann. Mycol., 16, 60-66.
TYRRELL, D. 1967. The fatty acid composition of 17 *Entomophthora* isolates. Can. J. Microbiol., 13, 755-760.
TYRRELL, D. 1971. The fatty acid composition of some *Entomophthoraceae*. III. Can. J. Microbiol., 17, 1115-1118.
TYRRELL, D. & J. WEATHERSTON. 1976. The fatty acid composition of some *Entomophthoraceae*. IV. The occurence of branched chain fatty acids in *Conidiobolus* species. Can. J. Microbiol., 22, 1058-1060.

MYCOTAXON

Vol. XI, No. 1, pp. 269-321 April-June 1980

REVISION SYSTEMATIQUE DE ENTOMOPHTHORA APHIDIS HOFFM. IN FRES. DESCRIPTION DE DEUX NOUVEAUX PATHOGENES D'APHIDES

G. REMAUDIERE

Unité de Lutte Biologique contre les Insectes
Institut Pasteur
25, rue du Dr Roux 75724 Paris Cedex 15, France

G.L. HENNEBERT

Laboratoire de Mycologie systématique et appliquée
Université catholique de Louvain, Place Croix du Sud, 3
B1348 Louvain-la-Neuve, Belgique

A B S T R A C T

Originally attributed to an aphid pathogen on *Cornus*, the name *Entomophthora aphidis* Hoffm. in Fres. was erroneously applied to the most common pathogen encountered in aphid populations. The various conidial forms including capilloconidia are fully described from new material collected in the Alps ex *Aconcia* on *Cornus*. The species, designated as *Zoophthora aphidis* (Hoffm. in Fres.) Batko, is closely allied to *Z. radicans* (Bref.) Batko from which it differs mainly by having broader capilloconidia and much larger resting spores.

The subgeneric divisions introduced by Batko in *Zoophthora* Batko are discussed. The application of this genus name is restricted to the species giving capilloconidia. The subgenus *Pandora* established by Batko, with *aphidis* Hoffm. in Fres. as type species, becomes synonymous with *Zoophthora*. The other species classified in the subgenera *Erynia*, *Pandora* and *Furia* are brought together in *Erynia* Nowak. which is re-established to the genus level.

The species *Entomophthora ferruginea* Phill. in Hought. & Phill. and *Entomophthora exitialis* Hall & Dunn are considered as *nomina confusa*.

Erynia neoaphidis sp. nov. is described;"*E. aphidis*" sensu Nowak. or sensu Thaxter is identical to this species.

Erynia nouryi sp. nov. is described;"*E. aphidis*" sensu Petch 1939 and "*E. exitialis*" sensu Gustafsson are identical to this species.

SOMMAIRE

Dans un récent article, Remaudière et al. (1978) considèrent que trois entités spécifiques sont apparemment confondues sous le même taxon *Entomophthora aphidis* Hoffm. in Fres.:

- *Entomophthora aphidis* Hoffm. in Fres. (1858), espèce à spores durables volumineuses, originellement décrite comme pathogène d'un puceron vivant sur *Cornus sanguinea*,
- *"Entomophthora aphidis"* sensu Nowak. (1883) (= sensu Thaxter 1888), espèce la plus commune dans les populations d'un très grand nombre d'Aphides qui ne forme probablement jamais de spores durables chez les pucerons,
- *"Entomophthora aphidis"* sensu Grobler et al. (1962) à spores durables plus petites que celles de *Entomophthora aphidis* Hoffm. in Fres., espèce seulement connue comme pathogène du puceron *Schizolachnus piniradiatae* Davidson sur *Pinus resinosa*.

L'étude des données historiques fournies par la littérature, celle des syntypes de *Entomophthora aphidis* Hoffm. in Fres. et la redécouverte de l'espèce sous toutes ses formes nous conduisent à en donner une description complète et à montrer que son nom a été appliqué par erreur à plusieurs autres espèces dont nous pouvons maintenant préciser le statut.

---

1 HISTORIQUE

Dans cette partie, nous rappelons les principaux travaux consacrés à *Entomophthora aphidis* ainsi que ceux traitant de *Entomophthora ferruginea* Phill. in Hought. & Phill. (1886) et de *Entomophthora exitialis* Hall & Dunn (1957), espèces qui ont été comparées à *Entomophthora aphidis* par plusieurs auteurs.

A. DESCRIPTION ORIGINALE ET APPLICATIONS SUCCESSIVES DU NOM *ENTOMOPHTHORA APHIDIS*

a) *LA DESCRIPTION ORIGINALE DE HOFFMANN IN FRESENIUS ET L'EXAMEN DES SYNTYPES*

D'après la description originale de Fresenius (1858), *Entomophthora aphidis* Hoffm. in Fres. a été découvert en automne à Giessen par H. Hoffmann, chez un puceron "vraisemblablement *Aphis cerni*" vivant sur les feuilles de *Cornus sanguinea*:

Les petits spécimens aptères de cette espèce d'insecte sont remplis de grosses spores sphériques, tandis qu'un grand ailé présente du mycélium dans la cavité abdominale. Fresenius précise que "le mycélium apparaît pauvrement développé et formé de filaments bruns, courts, branchus, plus ou moins torsadés, qui produisent les spores à leur extrémité ou sur de très courtes ramifications latérales. Ces dernières (les spores durables) demeurent attachées aux filaments résiduels si bien que leur séparation ne réussit pas aussi aisément que chez les autres espèces" (traduit de l'allemand). La dimension des spores varie de 1/30 à 1/23 mm (soit 33,3 à 43,5 µm), le plus souvent 1/27 à 1/25 mm (soit 37 à 40 µm). Les figures originales 61 à 64 (Fig. 1) montrent que les spores sont lisses. La forme conidienne n'est pas mentionnée.

Le matériel authentique récolté par Hoffmann en 1857 se trouve sous le N° 768 dans l'édition II du Rabenhorst: Klotzschii herbarium vivum mycologicum (1858) accompagné de l'étiquette suivante:

Rabenhorst, Herb. mycologicum. Ed. II.
768. Entomophthora Aphidis H. Hoffm.
Cf. Fresenius in Abhandl. d. Senckenb. naturf. Ges. Bd. II.
1858. p. 208. T. IX. F. 59—67.
In foliis Corni sanguineae pr. Giesen 1857 leg. Hoffmann.

Les exsiccata conservés au Muséum de Paris (PC), à l'Institut botanique de Pavie (PAV) et au Royal Botanic Gardens de Kew (K) ont été examinés; ils comportent une feuille de *Cornus sanguinea* avec quelques cadavres de sexués

d'*Anoecia* sp. de couleur noire, remplis de spores et parfois des ailés sexupares du même puceron.

Le Royal Botanical Garden d'Edinburgh (E) nous a communiqué un exsiccatum de la collection Siemaszko récolté en Pologne en octobre 1926 sur feuilles de *Cornus sanguinea*: le puceron hôte est également une espèce du genre *Anoecia* et son pathogène est semblable à celui du matériel d'Hoffmann.

Les mensurations des spores extraites de ces échantillons puis montées dans le bleu trypan lactophénol sont données dans le tableau 1.

Les valeurs moyennes obtenues varient de 36,4 à 40,1 µm et concordent parfaitement avec les dimensions les plus fréquentes mentionnées dans la description originale (37 à 40 µm); les valeurs extrêmes (27 à 48 µm) encadrent bien celles publiées par Fresenius (33,3 à 43,5 µm).

L'examen du matériel authentique permet d'apporter les précisions suivantes: les spores durables présentent une épispore brune, amorphe qui se dilacère lorsqu'on veut les séparer, elles apparaissent alors hyalines avec une paroi épaisse et présentent souvent des fragments d'épispore. La difficulté rencontrée par Fresenius pour isoler les spores paraît davantage résulter de la cohésion des épispores que de l'attachement des spores au mycélium résiduel, les hyphes étant peu nombreux dans les cadavres remplis de spores mûres (Fig. 21).

Les exsiccata du Rabenhorst Klotzschii herbarium vivum mycologicum ed. II n. 768 sont des syntypes de l'espèce *Entomophthora aphidis* Hoffm. in Fres. Les syntypes de Pavie et de Kew sont très pauvres (2 pucerons avec spores durables); celui de Paris, qui renferme 5 cadavres pleins de spores, est désigné ici comme lectotype de *Entomophthora aphidis* Hoffm. in Fres.

Le genre *Entomophthora* Fresenius 1856 a été créé explicitement par Fresenius pour remplacer *Empusa* Cohn 1855 qui était préoccupé par *Empusa* Lindney 1824 (*Orchidaceae*); il conserve de ce fait, en tant que *nomen novum*, l'espèce type de *Empusa* Cohn, *Empusa muscae* Cohn, renommée *Entomophthora muscae* (Cohn) Fres. 1856. Toute lectotypification postérieure à 1856 ne confirmant pas *Empusa muscae* Cohn et qui désigne l'une des deux autres espèces originales de *Entomophthora* Fres. 1856, *E. grylli* Fres. 1856 ou *E. sphaerosperma* Fres. 1856 est erronée parce que contraire à l'article 7 du code (code international de nomenclature botanique, Stafleu 1972).

TABLEAU 1

Mesures (en µm) du diamètre des spores durables de *Entomophthora aphidis* sur matériel authentique de l'herbier Rabenhorst (Paris, Pavie et Kew) et sur matériel polonais de Siemaszko (n = nombre de spores mesurées)

ORIGINE	INDIVIDU		n	min	MOY	max
Rabenhorst	I	CP	50	33	40,I	48
	2	CP	50	33	37,6	4I
	3	PAV	7I	30	36,5	44
	4	K	28	3I	37,7	4I
Siemaszko	I	E	50	33	39,9	46
	2	E	50	27	36,4	42
	3	E	50	30	36,7	44

C'est le cas de la typification de von Arx (1970) qui désigne à tort *E. sphaerosperma* Fres. comme espèce type de *Entomophthora* Fres.

En 1858, *Entomophthora* Fres. est l'unique genre valide de la famille des *Entomophthoraceae* Nowak. 1883 (ut *Entomophthoreae*) *Pamietn. Wydz. Akad. Umiej. w. Krakôw.* 8: 154 (= *Entomophthoraceae* Warning 1884). En plus des 3 espèces originales, ce genre comprend *Entomophthora aphidis* Fres. ainsi que trois autres espèces: *Entomophthora tenthredinis* Fres., *Entomophthora tipulae* Fres. et *Entomophthora culicis* (A. Braun) Fres.

b) *LA NOUVELLE COMBINAISON DE COHN*

Bien qu'il considère que les conidies et les spores durables représentent deux formes du cycle des champignons qu'il étudie, Cohn (1870) - qui ne reconnaît pas la valeur du genre *Entomophthora* Fresenius - restreint l'application de son genre *Empusa* aux espèces dont on connaît seulement la forme conidienne et crée le genre *Tarichium* pour celles qui ne sont connues que par la forme spores durables, sur la base de *T. megaspermum* Cohn 1870 (espèce type). Dans ce dernier genre, il inclut deux autres espèces pour lesquelles il précise les nouvelles combinaisons suivantes: *Tarichium aphidis* (Hoffm. in Fres.) Cohn et *Tarichium sphaerospermum* (Fres.) Cohn.

Schneider (1873) utilise les mêmes combinaisons.

c) *LES OBSERVATIONS DE SOROKIN*

L'extrait de l'article de Sorokin (1880) publié par Batalin (1881) signale à propos de *Entomophthora aphidis*:

"en dehors des spores déjà connues et habituellement allongées qui se forment à la surface du corps des insectes" (les conidies) "il se développe aussi à l'intérieur du corps des *Aphis* et à partir des mêmes filaments d'*Entomophthora*, des spores durables..." (traduit de l'allemand). Cette affirmation est surprenante parce qu'inverse de la réalité: en effet, en 1880, la seule forme connue pour cette espèce est la spore durable décrite par Fresenius, puis mentionnée par Cohn en 1870 et par Schneider 1873.

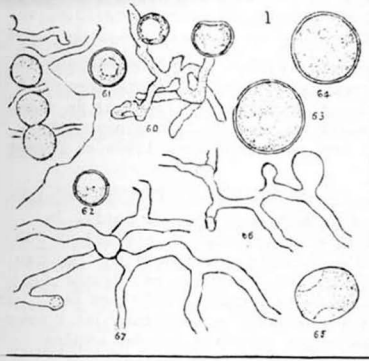
Dans le même extrait, Batalin rapporte que les spores durables sont décrites comme "rondes et grandes, à membrane stratifiée de couleur brune et couverte de reliefs (Erhöhungen)" (traduit de l'allemand); il est en outre précisé que les "spores habituelles" (c'est-à-dire les conidies) donnent des "sporidies secondaires de forme ronde". Aucune indication n'est fournie sur l'espèce de puceron attaquée, ni sur sa plante hôte.

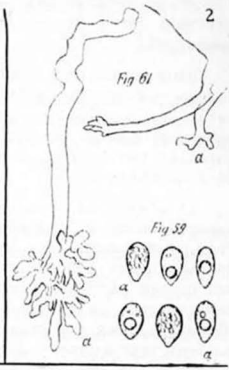
La présence de reliefs sur les spores brunes de Sorokin peut laisser penser que les spores décrites par Fresenius avaient perdu leur épispore, mais il semble plutôt que ces auteurs traitent d'espèces distinctes, les conidies secondaires "rondes" de Sorokin ne pouvant pas être celles de *Entomophthora aphidis*.

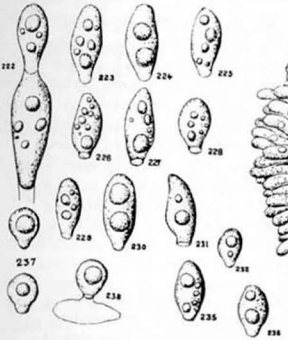
d) *LES OBSERVATIONS DE WINTER*

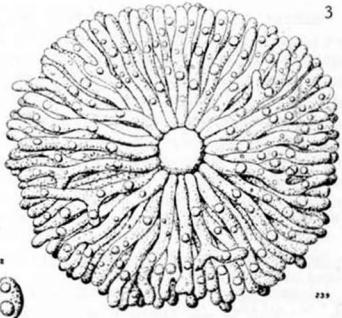
Winter (1881) retrouve une mycose sur le puceron du *Cornus sanguinea* en automne 1880: les feuilles étaient densément couvertes de pucerons; certains, de couleur brun clair avec l'abdomen fortement renflé, étaient remarquables par le duvet blanc (conidiophores + conidies) qui les recouvrait tandis que sur les mêmes feuilles d'autres pucerons, momifiés, ridés, renfermaient des spores durables correspondant à celles décrites par Hoffmann in Fresenius pour *Entomophthora aphidis*. Winter en conclut que les pucerons couverts de duvet blanchâtre hébergent une autre forme de la même espèce fongique; il décrit ainsi les conidies présentes sur les spécimens blanchâtres: "spores elliptiques, en forme de fuseau, souvent dissymétriques, rarement un peu courbées, le plus souvent avec une petite pointe, incolores; longueur 26-30 µm, épaisseur 10-16 µm" (traduit de l'allemand).

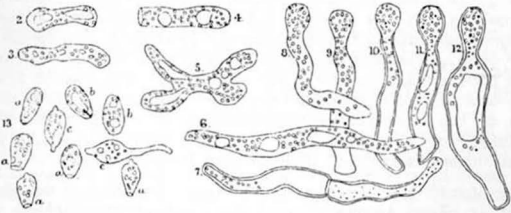
Fig. 1-4. Reproduction partielle des figures originales 1, de Fresenius 1858, *Entomophthora aphidis* Hoffm. in Fres.; 2, de Nowakowski 1883, "*Entomophthora aphidis*" sensu Nowak.; 3, de Thaxter 1888, "*Entomophthora aphidis*" sensu Thaxter; 4, de Houghton & Phillips 1886, *Entomophthora ferruginea* Phill. in Hought. & Phill.


1
61
60
64
63
62
66
67
65


2
Fig 61
a
Fig 59
a
a
a


222
223
224
225
226
227
228
229
230
231
232
237
238
235
236


3
239


4
2
3
4
5
6
7
8
9
10
11
12
13
a
b
c
d
e
f
g
h
i
k
l
m
n
o
p
q
r
s
t
u
v
x
y
z
α

Winter ne précise pas la position (basale ou apicale) de la petite pointe; il ne signale pas la présence de conidies secondaires.

Dans un travail postérieur, Winter (1884) décrit aussi les spores durables: "terminales ou sur de courtes branches latérales du mycélium qui est brunâtre..., 33-43 µm de diamètre, brunâtres lorsqu'elles sont jeunes, incolores lorsqu'elles sont mûres, avec une paroi épaisse, lisse et formée de 2 couches."

Il n'est pas douteux que les spores décrites par Winter appartiennent à l'espèce *Entomophthora aphidis* Hoffm. in Fres. Cet auteur cite en effet l'exsiccatum original N° 768 du Rabenhorst auquel il n'a sûrement pas manqué de comparer son propre matériel. Les conidies observées par Winter sur des cadavres de la même espèce de puceron fixés sur les mêmes feuilles que ceux contenant les spores durables correspondent probablement à une autre forme de la même espèce fongique, malgré l'absence de preuve expérimentale.

Winter (1884) n'accepte pas les genres *Empusa* Cohn (préoccupé) et *Tarichium* Cohn 1870 (créé pour les espèces dont seules les spores durables sont connues). Il place toutes les espèces d'Entomophthorées dans le genre *Entomophthora* Fres. et distingue, à l'intérieur de ce genre, 3 groupes: (A) celui dont seules les "basidiospores" (les conidies) sont connues à l'époque, (B) celui dont seules les spores durables sont connues à l'époque, (C) dont les espèces sont complètement connues (conidies + spores durables); c'est dans ce dernier groupe qu'il place *Entomophthora aphidis* Hoffm. in Fres. et *E. sphaerosperma* Fres.

e) *LES OBSERVATIONS DE NOWAKOWSKI*

Nowakowski (1883) applique le nom de *Entomophthora aphidis* Hoffm. in Fres. à un champignon qu'il rencontre communément sur différentes espèces d'Aphides. Les précisions qu'il donne sur les pucerons attaqués permettent de reconnaître les six espèces suivantes: *Macrosiphum rosae* L., *Brachycaudus cardui L.*, *Brevicoryne brassicae* L., *Aphis fabae* Scop., *Myzus persicae* Sulz. et *Aphis verbasci* Schrank, aucun puceron des *Cornus* n'est mentionné. Nowakowski précise qu'il n'a pas vu les spores durables néanmoins, et en l'absence de tout élément de comparaison, il n'hésite pas à considérer qu'il a affaire à l'espèce dont le mycélium et les spores durables ont été décrits par Fresenius.

Il décrit les conidies comme étant ovoïdes et de même aspect et mêmes dimensions que celles de *Entomophthora*

ovispora Nowak. 1877 (c'est-à-dire avec une papille basale et mesurant 22,8-28,5 x 14,2 µm). Les hôtes portent des "paraphyses" (cystides) et sont fixés par des rhizoïdes (voir les figures 59 et 61 de cet auteur: Fig. 2).

On remarquera que les conidies de "*Entomophthora aphidis*" sensu Nowakowski ne présentent pas la petite pointe signalée par Winter, ni en position apicale, ni en position basale.

f) *LES OBSERVATIONS DE THAXTER*

Thaxter, en 1888, applique la combinaison nouvelle *Empusa aphidis* Hoffm. in Fres. à l'une des Empusées les plus communes aux Etats-Unis qu'il rencontre sur de très nombreux genres d'Aphides dont il ne précise pas les noms. Malgré l'étude d'un nombre considérable de spécimens infectés par ce champignon, Thaxter n'a jamais trouvé les spores durables; il reconnaît que, dans ces conditions, il est impossible d'affirmer que la description de Fresenius se rapporte réellement à cette espèce.

Les conidies primaires (figures 223-236 de cet auteur: Fig. 3) sont ovoïdes à elliptiques ou subfusiformes, communément asymétriques et très variables, avec une papille basale; mensurations: moyenne 25 x 12 µm, maximum 40 x 16 µm. Thaxter ne doute pas de l'identité de cette forme conidienne avec, d'une part celles décrites pour la première fois par Winter 26-30 x 10-16 µm et d'autre part, celles décrites et figurées par Nowakowski.

L'identité des conidies et, par suite, celle des espèces considérées par Nowakowski et par Thaxter n'est pas contestable; en revanche nous devons reconnaître à nouveau que les conidies de Nowakowski et Thaxter diffèrent de celles de Winter par l'absence de la "petite pointe". "*Entomophthora aphidis*" sensu Nowakowski et sensu Thaxter représentent donc une même espèce, distincte de *E. aphidis* Hoffm. in Fres.

Thaxter décrit en outre une structure particulière caractérisée par "une cellule centrale", très réfringente et entourée d'une masse d'hyphes rayonnants. La figure 239 de cet auteur (Fig. 3) permet d'estimer le diamètre de cette cellule centrale à 40 µm. Brobyn & Wilding (1977) ont démontré la nature et la fonction de cette structure: la "cellule centrale" est en réalité la cellule mère d'une cystide qui va percer la cuticule de l'hôte tandis que les hyphes qui convergent vers elle, vont profiter de cette perforation pour sortir et devenir conidiophores.

g) *LES OBSERVATIONS DE PETCH*

Petch (1939) applique le nom de *Entomophthora aphidis* Hoffm. in Fres. à un pathogène de *Pemphigus* trouvé sur racine de *Lactuca*; l'abdomen des pucerons était transformé en une masse blanche et fragile de spores durables sphériques, lisses, hyalines à paroi très épaisse (diamètre 23 à 32 µm); un unique spécimen portait des conidies ayant l'aspect de celles de *Entomophthora aphidis* mais mesurant seulement 12-18 x 9-12 µm. Pour expliquer la discordance existant entre les mensurations de ses spores (23-32 µm) et celles de la description originale de l'espèce (33-43 µm), Petch considère les "cellules centrales" figurées par Thaxter (1888) dont le diamètre, estimé à 40 µm, est comparable à celui des spores de Fresenius; s'appuyant sur la remarque de Fresenius concernant la difficulté anormale qu'il rencontre pour séparer les spores durables du mycélium chez *Entomophthora aphidis*, Petch pense que Fresenius a pu, par erreur, interpréter ces "cellules centrales" comme étant des spores durables. Le simple examen des figures 59 et 60 de Fresenius (Fig. 3) et celui des syntypes (Fig. 15) obligent à rejeter cette interprétation et dès lors à reconnaître que "*Entomophthora aphidis*" sensu Petch est une espèce distincte de *Entomophthora aphidis* Hoffm. in Fres. et, probablement aussi, différente de "*Entomophthora aphidis*" sensu Nowak. ou sensu Thaxter (en raison des dimensions très faibles des conidies et de la présence de spores durables).

h) *LES OBSERVATIONS DE KRENNER*

Krenner (1961), après une critique sévère et confuse de tous les travaux antérieurs sur *Entomophthora aphidis*, présente un fatras d'observations sur ce champignon qu'il a rencontré sur *Acyrthosiphon pisum* Harris sur luzerne. En conclusion, cet auteur donne une liste hautement fantaisiste des synonymes nouveaux de "*Entomophthora aphidis* Hoffm. emend. Krenner"; cette liste confond des espèces aussi différentes que *Empusa fresenii* Nowakowski, *Entomophthora obscura* Hall & Dunn (= *Entomophthora thaxteriana* Petch = "*Empusa planchoniana* Cornu?" de Thaxter) (Remaudière et al. 1979), *Empusa lageniformis* Thaxter et *Empusa occidentalis* Thaxter !

i) *LES OBSERVATIONS DE GROBLER ET AL.*

Grobler et al. (1962) appliquent le nom de *Entomophthora aphidis* Hoffm. in Fres. à l'un des pathogènes qu'ils observent communément sur *Schizolachnus piniradiatae* Davidson et qu'ils caractérisent par ses conidies subcylindriques mesurant (16,5)25,5(38,5) x (7)12(18) µm et ses spores durables

de (29)34(43) µm (*a*) à épispore brun rougeâtre, réticulée et facilement détachable. Ultérieurement Tyrrell et al. (1975) montrent chez cette espèce l'existence de capilloconidies en forme de croissant (33 x 9 µm) qui naissent au sommet d'un tube capillaire émis par les conidies primaires.

Cette espèce particulière est aujourd'hui décrite sous le nom de *Entomophthora canadensis* MacLeod, Tyrrell & Soper (1979).

j) *LES OBSERVATIONS DE GUSTAFSSON*

Gustafsson (1965) décrit ainsi le matériel suédois qu'il rapporte à *Entomophthora aphidis*: conidies sur insectes, (18)21(25) x (7)11(14) µm, conidies obtenues de 5 cultures, 29x13, 29x15, 30x19, 32x17 et 37x17 µm (moyennes de 100 mesures); ces conidies, illustrées par la figure 75 de l'auteur (Fig. 7), se rapportent clairement aux conidies de "*Entomophthora aphidis*" sensu Nowak. et sensu Thaxter.

Parmi les 62 récoltes faites par Gustafsson entre 1959 et 1963, une seule (sur *Aphis fabae* Scop.) comportait des spécimens contenant des jeunes spores durables hyalines à brunes, avec épispore à profil étroitement cannelé, mesurant (21)30(35) µm. Ces spores durables ne peuvent se rapporter à "*Entomophthora aphidis*" sensu Nowak. qui n'en a pas; elles ont un diamètre voisin de celui des spores de "*Entomophthora aphidis*" sensu Petch mais s'en distinguent par leur pigmentation et leur ornementation; selon nous, elles pourraient être rapportées à des jeunes spores de *Zoophthora erinacea* Ben Ze'ev & Kenneth.

k) *LA NOUVELLE COMBINAISON DE BATKO*

Batko (1964b) crée le nouveau genre *Zoophthora* avec, pour espèce type, *Z. radicans* (Bref.) Batko. Dans une publication ultérieure, Batko (1964d) établit de nouvelles combinaisons parmi lesquelles *Zoophthora aphidis* (Hoffm. in Fres.) Batko. Deux ans plus tard, Batko (1966b) divise son genre *Zoophthora* en 4 sous-genres dont le subg. *Pandora* Batko 1966 avec *Zoophthora* (*Pandora*) *aphidis* (Hoffm. in Fres.) Batko comme espèce type.

La diagnose du sous-genre *Pandora* (conidies ovales, ovoïdes..., du type subpapillata... légèrement asymétriques,)

(*a*) Lorsque la ou les valeurs centrales des mensurations sont soulignées, elles expriment la moyenne ou la fourchette des moyennes de 1 ou plusieurs échantillons; exemple: (13)15(18) ou (10)12-14(20) µm.

montre que Batko applique le nom spécifique *aphidis* Hoffm. in Fres. à "*Entomophthora aphidis*" sensu Nowak. et sensu Thaxter et non à *Entomophthora aphidis* Hoffm. in Fres. dont les conidies présentent, selon Winter, une "petite pointe".

B. DESCRIPTION ORIGINALE ET APPLICATIONS DU NOM *ENTOMOPHTHORA FERRUGINEA*

a) *LA DESCRIPTION ORIGINALE DE PHILLIPS*

E. ferruginea Phill. in Hought. & Phill. (1886) est un pathogène de *Aphis fabae* Scop. sur betterave découvert en Grande-Bretagne. La description originale est imprécise; l'auteur n'a pas rencontré les spores durables mais seulement les conidies qui sont elliptiques ou subovales; les dimensions ne sont pas précisées. Les figures 8 à 12 qui accompagnent la description montrent des conidiophores portant des conidies en formation et la figure 13 représente des conidies à base tronquée, d'aspect varié avec des tubes germinatifs (Fig. 4).

Phillips a examiné un spécimen authentique de *Entomophthora aphidis* Hoffm. sur *Aphis* de *Cornus sanguinea* communiqué par M.C. Cooke (sans doute s'agit-il d'un des exsiccata N° 768 de Rabenhorst, 1858). Phillips déclare que cette espèce est essentiellement différente de son matériel trouvé sur betterave. En revanche il considère que *E. ferruginea* est très proche de l'espèce qui attaque et tue la mouche domestique, "*Empusa*" *muscae* Cohn.

Selon Hawksworth (1974), le matériel de W. Phillips est conservé dans l'herbier du Royal Botanic Gardens de Kew; malheureusement aucune trace du matériel type de *E. ferruginea* n'a été retrouvée dans cet herbier (D.A. Reid, communication personnelle).

b) *INTERPRETATION DE THAXTER ET DE LAKON*

Malgré l'affirmation de Phillips selon laquelle *Entomophthora aphidis* et *Entomophthora ferruginea* sont deux espèces distinctes qu'il a effectivement comparées, Thaxter (1888), qui n'a pu consulter le matériel authentique de *Entomophthora aphidis*, estime que la description et les figures de *Entomophthora ferruginea* concordent avec celles de l'espèce à laquelle il applique le nom de *Empusa aphidis* (="*Entomophthora aphidis*" sensu Nowak.). En conséquence, il place *Entomophthora ferruginea* en synonymie de *Empusa aphidis* (Hoffm. in Fres.) Thaxter sur la base de sa ressemblance avec "*E. aphidis*" sensu Thaxter. Il est suivi par Lakon (1919).

c) *INTERPRETATION DE PETCH, DE GUSTAFSSON ET DE MACLEOD ET AL.*

Petch (1937) constate que certaines figures originales de *Entomophthora ferruginea* montrent des conidies étroitement campanulées, parfois avec une pointe apicale. Ayant recherché, comme nous sans succès, les spécimens types, Petch considère *Entomophthora ferruginea* comme un synonyme nouveau de *Entomophthora planchoniana* Cornu 1873.

Gustafsson (1965) reprenant l'interprétation de Petch écrit que la description assez incomplète de Phillips indique indubitablement cette synonymie et non celle établie erronément par Thaxter avec *Entomophthora aphidis*.

MacLeod et al. (1976) adoptent une position moins catégorique et admettent que *Entomophthora ferruginea* est "probablement un synonyme de *Entomophthora planchoniana* plutôt que de *Entomophthora aphidis*".

d) *POSITION DE BATKO*

Batko (1966b), sans toutefois justifier sa position, accepte *Entomophthora ferruginea* qu'il considère comme une espèce voisine mais distincte de *Entomophthora aphidis* Hoffm. in Fres.; il place ainsi *E. ferruginea* dans son nouveau sous-genre *Zoophthora* (subg. *Pandora*) dont *E. aphidis* est l'espèce type.

C. DESCRIPTION ORIGINALE ET APPLICATION DU NOM *ENTOMOPHTHORA EXITIALIS*

a) *LA DESCRIPTION ORIGINALE DE HALL & DUNN*

Entomophthora exitialis Hall & Dunn (1957) est décrit de Californie comme l'un des 5 pathogènes trouvés dans les populations de *Therioaphis trifolii* Monell (= *T. maculata* Buckton) sur luzerne. L'espèce est décrite comme caractérisée par des conidies primaires ovoïdes à elliptiques, arrondies aux extrémités mesurant (17)20(23) x (9)11(12) µm, des conidies secondaires semblables aux primaires et des spores durables de (24)27(32) µm de diamètre, à épispore lisse. Selon les auteurs, le champignon présente une légère ressemblance avec *Entomophthora aphidis* ("*Entomophthora aphidis*" sensu Nowak. et sensu Thaxter, la seule interprétation qu'ils connaissent).

Alors que le texte concerne des conidies primaires dont le rapport Longueur moyenne/Diamètre moyen (Lm/Dm) est de 1,8, les photographies (figures 8 et 9 de Hall & Dunn: Fig.

5-6) montrent des conidies dont les rapports L/D varient de 2,3 à 3,7 (L/D moyen pour 9 conidies mesurables = 3,0). L'aspect de ces conidies, subcylindriques, avec une papille basale subtriangulaire surmontée d'un épaulement caractéristique est semblable à celui des conidies de *Zoophthora radicans* (Bref.) Batko et ne correspond pas du tout à celui des conidies de "*Entomophthora aphidis*" sensu Nowak.

Travaillant sur une culture de *Entomophthora exitialis* Hall & Dunn, reçue comme authentique de I.M. Hall (Dept. of Biol. Control, Univ. of California, Riverside), Krejzova (1973) en publie des photographies (ses figures 6 à 8) montrant des conidies allongées, subcylindriques comparables à celles figurées par Hall & Dunn.

En l'absence d'exsiccatum type (Hall, communication personnelle), il n'est pas possible d'expliquer la divergence constatée entre le texte de la description originale et l'illustration qui l'accompagne.

b) *APPLICATION DU NOM* E. EXITIALIS *PAR GUSTAFSSON*

Nous avons rappelé que Gustafsson (1965) a trouvé une fois sur *Aphis fabae* des spores durables hyalines à brunes avec épispore cannelée auxquelles il applique le nom de *Entomophthora aphidis* ("*Entomophthora aphidis*" sensu Nowak.) et nous avons montré que ces spores sont voisines quoique distinctes de celles de "*Entomophthora aphidis*" sensu Petch.

Dans la même publication, Gustafsson applique le nom d'*Entomophthora exitialis* Hall & Dunn à une autre espèce d'Entomophthorales trouvée, comme la précédente, sur *Aphis fabae* sur betterave; il considère son matériel probablement co-spécifique de celui décrit par Petch (1939) sous le nom d' "*Entomophthora aphidis*" dont les spores durables sont hyalines et de même diamètre (23-32 µm) que les siennes (23-39 µm) et dont les mensurations de conidies (12-18 x 9-12 µm) lui paraissent "mieux correspondre à *E. exitialis* qu'à *E. aphidis*".

Gustafsson distingue son "*Entomophthora exitialis*" de son "*Entomophthora aphidis*" (c'est-à-dire de "*Entomophthora aphidis*" sensu Nowak.) par la rareté des cystides; il reconnaît qu'il est impossible de séparer ces deux espèces au champ et que l'on risque également de les confondre lors de l'examen des préparations.

Nous considérons que "*E. exitialis*" sensu Gustafsson et "*E. aphidis*" sensu Petch sont co-spécifiques et différents de "*E. aphidis*" sensu Nowak.

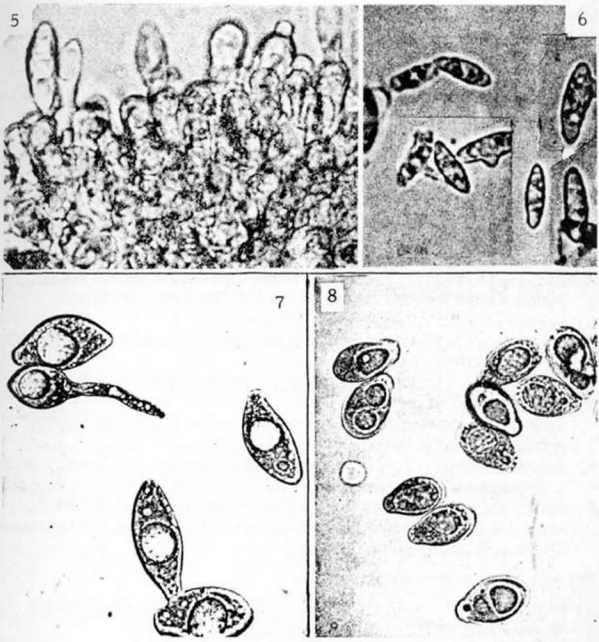


Fig. 5-8. Reproduction partielle des figures originales, 5-6, de Hall & Dunn 1957, conidiophores et conidies de *Entomophthora exitialis* Hall & Dunn; 7-8, de Gustafsson 1965, 7, conidies de *"Entomophthora aphidis"* sensu Nowak., 8, conidies de *"Entomophthora exitialis"* sensu Gustafsson.

On remarquera que les figures de *Entomophthora exitialis* publiées par Gustafsson (Fig. 8) présentent une certaine concordance avec le texte de la description originale de Hall & Dunn mais qu'elles ne correspondent pas aux photographies de conidies publiées par ces auteurs (Fig. 5-6) et par Krejzova (1973).

D. RECAPITULATION DES TAXONS IMPLIQUES

On peut résumer de la façon suivante la situation des différents taxons considérés dans les pages précédentes

(les taxons reconnus sont imprimés en capitales lors de leur première description).

Entomophthora aphidis

a) Fresenius (1858), *ENTOMOPHTHORA APHIDIS* HOFFM. IN FRES. 1858.
b) Cohn (1870), *Tarichium aphidis* (Hoffm. in Fres.) Cohn ≡ *E. aphidis* Hoffm. in Fres.
c) Sorokin (1880), douteux (présence de conidies, description insuffisante).
d) Winter (1881, 1884) = *Entomophthora aphidis* Hoffm. in Fres.
e) Nowakowski (1883) = "*ENTOMOPHTHORA APHIDIS*" SENSU NOWAK.
f) Thaxter (1888) = "*Entomophthora aphidis*" sensu Nowak.
g) Petch (1939) = "*ENTOMOPHTHORA APHIDIS*" SENSU PETCH.
h) Krenner (1961), mélange de 5 espèces.
i) Grobler et al. (1962) = *ENTOMOPHTHORA CANADENSIS* MACLEOD ET AL. 1979.
j) Gustafsson (1965), conidies = "*Entomophthora aphidis*" sensu Nowak.;
spores durables: douteux, voisin mais distinct de "*E. aphidis*" sensu Petch.
k) Batko (1964d), *Zoophthora aphidis* (Hoffm. in Fres.) Batko ≡ *Entomophthora aphidis* Hoffm. in Fres. 1858, espèce type désignée pour *Zoophthora* subg. *Pandora* Batko (1966b), mais la description du sous-genre s'applique à "*Entomophthora aphidis*" sensu Nowak.

Entomophthora ferruginea

a) Phillips in Houghton & Phillips (1886), *Entomophthora ferruginea* Phill. in Hought. & Phill.
b) Thaxter (1888), Lakon (1919) = "*Entomophthora aphidis*" sensu Nowak.
c) Petch (1937), Gustafsson (1965), MacLeod et al. (1976), synonymie *Entomophthora ferruginea* = *Entomophthora planchoniana* Cornu 1873.
d) Batko (1966b), *Zoophthora* (*Pandora*) *ferruginea* (Phill. in Hought. & Phill.) Batko 1966 ≡ *Entomophthora ferruginea* Phill. in Hought. & Phill.

Entomophthora exitialis

a) Hall & Dunn (1957), *Entomophthora exitialis* Hall & Dunn = mélange de 2 espèces.
b) Gustafsson (1965) = "*Entomophthora exitialis*" sensu Gustafsson = "*Entomophthora aphidis*" sensu Petch.

En conclusion, le nom *Entomophthora aphidis* a été appliqué à 4 taxons reconnaissables:

- *Entomophthora aphidis* Hoffm. in Fres. (1858), qui sera dénommé *Zoophthora aphidis* (Hoffm. in Fres.) Batko 1964.
- "*Entomophthora aphidis*" sensu Nowak. (1883), qui sera dénommé *Erynia neoaphidis*, nov. sp.
- "*Entomophthora aphidis*" sensu Petch (1939), qui sera dénommé *Erynia nouryi*, nov. sp.
- "*Entomophthora aphidis*" sensu Grobler et al. (1962) est décrit sous le nom de *Entomophthora canadensis* MacLeod, Tyrrell & Soper 1979.

Les deux taxons *E. ferruginea* et *E. exitialis* seront classés comme confus.

2 REEVALUATION DE ENTOMOPHTHORA APHIDIS DE E. FERRUGINEA ET DE E. EXITIALIS

A. *ENTOMOPHTHORA APHIDIS* HOFFM. IN FRES., SA POSITION DANS *ZOOPHTHORA* BATKO

a) *REDECOUVERTE ET CARACTERISTIQUES DE L'ENTOMOPHTHOROSE DES* ANOECIA

Les prospections réalisées en France au cours des dernières années ont permis de retrouver et de caractériser l'entomophthorose des sexupares et sexués d'*Anoecia* sur *Cornus sanguinea*, d'identifier son agent à l'espèce *Entomophthora aphidis* Hoffm. in Fres. et, pour la première fois depuis Winter 1881, de relier ses formes conidiennes à sa forme spore durable.

En automne, la haute vallée du Giffre et la vallée de l'Arve (Haute-Savoie, France), par les nuits fraîches, se couvrent souvent d'une chape de brume qui se dissipe lentement dans la matinée. Ces conditions sont très propices au développement des mycoses à *Entomophthora* dans les populations aphidiennes et en particulier dans les colonies d'*Anoecia* rencontrées à la face inférieure des feuilles de *Cornus sanguinea* après l'installation des ailés sexupares. De nombreux sexupares d'*Anoecia* et leur descendance sexuée, atteints de mycose, ont été trouvés en septembre et octobre pendant 5 années consécutives, de 1975 à 1979. Une trentaine de souches du champignon pathogène d'*Anoecia* ont été isolées, tantôt par récupération des conidies projetées par les cadavres, tantôt par ensemencement direct de ceux-ci sur le milieu après stérilisation superficielle selon les méthodes décrites par Remaudière et al. (1976). Les conidies primaires projetées des cadavres ou des cultures sont recueillies sur lame flambée, puis sont conservées à sec ou incubées

pendant une quinzaine d'heures en atmosphère saturée pour l'obtention des conidies secondaires, elles-mêmes conservées à sec. Les conidies sont colorées et montées dans le bleu trypan lactophénol juste avant mensuration.

A la face inférieure des feuilles de *Cornus sanguinea* on peut rencontrer trois types de cadavres d'*Anoecia*:

- des ailés sexupares envahis de mycélium, fixés à une nervure par les stylets du rostre; des coussinets de conidiophores (sporodochies) se développent à l'emplacement des parties membraneuses, principalement entre la tête et le pronotum, entre le pronotum et le mésonotum, le métanotum et l'abdomen ainsi qu'au niveau des articulations coxales;
- des larves et adultes mâles et femelles ovipares (aptères) et leurs larves, fixés le plus souvent sur le limbe de la feuille par les stylets, de couleur brun ocre, puis blanche lors de la sporulation du champignon: l'hôte est alors fortement déformé par le développement de volumineux coussinets de conidiophores qui font saillie à la surface du corps (Fig. 9, 12);
- des larves et adultes mâles et femelles ovipares, de couleur noir mat, à la cuticule intacte ou un peu ratatinée, (Fig. 9a, 10) fixés sur le limbe et souvent contre les nervures de la base de la feuille; la fixation est généralement assurée par les stylets, toutefois certains spécimens sont hérissés de longues cystides (Fig. 11) et présentent une masse rayonnante et dense de rhizoïdes formant comme une toile qui les attachent très solidement au substrat; dans les cas de fortes infestations, on retrouve aussi des amas de cadavres noirs à la base des pétioles et à l'aisselle des bourgeons; tous les cadavres noirs sont remplis de spores durables.

Les cadavres des deux premiers types, lorsqu'on les installe sur ouate de cellulose imbibée d'eau , émettent des conidiophores et des conidies qui sont projetées à quelques millimètres; cystides et rhizoïdes n'ont jamais été observés sur ces cadavres. Placés dans les mêmes conditions, les cadavres noirs du troisième type ne produisent jamais de conidies mais de longues cystides se développent tout autour du corps (Fig. 11), formant, sous les insectes qui en étaient dépourvus, une large toile ou plaque rhizoïdale.

Les spores durables n'ont jamais été observées chez les ailés sexupares. Les sexués produisent soit des spores dura-

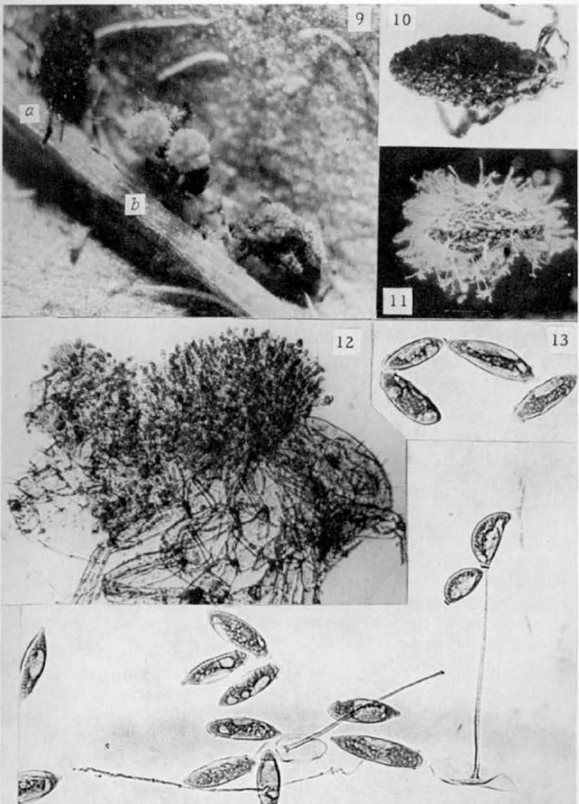


Fig. 9-13. *Zoophthora aphidis* (Hoffm. in Fres.) Batko; 9, cadavres de *Anoecia* sur *Cornus sanguinea*, a) avec spores durables, b) avec conidiophores groupés en sporodochies; 10, cadavre noir et bosselé rempli de spores durables; 11, cadavre avec spores durables ayant développé des cystides; 12, larve de *Anoecia* portant des conidiophores; 13, conidies primaires et capilloconidies.

bles, soit des conidies mais la coexistence des deux formes chez un même spécimen est exceptionnelle (1 cas observé sur près de 1000 étudiés).

Entomophthora aphidis Hoffm. in Fres. paraît hautement spécifique des *Anoecia* sur *Cornus*; il n'a jamais été rencontré sur des Aphides d'autres genres ni sur les formes estivales de ces pucerons qui colonisent les racines de Graminées.

Le puceron *Aphis salicariae* Koch (= *A. cornicella* Hille Ris Lambers) qui côtoie les *Anoecia* à la face inférieure des feuilles de *Cornus* n'a jamais été trouvé affecté par la même mycose mais seulement par "*E. aphidis*" sensu Nowak.; réciproquement "*Entomophthora aphidis*" sensu Nowak. n'a pas encore été rencontré sur *Anoecia*.

b) *IDENTIFICATION DE* ENTOMOPHTHORA APHIDIS *HOFFM. IN FRES.*

Compte-tenu du risque d'infection mixte d'un insecte par plusieurs espèces d'*Entomophthora* (Humber et al. 1977), il importait de vérifier expérimentalement la relation ontogénique des spores durables et des conidies. Trois séries de souches ont été isolées à partir des trois sortes d'inoculum suivantes:

- conidies projetées par des ailés sexupares (= cadavres du premier type);
- cadavres du 2e type stérilisés superficiellement; dans les tubes de culture ces cadavres projettent des conidies qui germent sur le milieu et émettent des filaments mycéliens qui contribuent aussi à la colonisation du milieu.
- cadavres du 3e type, noirs, remplis de spores durables; le milieu est colonisé exclusivement par le développement de cystides et rhizoïdes, car aucune conidie n'est projetée de ces cadavres.

Les trois séries de souches ainsi isolées se révèlent identiques, tant par les caractéristiques des cultures, que par la morphologie des fructifications qu'elles produisent. Ces faits montrent que les spores durables et les conidies observées sur *Anoecia* appartiennent bien à la même espèce d'Entomophthorale.

La description originale d'*Entomophthora aphidis* Hoffm. in Fres. et les syntypes de cette espèce que nous avons examinés en première partie, correspondent parfaitement à l'espèce trouvée en Haute-Savoie sur le même aphide hôte. Les spores durables de Haute-Savoie (Fig. 16 et Tabl. 2) sont identiques à celle des syntypes de l'espèce (Fig. 15 et Tabl. 1).

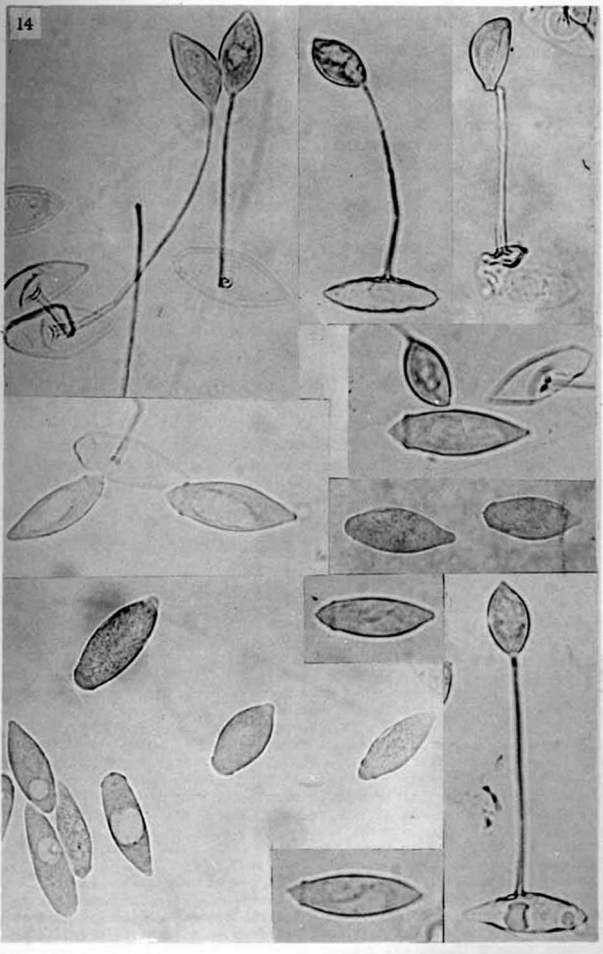


Fig. 14. *Zoophthora aphidis* (Hoffm. in Fres.) Batko, variabilité d'aspect des conidies primaires et capilloconidies ex culture.

Winter (1881) est le seul, après Hoffmann, à avoir mentionné l'entomophthorose des *Anoecia* sur *Cornus*. Sa description, brève mais plus complète que celle de Fresenius, en témoigne; les conidies qu'il décrit peuvent être rapportées aux conidies primaires, par leur aspect "en forme de fuseau, le plus souvent avec une petite pointe" ou aux capilloconidies "souvent dissymétriques, un peu courbées"; en effet, vue de face, la capilloconidie est fusiforme, vue de profil, son apex a l'aspect d'un bec émoussé, tandis que la conidie primaire est plus ou moins fusiforme et porte souvent une petite pointe au centre de la papille basale. La longueur des conidies mesurées par Winter (26-30 x 13 µm) s'accorde avec celle des conidies primaires que nous avons observées; en revanche le rapport moyen L/D, qui peut être estimé d'après les données de Winter, à 28/13 = 2,2, correspondrait aux valeurs que nous obtenons pour les capilloconidies (1,9 à 2,2).

Comme nous le montrons dans le chapitre 3, l'espèce *Entomophthora aphidis* Hoffm. n'étant pas congénérique de *Entomophthora muscae* (Cohn) Fres. mais de *Zoophthora radicans* (Bref.) Batko, en raison de ses conidies uninucléées et de ses capilloconidies amygdaliformes, c'est dans le genre *Zoophthora* Batko 1964 que nous classons le pathogène des *Anoecia*.

c) *REDESCRIPTION DE* ZOOPHTHORA APHIDIS (*HOFFM. IN FRES.*) *BATKO*

Le *mycélium* est formé de corps hyphaux, éléments sinueux, courtement ramifiés, de 60-150 x 6-10(13) µm, à contenu cytoplasmique granuleux, hyalin dans ses parties jeunes, à noyaux volumineux.
Les *conidiophores* sont plusieurs fois ramifiés de manière répétée et successive, groupés en sporodochies, cylindriques, souvent cloisonnés à la base de la ramification et produisant à chaque sommet une seule conidie apicale qui, à maturité, est libérée par projection.
Les *conidies primaires* (Fig. 13-14) sont subcylindriques à largement fusiformes, composées d'un corps à paroi double, lisse et hyaline et d'une papille basale triangulaire à semi-circulaire, séparée du corps par un léger épaulement, ornée souvent d'une petite pointe centrale et à paroi simple. Elles germent parfois en formant un court conidiophore qui projette une conidie secondaire morphologiquement semblable à la primaire mais, le plus souvent elles émettent un tube capillaire (30-130 x 1,5-2,5 µm) au sommet duquel se développe une capilloconidie qui est libérée par rupture.
Les *capilloconidies* (Fig. 13-14) sont largement amygdaliformes avec, à leur base, un coussinet annulaire; vues de profil, elles sont nettement asymétriques, renflées, avec une ligne externe semi-circulaire et une ligne interne sinuée, faiblement convexe au milieu, puis droite ou concave jusqu'à l'apex qui présente l'aspect d'un bec émoussé; vues de face, les capilloconidies apparaissent fusiformes et symétriques.
Les conidies primaires et secondaires, y compris les capilloconidies,

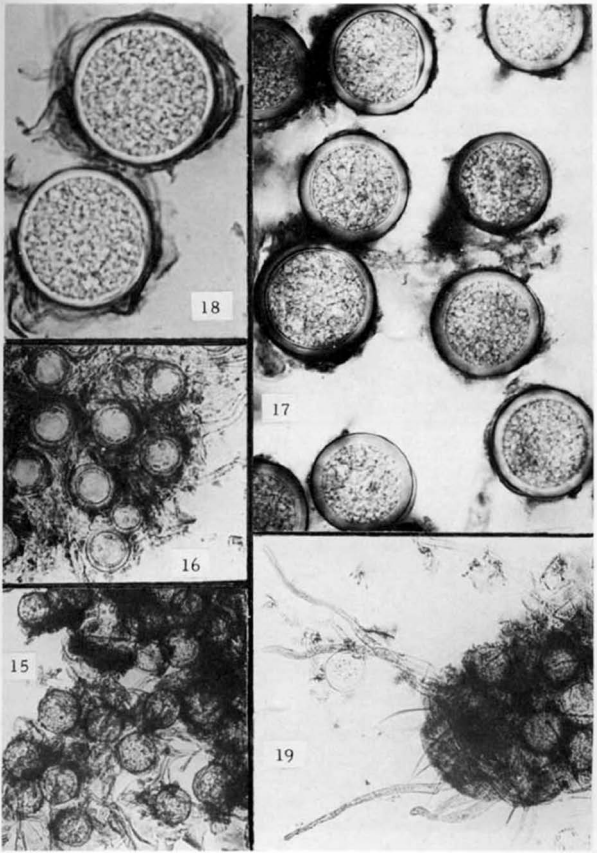


Fig. 15-19. Spores durables de *Zoophthora aphidis* (Hoffm. in Fres.) Batko; 15, ex syntype d'Hoffmann (Giessen, Allemagne 1857); 16, ex spécimen de Haute-Savoie, France 1979 (remarquer la gangue noirâtre entre les spores); 17, spores durables presque mûres, à paroi épaisse; 18, spores durables avec épispore détachée; 19, spécimen ayant développé quelques cystides.

TABLEAU 2

Mensurations de *Zoophthora aphidis* (Hoffm. in Fres.) Batko ex *Anoecia* sur *Cornus sanguinea* (exprimées en µm) (minimum, moyenne, maximum de 50 mesures par insecte ou par souche; entre parenthèses: valeurs Lm/Dm au lieu de moyenne L/D).
F: France (Haute-Savoie);
CH: Suisse (Zurich), mensurations S. Keller;
IPLB: souches Institut Pasteur, unité de Lutte Biologique.

	LONGUEUR			DIAMETRE			L/D		
	min	MOY	max	min	MOY	max	min	MOY	max
CONIDIES PRIMAIRES ex INSECTES									
F 1976	25	30,1	37	8	9,3	11	2,7	3,3	3,7
F 1977	26	32,0	37	8	10,1	12	2,7	3,2	3,9
F 1978	25	28,7	34	8	9,3	11	2,6	3,1	3,6
F 1979	27	30,4	34	9	10,3	11	2,5	2,9	3,4
F 1979	21	29,9	33	9	10,6	12	2,1	2,8	3,3
CH 26	24	27,5	33	9	10,3	11		(2,7)	
CH 37	24	29,7	36	10	12,1	15		(2,5)	
CH 44	24	30,3	38	10	12,0	16		(2,5)	
	ex CULTURES IPLB								
675	30	34,6	41	10	11,7	13	2,6	3,0	3,6
975	30	37,4	51	11	13,1	17	2,4	2,9	3,6
979	30	35,0	41	11	12,3	18	2,1	2,8	3,2
982	23	30,4	40	7	9,0	12	2,6	3,4	4,4
985	27	36,9	57	11	12,7	19	2,2	2,9	3,7
985	26	36,1	49	8	13,4	21	2,1	2,7	3,7
1274	29	37,2	49	11	12,5	15	2,3	3,0	4,3
1276	31	40,3	51	10	13,2	17	2,4	3,1	4,4
CAPILLOCONIDIES ex INSECTES									
F 1976	18	20,2	23	8	10,7	12	1,7	2,0	2,3
F 1977	16	23,3	30	8	12,0	16	1,5	1,9	2,5
F 1977	16	22,6	30	9	12,1	16	1,4	1,9	2,2
F 1978	15	21,7	25	8	10,0	12	1,9	2,2	2,5
F 1979	17	22,3	28	8	11,1	13	1,7	2,0	2,3
F 1979	17	22,2	27	9	10,6	14	1,6	2,1	2,5
CH	17	20,3	25	8	9,9	13		(2,1)	
	ex CULTURES IPLB								
975	22	28,7	36	12	13,8	16	1,7	2,1	2,5
979	19	25,1	33	10	12,3	15	1,8	2,1	2,4
985	19	25,1	33	10	11,6	15	1,8	2,2	3,0
985	16	25,2	33	8	12,1	16	1,8	2,1	2,4
1274	19	27,1	35	11	12,4	14	1,6	2,2	2,8
1276	22	27,0	33	12	13,5	15	1,7	2,0	2,4
SPORES DURABLES ex INSECTES									
F 1976				33	40,6	51			
F 1976				34	40,8	49			
F 1976				36	41,1	49			
F 1976				34	41,1	46			
F 1978				33	40,6	52			
F 1979				31	37,6	44			
F 1979				29	35,8	41			
F 1979				30	36,0	41			
F 1979				30	41,4	53			

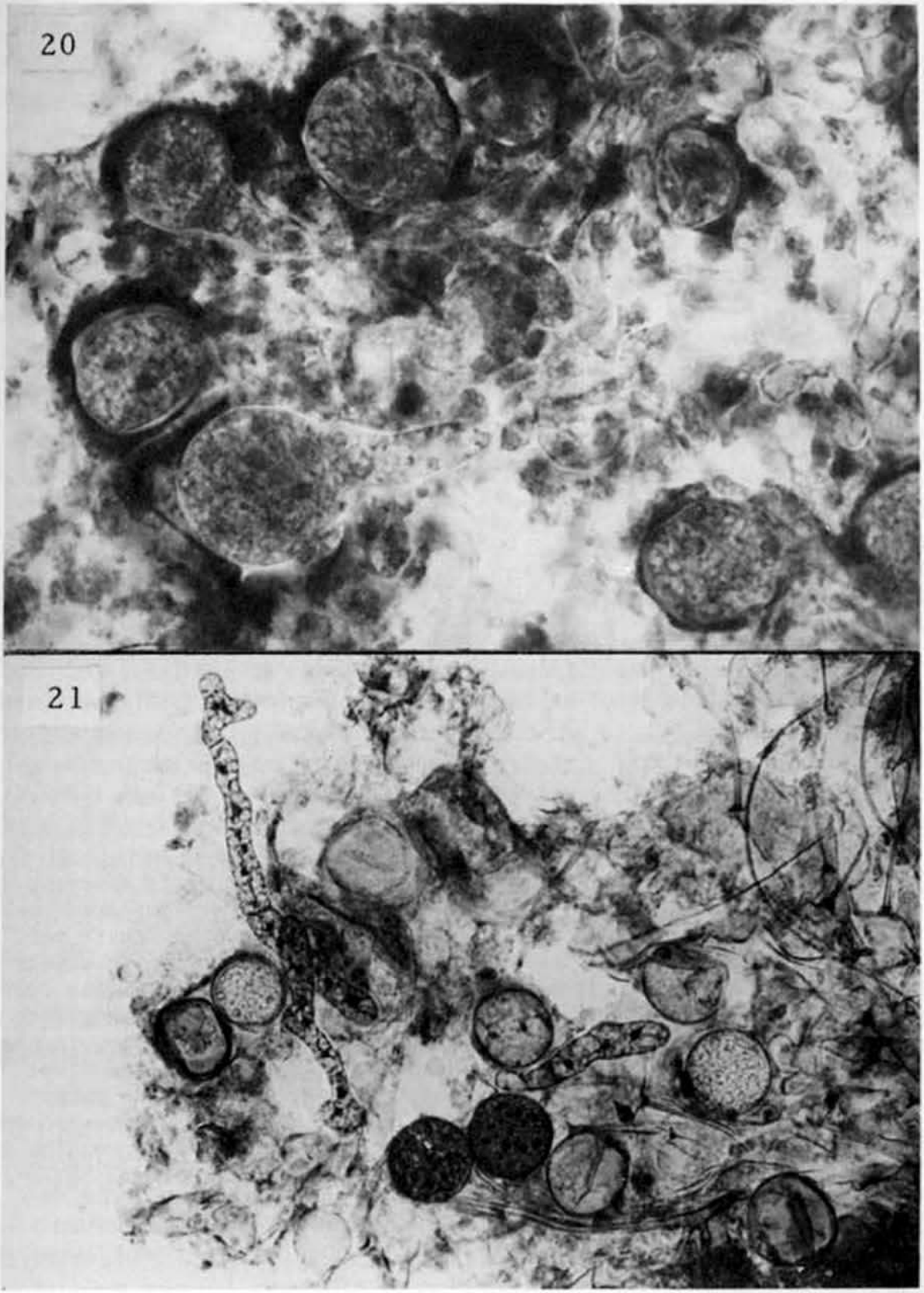


Fig. 20-21. Formation des spores durables de *Zoophthora aphidis* (Hoffm. in Fres.) Batko; 20, jeunes spores apparaissant à l'apex de corps hyphaux; 21, spores plus âgées entre lesquelles subsistent quelques hyphes interstitiels capables de former des cystides (remarquer les noyaux).

sont uninucléées, très rarement binucléées.
Les *spores durables* sont probablement des azygospores car aucune véritable image de conjugaison n'a été décelée dans les stades juvéniles; elles se forment le plus souvent à l'extrémité de segments d'hyphes internes, distincts, enchevêtrés, généralement appelés corps hyphaux; au début de leur développement, le contenu de l'hyphe s'y condense, elles deviennent pyriformes puis sphériques, elles comportent une dizaine de noyaux et sont déjà entourées d'une gangue amorphe ou membraneuse brunâtre (Fig. 20-21). A un stade plus avancé, la spore est sphérique, sa paroi s'épaissit (Fig. 17), son contenu devient uniformément granuleux; à maturité on distingue, au centre un gros globule lipidique et à la périphérie une épispore brune, fragile, ornée de légers reliefs irréguliers (Fig. 18); débarrassée de l'épispore, la spore apparaît hyaline et lisse. Dans les cadavres, les spores sont soudées par la gangue brunâtre dont il est difficile de les séparer sans léser l'épispore; en outre des corps hyphaux subsistent généralement entre les spores (Fig. 21) et peuvent donner des cystides.
Les *cystides* n'apparaissent que sur certains cadavres de sexués contenant déjà des spores durables (Fig. 19); elles sont longues, dressées, filamenteuses et indifférenciées (Fig. 12), évoluant sous le corps de l'insecte en s'enchevêtrant pour former une plaque ou subiculum rhizoïdal.

Dimensions: les valeurs moyennes des longueurs et diamètres et celles des rapports L/D des conidies primaires et des capilloconidies d'insectes et de cultures ainsi que des diamètres des spores durables d'insectes obtenues des différents lots mesurés (50 par lot), sont données dans le tableau 2 et comprises dans les fourchettes suivantes:

co. primaires insectes	27,5-33,0 x 9,3-12,1 µm; L/D 2,5-3,3
co. primaires cultures	30,4-40,3 x 9,0-13,4 µm; L/D 2,7-3,4
capilloconidies insectes	20,2-23,3 x 9,9-12,1 µm; L/D 1,9-2,2
capilloconidies cultures	25,2-28,7 x 12,1-13,8 µm; L/D 2,0-2,2
spores durables insectes	35,8-41,1 µm

Caractères culturaux. Le champignon se cultive et croît aisément sur milieu de Sabouraud enrichi de jaune d'oeuf (80/20); sur Sabouraud seul, la culture est également possible mais la croissance plus lente; sur malt, l'inoculum se développe très faiblement. La culture a un aspect blanc lisse et prend une légère couleur crème en vieillissant, la couleur du milieu n'est pas modifiée. Bien que des formations sphériques à paroi peu épaissie apparaissent parfois à partir du mycélium, il n'a jamais été rencontré de spores durables viables, le cytoplasme étant toujours lysé avant la fin d'évolution de ces structures. Une bonne croissance est également obtenue en milieu agité (eau de levure glucosée à 20g d'extrait de levure et 60g de glucose par litre); la formation de spores durables n'a pas non plus été constatée dans ce milieu liquide.

B. STATUT DE *ENTOMOPHTHORA FERRUGINEA* PHILL. IN H. & PH., *NOMEN CONFUSUM*

Ayant démontré que Nowakowski (1883), Thaxter (1888) et tous les auteurs postérieurs ont appliqué par erreur le nom de *Entomophthora aphidis* Hoffm. in Fres. à l'espèce la plus commune dans les populations de pucerons, il est nécessaire de désigner cette espèce "*Entomophthora aphidis*" sensu Nowak.

par un nom qui lui soit propre et de voir en priorité si un nom valablement publié doit lui être substitué. A ce titre, *Entomophthora ferruginea* Phill. in Hought. & Phill. peut être considéré comme un candidat.

Nous avons toutefois montré plus haut que les imprécisions de la description originale de Phillips ont conduit à trois sens différents:
- sens original comme espèce valable et distincte de "*Entomophthora aphidis*" sensu Nowak., que Batko (1966b) reclasse comme *Zoophthora* (*Pandora*) *ferruginea* (Phill. in Hought. & Phill.) Batko, mais sans en donner une redescription;
- sens de "*Entomophthora aphidis*" sensu Nowak. (Thaxter 1888; Lakon 1919);
- synonyme de *Entomophthora planchoniana* Cornu (Petch 1937; Gustafsson 1965) ou synonyme probable de *E. planchoniana* (MacLeod et al. 1976).

Phillips, qui a vu le matériel authentique de *Zoophthora aphidis* (Hoffm. in Fres.) Batko, n'a pu observer que les s p o r e s d u r a b l e s: fatalement les c o n i d i e s de son *Entomophthora ferruginea* lui sont apparues très différentes et évidemment beaucoup plus proches des conidies de *Entomophthora muscae*; ceci explique son allusion à l'étroite parenté de *Entomophthora muscae* et de *Entomophthora planchoniana* Cornu. Gustafsson et Petch ont, semble-t-il, accordé une importance trop grande à cette allusion de Phillips et mal interprété ses figures, croyant y reconnaître *Entomophthora planchoniana* Cornu; si c'était le cas, on devrait voir la pointe apicale des conidies sur les figures 10 et 12 qui représentent un stade de développement très avancé; en outre les figures 13c (Fig. 4), qui montrent deux conidies émettant un tube germinatif à chacune de leurs extrémités, ne représentent pas un mode habituel de germination de *Entomophthora planchoniana*.

Bien que l'identité de *Entomophthora ferruginea* et "*Entomophthora aphidis*" sensu Nowak. nous paraisse probable, cette hypothèse ne peut être démontrée, pas plus que celle d'une espèce distincte, d'ailleurs mal définie, suggérée par la classification de Batko. Dans ces conditions, plutôt que de rétablir un nom qui a fait l'objet d'applications contradictoires en lui donnant un statut qui, en l'absence du type pourra toujours être contesté, nous proposons de considérer *E. ferruginea* Phill. in Hought. & Phill. comme *n o m e n c o n f u s u m*.

C. STATUT DE *ENTOMOPHTHORA EXITIALIS* HALL & DUNN, *NOMEN CONFUSUM*

Avant d'examiner le statut à donner à "*Entomophthora aphidis*" sensu Nowak., il importe de clarifier celui de *Entomophthora exitialis*, espèce apparemment peu commune qui a été considérée par Gustafsson comme très voisine mais distincte de la précédente.

Nous avons étudié les souches suivantes qui sont enregistrées sous le nom de *E. exitialis* Hall & Dunn:
- la souche ATCC 14269 isolée de *Therioaphis trifolii* (= *T. maculata*) le 19 septembre 1955 par Hall & Dunn et qui est parvenue à l' ATCC en 1961;
- la souche CBS 180-60 reçue de Hall en 1960, qui a été remplacée en 1972 par la souche ATCC 14269;
- la souche authentique envoyée par I.M. Hall à J. Weiser à Prague (Krejzova 1973) = IPLB 1066, reçue de Mme Krejzova.

Les souches ATCC et CBS sont évidemment identiques. L'aspect des cultures, la forme sphérique des conidies, leur papille, leurs dimensions moyennes (22x18 µm) et celle des spores durables (19 µm) correspondent à *Conidiobolus thromboides* Drechsler (= *Entomophthora virulenta* Hall & Dunn d'après Latgé et al. 1980).

La souche de Prague donne des conidies primaires allongées, subcylindriques, semblables à celles qui illustrent la description originale de Hall & Dunn et des capilloconidies amygdaliformes; cette souche appartient à l'espèce *Zoophthora radicans* (Bref.) Batko dont nous donnons les caractéristiques dans le tableau 3.

Les difficultés d'interprétation de l'Entomophthorale décrite sous le nom de *Entomophthora exitialis* peuvent se résumer comme suit:
(1) il n'existe pas d'exsiccatum type (Hall, comm. pers.); aucun matériel type n'est désigné dans la description originale;
(2) la culture déposée à l' ATCC par Hall correspond à *Conidiobolus thromboides* Drechsler (= *Entomophthora virulenta* Hall & Dunn);
(3) la culture envoyée à Prague par I.M. Hall correspond à *Zoophthora radicans* (Brefeld) Batko;
(4) les illustrations originales montrent incontestablement, comme l'ont d'ailleurs récemment remarqué Milner & Teakle (1978), des conidies à épaulement, comme celles de *Zoophthora radicans*, avec un rapport L/D voisin de 3 tandis que la description originale donne des dimensions moyennes dont le rapport Lm/Dm = 20/11 = 1,8 est incompatible avec

celui des conidies figurées; ce texte pourrait s'appliquer à "*Entomophthora aphidis*" sensu Petch, comme l'a fait Gustafsson (= "*Entomophthora exitialis*" sensu Gustafsson); la description originale des spores durables ne permet pas de lever l'ambiguité car leur diamètre, (24)27(32) µm, est comparable aussi bien à celui des spores durables de *Z. radicans*, diamètre moyen compris entre 24 et 29 µm, qu'à celui de"*Entomophthora aphidis*" sensu Petch, (20)25-30(36) µm;

(5) un argument écologique peut incliner à considérer que les conidies photographiées et les spores durables décrites par Hall & Dunn correspondent effectivement à *Z. radicans* tandis que le reste de la description pourrait concerner les conidies de "*Entomophthora aphidis*" sensu Nowak. (les mesures de Hall & Dunn étant intermédiaires entre celles de "*E. aphidis*" sensu Petch et de "*E. aphidis*" sensu Nowak.); cette hypothèse est solidement étayée sur les données écologiques suivantes: en trois années de recherches assidues sur les pathogènes de *Therioaphis trifolii* en Californie, ces auteurs ont reconnu, à côté de *Entomophthora coronata* (Cost.) Kevork., 4 espèces nouvelles *E. obscura*, *E. ignobilis*, *E. exitialis* et *E. virulenta* sans jamais rencontrer - ce qui est fort surprenant - ni le très commun "*Entomophthora aphidis*" sensu Nowak., ni *Zoophthora radicans*, deux espèces pourtant fréquentes sur *T. trifolii* en Amérique du Nord; ces deux dernières espèces ont en effet été récemment isolées du même hôte dans les luzernières de la région de Mexico par J.P. Latgé (souches IPLB 1125: "*E. aphidis*" sensu Nowak. et 1117, 1118, 1181: *Z. radicans*);

(6) nous avons retourné à I.M. Hall la souche "*E. exitialis*" de Prague (*Zoophthora radicans*, selon nous); son avis est catégorique: cette culture n'est pas *E. exitialis*.

Constatant l'absence de matériel type, l'ambiguité taxonomique du protologue, l'identité de la culture originale déposée à l' ATCC à une espèce étrangère (*Conidiobolus thromboides* Drechsler) et le rejet par l'auteur d'une autre culture originale correspondant bien à l'illustration du protologue (*Zoophthora radicans*), nous devons considérer cette espèce comme un *n o m e n c o n f u s u m* et rechercher un nom applicable à "*Entomophthora exitialis*" sensu Gustafsson ="*Entomophthora aphidis*" sensu Petch.

3 REVISION DU GENRE ZOOPHTHORA BATKO DESCRIPTION DE ERYNIA APHIDIS ET DE E. NOURYI SPP. NOV.

A. REVISION DU GENRE *ZOOPHTHORA*

Comme nous l'avons rappelé dans la première partie, Fresenius (1856) reconnaît le genre *Empusa* Cohn (1855), *nomen illegitimum*, comme *Entomophthora* Fresenius, sur la base de l'espèce type *Empusa muscae* Cohn.

En 1881, Nowakowski crée le nouveau genre *Erynia* pour *Erynia ovispora* Nowak. 1877, *Erynia curvispora* Nowak. 1877 et *Erynia conica* (*nom. nudum* en 1881), trois espèces qu'il se refuse à maintenir ou à placer dans *Entomophthora*, à côté de *E. radicans* Bref. car, contrairement à cette dernière, les trois espèces précédentes présentent des zygospores issues d'une véritable conjugaison.

En 1883, il divise l'ensemble des espèces de *Entomophthora* Fres. en trois groupes:

- celui des espèces à conidiophores simples et sans rhizoïdes - dont l'espèce type de *Entomophthora* Fres., *E. muscae* Cohn - qu'il reclasse à tort dans *Empusa* Cohn, illégitime;
- celui de l'espèce *Entomophthora culicis* (A. Cohn) Fres. à conidiophores simples mais avec rhizoïdes, pour lequel il confirme son genre *Lamia* Nowak. déjà mentionné en 1881.
- celui des espèces à conidiophores ramifiés qu'il réunit sous le nom de "*Entomophthora*", créant ainsi un homonyme postérieur, "*Entomophthora* Nowak.", illégitime vu l'exclusion de son type; dans ce dernier groupe, il reprend *Entomophthora ovispora* et *Entomophthora curvispora*, il décrit *Entomophthora conica* et rejette explicitement *Erynia* Nowak. 1881 en synonyme de *Entomophthora* Nowak. 1883.

Thaxter (1888), lui aussi, maintient l'illégitime *Empusa* Cohn; il réduit *Entomophthora* au rang de sous-genre de *Empusa* dans lequel il classe des espèces telles que *Entomophthora sphaerosperma* Fres. (= *radicans* Bref.) et *Entomophthora aphidis* Hoffm. in Fres.; comme Nowakowski, il exclut de son sous-genre *Entomophthora* l'espèce type *muscae*; il crée en outre le nouveau sous-genre *Triplosporium* Thaxter et traite *Lamia* Nowak. comme synonyme de *Empusa* subg. *Empusa*.

Nieuwland (1916), observant que *Lamia* Nowak. est illégitime parce qu'homonyme de *Lamia* Endlich. 1841, le renomme

Culicicola avec la même espèce type *Empusa culicis* A. Braun et le resépare de *Empusa*.

Batko (1964a) réaffirme la typification obligatoire de *Entomophthora* Fres. comme nom nouveau d'*Empusa* Cohn et restreint le genre aux seules espèces congénériques de *Entomophthora muscae*, c'est-à-dire à conidies campanulées avec absence de rhizoïdes et de cystides.

Batko (1964b,c) élève le sous-genre *Triplosporium* Thaxter au rang de genre pour les espèces à conidiophores simples, à conidies subsphériques multinucléées, munies d'une papille tronquée, à capilloconidies et à zygospores formées par isogamie. Il crée le genre *Entomophaga* Batko pour les espèces à conidiophores simples, dépourvues de rhizoïdes, à conidies subsphériques non campanulées, unituniquées, multinucléées. Il reconnaît le genre *Culicicola* Nieuwl. (≡ *Lamia* Nowak.) pour les espèces à conidiophores simples, pourvues de rhizoïdes et à conidies unituniquées, campanulées ou non.

Négligeant apparemment la disponibilité du genre *Erynia* Nowak., il crée encore le nouveau genre *Zoophthora* Batko qu'il typifie par *Empusa radicans* Bref. 1870. Il y transfère ensuite (Batko 1964d) 24 autres espèces dont *Entomophthora aphidis* Hoffm. in Fres. ainsi que *Entomophthora ovispora* Nowak., *Entomophthora curvispora* Nowak. et *Entomophthora conica* Nowak., les 3 espèces originales de *Erynia* Nowak. Ainsi *Zoophthora* regroupe les espèces à conidiophores ramifiés, pourvues de rhizoïdes, à conidies bituniquées, uninucléées, non campanulées.

Poursuivant son essai de clarification de la systématique des *Entomophthoraceae*, Batko (1966b) scinde son genre *Zoophthora* en 4 sous-genres:

- subg. *Zoophthora* Batko 1966, holotype *Empusa radicans* Bref. 1870;
- subg. *Erynia* (Nowak. 1881) Batko 1966, type *Entomophthora ovispora* Nowak. 1877 (lectotype pour *Erynia* Nowak. 1881);
- subg. *Pandora* Batko 1966, holotype *Entomophthora aphidis* Hoffm. in Fres. 1858;
- subg. *Furia* Batko 1966, holotype *Empusa virescens* Thaxter 1888.

Les bases morphologiques sur lesquelles s'appuie Batko pour différencier ces 4 sous-genres sont notamment la diversité des types conidiens selon la classification de Lakon (1919), le degré de vacuolisation du cytoplasme des conidies, l'épaisseur relative des conidiophores, des cystides et des rhizoïdes ainsi que les particularités des expansions terminales de ces derniers. Ces caractères, déjà subtils et

variables, souvent communs à plusieurs de ces sous-genres, ne permettent ni une définition univoque de chacun d'eux, ni *a fortiori* leur maintien.

Par ailleurs, la diagnose du sous-genre *Pandora* ne correspond pas à son espèce type, *Entomophthora aphidis* Hoffm. in Fres., mais à "*Entomophthora aphidis*" sensu Nowak. par tous les éléments de la description et en particulier la forme des conidies primaires décrites et illustrées comme généralement ovales, ovoïdes, souvent à faible symétrie bilatérale, au lieu de subcylindriques allongées.

De plus, pouvant affirmer que *E. aphidis* Hoffm. in Fres., holotype de *Zoophthora* subg. *Pandora* est si proche de *Empusa radicans* Bref. 1870, holotype de *Zoophthora* Batko 1964b (et de *Z.* subg. *Zoophthora*) au point d'être nécessairement congénérique, nous devons considérer *Zoophthora* subg. *Pandora* Batko 1966 , synonyme de *Zoophthora* Batko 1964b, prioritaire, ceci en dépit des différences relevées dans les diagnoses de ces sous-genres (Article 11 du code international de nomenclature botanique).

Enfin, contrairement à ce qu'écrit Batko (1966b), le taxon *Erynia* n'a pas été invalidé par le fait que Nowakowski l'ait rejeté deux ans après l'avoir créé. En réalité, Nowakowski (1883) en a fait un synonyme facultatif (taxonomique) du genre *Entomophthora*. En rétablissant *Erynia* Nowak. 1881 au rang de sous-genre de *Zoophthora* Batko 1964, Batko ne respectait pas la règle de priorité qu'impliquait la priorité de *Erynia* sur *Zoophthora* par le fait de l'inclusion de son espèce type.

Parmi les 25 espèces classées dans le genre *Zoophthora* par Batko (1964b), nous constatons l'existence d'un premier groupe très homogène et bien caractérisé par l'aptitude à former des capilloconidies à symétrie bilatérale, de type amygdaliforme ou falciforme; les espèces du groupe ont des conidies primaires produites sur des conidiophores ramifiés; ces conidies sont subcylindriques, allongées, généralement uninucléées, avec une papille basale séparée du corps de la conidie par un léger épaulement. Le nom générique *Zoophthora* Batko 1964 s'applique à ce groupe d'espèces puisque son type *Empusa radicans* Bref. en fait lui-même partie.

Nous proposons de réunir en un second groupe les autres espèces à conidies primaires généralement uninucléées et produites sur conidiophores ramifiés (comme dans le groupe précédent, *Zoophthora*) mais qui ne donnent jamais de capilloconidies. Bien que moins homogène, ce deuxième groupe mérite d'être rassemblé dans un même taxon générique auquel le nom

Erynia Nowak. 1881 s'impose du fait de l'inclusion de son lectotype *E. ovispora* (Nowak. 1877) Nowak. 1881, désigné par Batko (1966b).

En conclusion, nous distinguons deux genres d'Entomophthoracées présentant des conidiophores ramifiés, des conidies généralement uninucléées et souvent aussi des rhizoïdes: *Zoophthora* Batko et *Erynia* Nowak.

1. Genre *ZOOPHTHORA* Batko 1964 (*Bull. Acad. Polon. Sci. cl. II, ser. Sci. biol. 12*: 323-324)

≡ *Zoophthora* subg. *Zoophthora* Batko 1966 (*Acta mycol. 2*: 16-18)
= *Zoophthora* subg. *Pandora* Batko 1966 (*Acta mycol. 2*: 18-19)

Espèce type: *Empusa radicans* Bref. 1870 (*Bot. Zeitg. 28*: 161-166, 177-186) ≡ *Z. radicans* (Bref. 1870) Batko 1964 (*Bull. Acad. polon. Sci. cl. II, ser. Sci. biol. 12*: 323-324) (= "*Empusa sphaerosperma* Fres." sensu Thaxter 1888).

Principal caractère distinctif: présence de capilloconidies.
Principales espèces du genre:

Z. aphidis (Hoffm. in Fres. 1858) Batko 1964;
Z. canadensis (MacLeod et al. 1979) comb.nov. ≡ *Entomophthora canadensis* MacLeod et al. 1979 (*Can. J. Bot. 57*: 2663-2672);
Z. elateridiphaga (Turian 1978) Ben Ze'ev & Kenneth 1980;
Z. geometralis (Thaxter 1888) Batko 1964;
Z. occidentalis (Thaxter 1888) Batko 1964;
Z. phalloides Batko 1966;
Z. phytonomi (Arthur 1886) Batko 1964.

2. Genre *ERYNIA* Nowak. 1881 (*Djenn. III Zjazdu Lek. Przyr. Polsk. Kraków 6*: 67)

≡ *Zoophthora* subg. *Erynia* (Nowak. 1881) Batko 1966 (*Acta mycol. 2*: 18)
= *Zoophthora* subg. *Furia* Batko 1966 (*Acta mycol. 2*: 20) syn. nov.

Espèce lectotype: *Entomophthora ovispora* Nowak. 1877 (*Bot. Zeitg. 35*: 220) ≡ *Erynia ovispora* (Nowak. 1877) Nowak. 1881 (*Djenn. III Zjazdu Lek. Przyr. Polsk. Kraków 6*: 67).

Principal caractère distinctif: absence de capilloconidies.
Principales espèces du genre:

E. americana (Thaxter 1888) comb. nov. ≡ *Empusa americana* Thaxter 1888 (*Mem. Boston Soc. Nat. Hist. 4*: 179-180, fig. 262-273);
E. aquatica (Anderson & Ringo 1969) comb. nov. ≡ *Entomophthora aquatica* Anderson & Ringo 1969 (*J. Invert. Pathol. 13*: 386-393, fig. 1-12);

E. blunckii (Lakon ex Zimm. 1978) comb. nov. ≡ *Entomophthora blunckii* Lakon ex Zimm. 1978 (*Entomophaga 23*: 181-187, fig. 1-5 (*Entomophthora blunckii* Lakon 1935 est *nomen invalidum* car sans diagnose latine);
E. brahminae (Bose & Mehta 1953) comb. nov. ≡ *Entomophthora brahminae* Bose & Mehta 1953 (*Trans. Brit. Mycol. Soc. 36*: 52-56, fig. 1-11);
E. bullata (Thaxter in Povah 1935) comb. nov. ≡ *Entomophthora bullata* Thaxter in Povah 1935 (*Papers Mich. Acad. Sci. 20*: 120);
E. calliphorae (Giard 1879) comb. nov. ≡ *Entomophthora calliphorae* Giard 1879 (*Bull. Sci. Fr. et Belg. 11*: 356-358);
E. caroliniana (Thaxter 1888) comb. nov. ≡ *Empusa caroliniana* Thaxter 1888 (*Mem. Boston Soc. Nat. Hist. 4*: 167, fig. 91-105);
E. conica (Nowak. 1883) comb. nov. ≡ *Entomophthora conica* Nowak. 1883 (*Pamietn. Wyda. Akad. Umiej.w. Krakŏw 8*: 155-160, fig. 1-32 (la combinaison *Erynia conica* Nowak. 1881 est invalide, l'épithète *conica* étant nomen nudum en 1881, comme d'ailleurs en 1882 sous la combinaison *Entomophthora conica* Nowak. 1882);
E. creatonoti (Yen 1962) comb. nov. ≡ *Entomophthora creatonoti* (ut "*creatonotus*") Yen 1962 (*J. Insect Pathol. 4*: 88-94, fig. 1-4);
E. curvispora (Nowak. 1877) Nowak. 1881;
E. dipterigena (Thaxter 1888) comb. nov. ≡ *Empusa dipterigena* Thaxter 1888 (*Mem. Boston Soc. Nat. Hist. 4*: 177, fig. 241-250);
E. echinospora (Thaxter 1888) comb. nov. ≡ *Empusa echinospora* Thaxter 1888 (*Mem. Boston Soc. Nat. Hist. 4*: 180, fig. 286-305);
E. erinacea (Ben Ze'ev & Kenneth 1979) comb. nov. ≡ *Zoophthora erinacea* Ben Ze'ev & Kenneth 1979 (*Mycotaxon 10*: 219-232, fig. 1-10);
E. gloeospora (Vuillemin 1886) comb. nov. ≡ *Entomophthora gloeospora* Vuillemin 1886 (*Bull. Soc. Sci. Nat. Nancy, sér. 2, 19*: 34-46, fig. 1-16);
E. gracilis (Thaxter 1888) comb. nov. ≡ *Empusa gracilis* Thaxter 1888 (*Mem. Boston Soc. Nat. Hist. 4*: 185-186, fig. 379-391);
E. montana (Thaxter 1888) comb. nov. ≡ *Empusa montana* Thaxter 1888 (*Mem. Boston Soc. Nat. Hist. 4*: 180, fig. 274-285);
E. myrmecophaga (Turian & Wuest 1977) comb. nov. ≡ *Zoophthora myrmecophaga* Turian & Wuest 1977 (*Bull. Soc. ent. Suisse 50*: 285-289, fig. 1-4) (*Entomophthora myrmecophaga* Turian & Wuest 1969 est *nomen invalidum* car sans diagnose latine);
E. phalangicida (Lagerheim 1898) comb. nov. ≡ *Empusa phalangicida* Lagerheim 1898 (*Bihang Till K.Sv. vet. Akad. Handl. 24 III*: 12-15, fig. 1-7);
E. rhizospora (Thaxter 1888) comb. nov. ≡ *Empusa rhizospora* Thaxter 1888 (*Mem. Boston Soc. Nat. Hist. 4*: 183-185, fig. 347-378);
E. sepulchralis (Thaxter 1888) comb. nov. ≡ *Empusa sepulchralis* Thaxter 1888 (*Mem. Boston Soc. Nat. Hist. 4*: 181-182, fig. 306-326);
E. variabilis (Thaxter 1888) comb. nov. ≡ *Empusa variabilis* Thaxter 1888 (*Mem. Boston Soc. Nat. Hist. 4*: 183, fig. 327-346);
E. virescens (Thaxter 1888) comb. nov. ≡ *Empusa virescens* Thaxter 1888 (*Mem. Boston Soc. Hist. Nat. 4*: 178, fig. 251-261);
E. vomitoriae (Rozsypal 1966) comb. nov. ≡ *Zoophthora vomitoriae* Rozsypal 1966 (*Acta mycol. 2*: 23-24).

Les deux nouvelles espèces décrites à la fin du présent article sont également à ranger dans le genre *Erynia*: *E. neoaphidis* sp. nov. et *E. nowryi* sp. nov.

La question peut se poser de savoir pourquoi nous maintenons, à l'instar de Batko (1964b), l'épithète *radicans*

Bref. 1870 plutôt que d'user de l'épithète prioritaire *sphaerosperma* Fres. 1856.

Brefeld (1877b) a démontré la bonne correspondance des spores durables de son espèce avec les caractères révélés par Fresenius sur *Entomophthora sphaerosperma*, montrant ainsi, d'une certaine manière, l'identité des espèces, sans toutefois tirer la conclusion logique de la priorité de l'épithète *sphaerosperma* Fres. sur *radicans* Bref. (comme allaient le faire plus tard, Giard 1879, Winter 1884, Thaxter 1888, et de nombreux autres auteurs).

Batko (1964b) rejette comme nomen confusum *Entomophthora sphaerosperma* en vertu de l'article 70 du code international de nomenclature permettant de rejeter un nom dont le type est hétérogène. En effet, dans les illustrations originales de *Entomophthora sphaerosperma* Fres. (seul élément type en l'absence du matériel type, en vertu de l'article 9, note 1), Batko reconnaît des éléments discordants comme les hyphes de la figure 69 de Fresenius qui, probablement, appartiennent à un champignon non Phycomycète.

Nous appuyant sur le même article 70 du code (selon lequel on peut ne pas rejeter un type hétérogène s'il est possible de retenir comme type satisfaisant un seul de ses éléments), nous retenons les figures 72 à 78 de Fresenius comme lectotype de *Entomophthora sphaerosperma* qui représentent bien les corps hyphaux et les spores durables d'une espèce d'*Entomophthora* que nous classons *n o m e n d u b i u m* (et non *nomen confusum*), tant que la découverte d'un matériel type ou authentique ou celle d'un matériel postérieur de l'auteur n'aura pas permis de préciser et confirmer l'espèce de Fresenius.

Par l'application d'une démarche rigoureuse, nous avons réussi à reconnaître et à classer *Entomophthora aphidis* Hoffm. in Fres., ce qui n'était pas possible avant la redécouverte du type, la parfaite connaissance des deux formes de l'espèce et la démonstration de leur lien ontogénique.

Cette démarche est la seule qui permette de décider du statut d'espèces telles que *Entomophthora sphaerosperma* Fres., *Tarichium megaspermum* Cohn et *Tarichium* spp., toutes décrites à l'origine - comme *Entomophthora aphidis* - sur la seule forme spore durable.

Ainsi Bucher & MacLeod (1974) ont eu raison de ne pas conclure hâtivement à une synonymie entre *Tarichium megaspermum* Cohn et *Entomophthora virescens* Thaxter, espèces qui, selon ces auteurs, coexistent dans les populations de deux

Lépidoptères *Noctuidae* du genre *Euxoa*. En l'absence de comparaison avec le matériel type, il n'est pas démontré que les spores durables qu'ils observent soient celles de *T. megaspermum*, bien que, dans ce cas, la présomption soit forte. La relation entre ces spores durables et les conidies de *Entomophthora virescens* n'est pas prouvée: les deux formes n'ont pas encore été observées sur un même individu et, même si c'était le cas, il resterait encore à démontrer que cette coexistence n'est pas le résultat d'une infection mixte par deux espèces distinctes.

La prudence manifestée par Bucher & MacLeod est d'autant plus justifiée qu'il s'agit d'une espèce type (*megaspermum* est le type de *Tarichium* Cohn 1870), toute synonymie impliquant dès lors des remaniements de la nomenclature générique.

B. DIAGNOSE DE *ZOOPHTHORA APHIDIS* HOFFM. IN FRES.

Zoophthora aphidis (Hoffm. in Fres.) Batko 1964
- ≡ *Entomophthora aphidis* Hoffm. in Fres. 1858
- ≡ *Tarichium aphidis* (Hoffm. in Fres.) Cohn 1870
- ≡ *Empusa aphidis* (Hoffm. in Fres.) Thaxter 1888, non "*Empusa aphidis* (Hoffm. in Fres.) Thaxter" sensu Thaxter 1888.

Diagnose (Fig. 1, 9-21):

Conidiophores ramifiés. *Conidies primaires* uninucléées, subcylindriques à fusiformes avec papille basale souvent conique pointue, plus rarement arrondie, bordée d'un épaulement, (21)27-32(38) x (8)9-12(16) µm, rapport L/D (2,1)2,5-3,2(3,9). *Conidies secondaires* parfois du même type que les primaires et formées sur des conidiophores épais, de longueur variable; plus souvent du type capilloconidies, apparaissant au sommet d'un tube capillaire. *Capilloconidies* largement amygdaliformes avec un bec émoussé, (15)20-23(30) x (8)10-12(16) µm, rapport L/D (1,4)1,9-2,2(2,5). *Spores durables*, probablement azygospores, volumineuses, coalescentes, à épispore brune pourvue de légers reliefs amorphes et irréguliers, (29)37-40(53) µm. *Corps hyphaux* sinueux, courtement ramifiés 60-150 x 6-10(13) µm. *Cystides* longues, flexueuses, rencontrées seulement sur spécimens remplis de spores durables et ayant été en présence d'eau, évoluant sous l'insecte en un subiculum rhizoïdal.
Hôte: Anoecia spp. (*Hom. Aphididae*) sur *Cornus sanguinea*.
Distribution géographique: Allemagne, Pologne, Suisse et France.
Type: Rabenhorst Klotzschii herbarium vivum mycologicum Ed. II Cent. VIII n. 768, *Entomophthora aphidis* Hoffmann sur *Anoecia* sp. sur *Cornus sanguinea*, Giessen, automne 1857, H. Hoffmann (lectotype: Herb. PC); autres syntypes Herb. PAV, K).
Autres collections, toutes sur *Anoecia* spp. sur *Cornus sanguinea:* (1) Puławy Pologne, octobre 1926, W. Siemaszko (Herb. E); (2)18 récoltes, Samoëns et Sixt dans la vallée du Giffre, Sallanches et Passy dans la

vallée de l'Arve, Haute-Savoie, France, automnes 1975 à 1979, G. Remaudière, J.P. Latgé et B. Papierok (coll. G.R., Institut Pasteur Paris) (Tableau 2); (3) 1 récolte Le Creux-de-Miège, Hérault, septembre 1977, France, Mme Matile (coll. G.R.); (4) 1 récolte Brie-Comte-Robert, Seine-et-Marne, France, octobre 1979, G. Remaudière (coll. G.R.); (5) Zurich, Suisse, octobre 1977, S. Keller (coll. S.K.).

Cultures: N° IPLB 670 à 675, 975 à 982, 985, 997, 1274 à 1280, Institut Pasteur, unité de Lutte Biologique contre les Insectes. La souche IPLB 1274 est déposée à l' ATCC, au CBS et à l' IMI (N° IMI 245781).

Principales applications et descriptions erronées: Depuis Nowakowski (1883) et jusqu'à ce jour, tous les auteurs font une application erronée du nom *E. aphidis* Hoffm. in Fres. Dans la première partie, nous avons discuté les principaux articles présentant un intérêt taxonomique: Nowakowski (1883), Thaxter (1888), Petch (1939), Krenner (1961), Grobler et al. (1962), Gustafsson (1965), Batko (1966b), Tyrrell et al. (1975). Dans les très nombreuses publications parues durant cette période de près d'un siècle et traitant du comportement, du spectre d'hôtes et de l'épizootiologie de l'espèce fongique la plus fréquente dans les populations aphidiennes, le nom de *E. aphidis* Hoffm. in Fres. est quasi invariablement utilisé par erreur pour désigner le taxon différent "*E. aphidis*" sensu Nowak.

Comparaison de *Z. aphidis* avec les autres *Zoophthora* pathogènes d'Aphides

Hormis *Zoophthora aphidis*, 4 autres espèces de ce genre sont connues comme pathogènes stricts ou occasionnels d'Aphides:

Z. radicans (Bref.) Batko, qui attaque des insectes de divers ordres,

Z. phalloides Batko, qui se rencontre sur plusieurs genres d'Aphides,

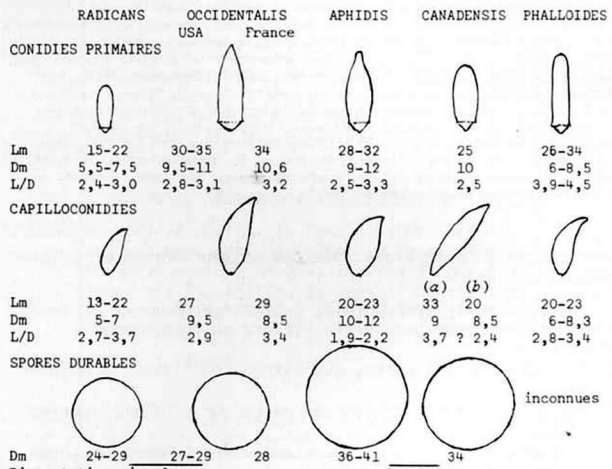
Z. canadensis (MacLeod et al.) Remaudière & Hennebert, pathogène des *Schizolachnus*,

Z. occidentalis (Thaxter) Batko, surtout connu sur pucerons du bouleau.

La comparaison des caractères morphologiques de ces espèces et la clé d'identification se basent sur les données de la littérature, complétées par nos données personnelles. Dans le cas de *Z. occidentalis*, cette espèce n'ayant été signalée qu'une fois (Petch 1948) depuis la description originale (Thaxter 1888), nous avons étudié le matériel conservé au Farlow Herbarium (FH): matériel type N° 4345 et authentique N° 4344, 4346, 4347 et 6416 de Thaxter. Selon Thaxter, les hôtes sont des pucerons vivant sur *Betula populifolia*; l'examen de ses spécimens permet de reconnaître une espèce du genre *Euceraphis* (probablement *E. betulae* Koch). En France, à Pontcarré (Seine-et-Marne) nous avons retrouvé *Z. occidentalis* dans une population d'*Euceraphis betulae* Koch sur *Betula verrucosa* le 5 novembre 1977 et

TABLEAU 3

Comparaison des 5 espèces de *Zoophthora* rencontrées sur Aphides: *Z. radicans*, *Z. occidentalis*, *Z. aphidis*, *Z. canadensis* et *Z. phalloides* (fourchettes des longueurs ou diamètres moyens, Lm et Dm en µm et fourchettes des rapports moyens L/D moy.).



(*a*) selon Tyrrell & al.(1975)
(*b*) selon MacLeod & al.(1979)

nous avons isolé une série de souches de ce pathogène (IPLB 1005 à 1010).

Les valeurs mentionnées dans le tableau 3 et dans la clé sont les fourchettes des moyennes obtenues sur des séries de 50 conidies ou spores durables issues d'insectes hôtes (dans le cas de *Z. canadensis*, le nombre d'individus sur lesquels portent les moyennes ne peut être précisé). Les abréviations suivantes ont été retenues:

co., conidie primaire — Lm, longueur moyenne
cap., capilloconidie — Dm, diamètre moyen
sp.d., spore durable — L/Dmoy moyenne des rapports L/D

La clé suivante permet assez facilement de séparer les 5 espèces considérées ici:

1 - *co.* L/Dmoy 3,9-4,5, Lm 26-34 µm; *cap.* arquée. . . . *Z. phalloides*
- *co.* L/Dmoy ⩽3,5. 2

2 - *sp.d.* incolore, Dm 30 µm 3
- *sp.d.* à épispore brune, Dm 33 µm 4

3 - *co.* Lm 15-22 µm, cylindriques; *cap.* Lm 13-22 µm . . *Z. radicans*
- *co.* Lm 30-35 µm, apex souvent conique; *cap.* Lm 27-29 µm . . . . . *Z. occidentalis*

4 - *co.* Lm 28-32 µm, apex souvent conique; *cap.* L/Dmoy 1,9-2,2; *sp.d.* 36-41 µm . . . . . *Z. aphidis*
- *co.* Lm 25 µm, cylindrique; *sp.d.* 34 µm . . . . . *Z. canadensis*

Ainsi *Zoophthora aphidis* se distingue de *Z. phalloides* par ses conidies primaires et ses capilloconidies bien plus larges, de *Z. radicans* par ses conidies et spores durables beaucoup plus grandes; *Z. aphidis* se rapproche de *Z. occidentalis* par la forme des conidies primaires souvent coniques à l'apex mais ses spores sont brunes; elle se rapproche aussi de *Z. canadensis* par ses spores brunes et volumineuses mais celles-ci ne sont pas cannelées et ses conidies primaires et capilloconidies ont une forme très différente (voir Tableau 3).

C. DESCRIPTION DE *ERYNIA NEOAPHIDIS* SP. NOV.

Erynia neoaphidis sp. nov.
(= "*Entomophthora aphidis*" sensu Nowak. 1883, sensu Thaxter 1888, sensu auctorum posteriorum; non sensu Petch 1939; non sensu Grobler et al. 1962, non sensu Tyrrell et al. 1975).

Diagnose (latine et française) (Fig. 22-25).

Fungus entomogeneus (Entomophthoraceae). Conidiophori *ramosi, varii, 55-130 x 6-10 µm, paliformibus.* Primaria conidia *uninucleata, hyalina, ovoidea vel elliptica, dorso-ventraliter asymetrica, in apice rotunda, cum angusta, sine conidiophori vestigio, pariete ad conidii corporem continuo, papilla, varia, in insectis (15)21-32(40) x (9)11-14(16) µm, L/D (1,4)1,7-2,3(2,9), in cultura (15)21-37(42) x (7)11-17,5(22) µm, L/D (1,2)1,6-2,6(3,5) (ultima et media dimensio).* Secondaria conidia *sive primariis conidiis similia atque parvioria, ovoidea, L/D minore, sive subsphaerica, cum conspicua papilla, saepe cum minuto, punctiformi, obscuriore atque* Entomophthora muscae *simili apiculo in apice ornata, (14)19(24) x (11)16(20) µm, L/D (1,1)1,2(1,4).* Hyphalia corpora *vere varia 32-260 x 6-13 µm, saepe multivamosa, cum vacuoloso cytoplasmate et 1-12, 6-8 µm latis nucleis.* Cystidia *e globosa, 30-40 µm diam., matricali cellula ennata, basaliter 12-14 µm lata, ad apicem 7-3 µm attenuata et rotundata, 120-240 µm longa, conidiophoribus supersedentia, 10-15 nucleata.* Rhizoidea *hyalina, tenua, una hypha composita, numerosa (15-30), e thoraci et ventre hospitis ennata, varie longa, 80-400 µm, 10-25 µm diam., ad substratum cum irregulare terminali disco affixa.*

Perdurantes sporae *ignotae*. Hospes: *in Homopteris, Aphididis. Vere frequens in Asia, Europa, Africa septentrionali, America septentrionali, Australia, rarior in tropicalibus regionibus.* Typus: *in* Nasonovia ribisnigri *Mosley ad* Ribem alpinum, *Samoens, Alta Savoya, Francia, 25 oct. 1979 (G. Remaudière) in PC herbario; isotypus: IPLB 1284, cultura exsiccata in K, E, PAV, FH herbariis deposita.*

Conidiophores ramifiés, de longueur et de diamètre variables 55-130 x 6-10 µm, disposés en palissade. *Conidies primaires* uninucléées, hyalines, ovoïdes à elliptiques, arrondies au sommet, généralement à asymétrie dorso-ventrale, avec une papille assez étroite, non séparée du corps de la conidie, sans marque d'attachement au conidiophore, de forme et dimensions très variables; dimensions moyennes et extrêmes (ex Tableau 4): ex insectes: (15)21-32(40) x (9)11-14(16) µm; rapport L/D (1,4)1,7-2,3(2,9) ex cultures: (15)21-37(42) x (7)11-17,5(22) µm; rapport L/D (1,2)1,6-2,6(3,5). *Conidies secondaires* généralement semblables aux primaires mais un peu plus petites, plus ovoïdes et à rapport L/D plus faible, ou bien subsphériques avec une papille bien marquée et parfois une petite bosse apicale ou apicule ponctiforme, moins évidente que chez *Entomophthora muscae* (Cohn) Fres. mais du même type, dimensions (14)19(24) x (11)16(20); rapport L/D (1,1)1,2(1,4). Corps hyphaux très variables 32-260 x 6-13 µm, avec souvent plusieurs ramifications, plus ou moins vacuolisés, avec 1 à 12 gros noyaux de 6-8 µm de diamètre. *Cystides* issues d'une cellule mère sphérique de 30 à 40 µm de diamètre, larges à la base (12-14 µm), plus fines à l'apex (7-9 µm), allongées (120-240 µm), plus longues que les conidiophores, arrondies à l'apex, contenant 10 à 15 noyaux. *Rhizoïdes* hyalins, très fins, monohyphaux, nombreux (15 à 30), issus du thorax et de l'abdomen de l'hôte, de longueur très variable liée à la distance entre le cadavre de l'hôte et la plante support (80 à 400 µm, diamètre 10 à 25 µm), fixés au substrat par une plaque adhésive irrégulièrement circulaire. *Spores durables* inconnues.

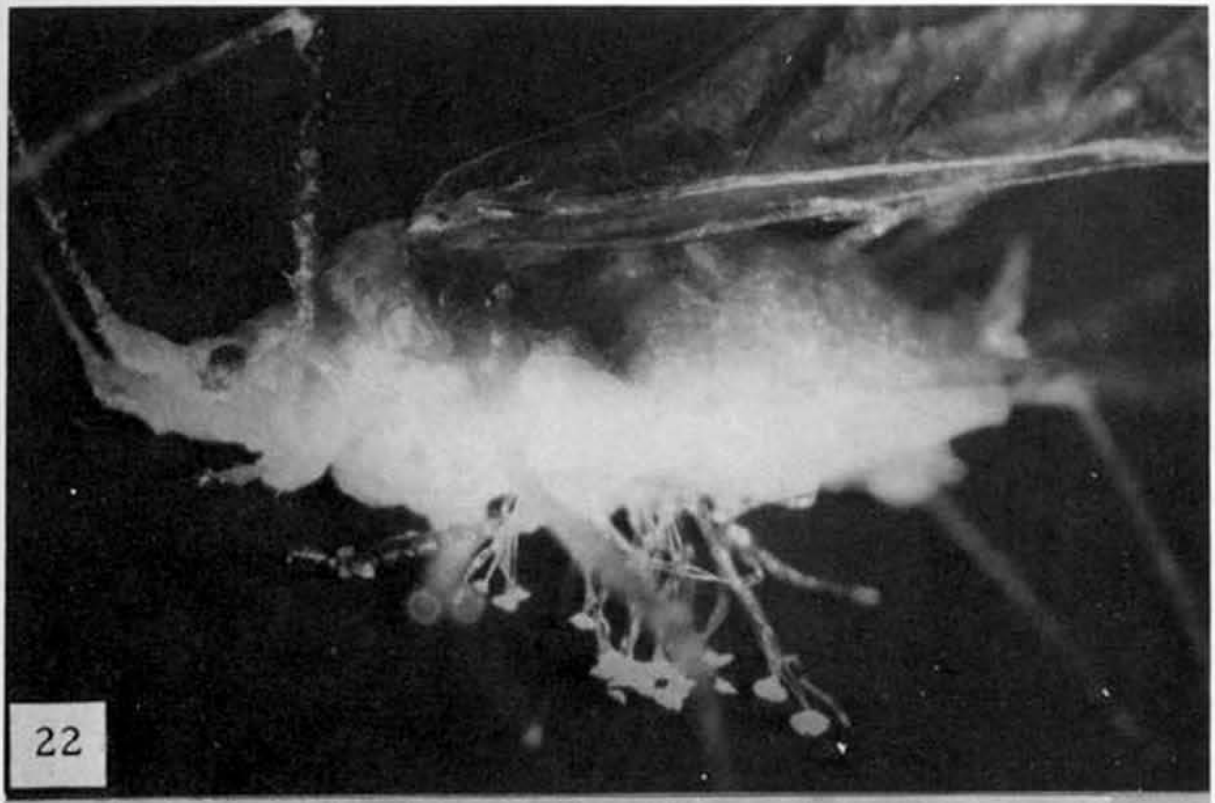
Hôtes: très nombreux genres d'Homoptères *Aphididae*.

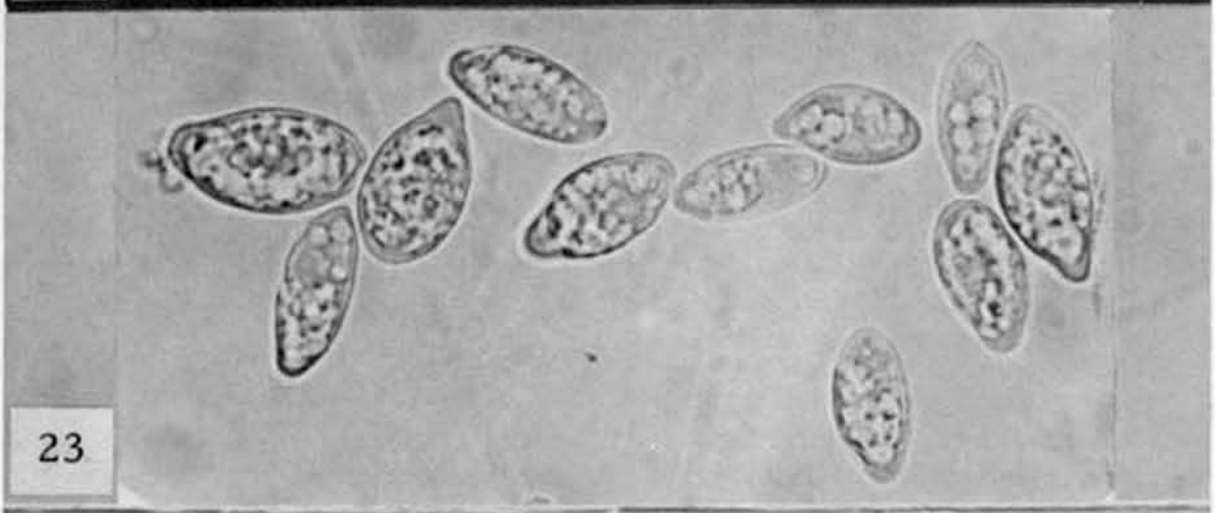
Distribution géographique: Asie, Europe, Afrique du Nord, Amérique du Nord, Australie; vraisemblablement commune partout quoique plus rare dans les régions tropicales.

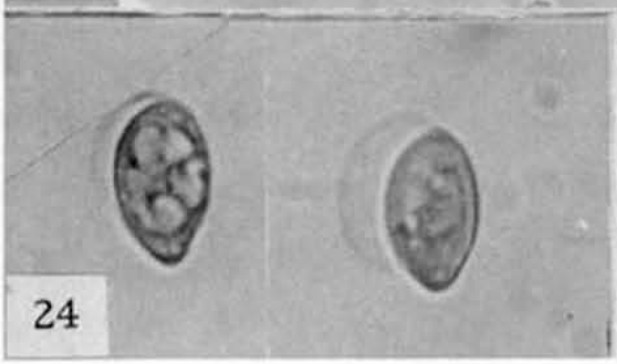
Holotype: un individu infecté (monté sur lame) de *Nasonovia ribisnigri* Mosley sur *Ribes alpinum*, Les Allamands, Samoëns, Haute-Savoie, France, 25 X 1979, G. Remaudière. *Isotypes*: les exsiccata de la culture IPLB 1284 isolée de l'individu holotype, les cadavres de *Acyrthosiphon pisum* Harris et de *Sitobion avenae* Fabricius infectés expérimentalement par cette culture et conservés en alcool à 70 % et à sec, les conidies primaires projetées de ces cadavres et de la culture IPLB 1284 et conservées en partie à sec sur lames et en partie montées dans le bleu trypan lactophénol. L'holotype et des isotypes sont déposés au Laboratoire de Cryptogamie du Muséum National d'Histoire Naturelle, Paris (PC); des isotypes sont déposés dans les herbiers suivants: K, E, PAV, FH.

Autres collections: 14 récoltes mentionnées dans le Tableau 4 et plusieurs centaines faites en France, au Moyen-Orient, en Amérique du Nord (Canada, USA, Mexique) par G. Remaudière, J.P. Latgé, B. Papierok et G. Thoizon; elles sont conservées dans la collection G.R., Institut Pasteur Paris.

Culture: la souche IPLB 1284, ex holotype, est maintenue à IPLB et déposée à l'ATCC, au CBS, et à l' IMI (N° IMI 245780).







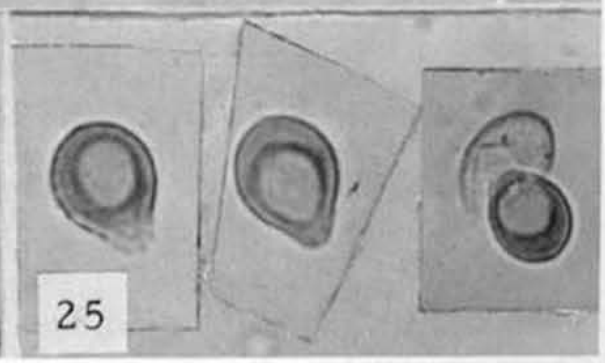


Fig. 22-25. *Erynia neoaphidis* sp. nov.; 22, rhizoïdes sur un ailé d'*Acyrthosiphon pisum* Harris infecté par la souche IPLB 1284; 23, conidies primaires ex culture IPLB 1284; 24, conidies primaires montrant la paroi bituniquée; 25, conidies secondaires subsphériques, pourvues d'un léger apicule.

TABLEAU 4

Mensurations (en µm) de conidies de *Erynia neoaphidis* sp. nov. projetées de pucerons (50 conidies mesurées par insecte)

	LONGUEUR			DIAMETRE			L/D		
	min	MOY	max	min	MOY	max	min	MOY	max
EUROPE: FRANCE									
1	22	26,8	32	10	12,2	15	1,7	2,21	2,8
2	16	25,1	30	9	12,7	16	1,6	1,99	2,4
3	23	31,9	40	12	14,0	16	1,6	2,29	2,9
4	15	24,0	30	10	12,2	15	1,5	1,97	2,3
5	16	23,7	28	10	11,3	13	1,4	2,10	2,5
6	22	25,3	28	12	13,4	15	1,6	1,88	2,3
7	20	24,1	30	11	12,1	14	1,6	2,00	2,6
AMERIQUE DU NORD: USA, MEXIQUE									
8	20	25,2	38	10	11,4	14	1,5	2,23	2,7
9	17	22,1	27	10	11,8	14	1,5	1,87	2,2
10	19	23,7	30	10	11,4	15	1,5	2,08	2,4
11	20	25,0	30	10	12,3	15	1,6	2,05	2,5
ASIE: TURQUIE, IRAN									
12	19	23,5	33	11	12,7	16	1,5	1,85	2,2
13	19	25,1	31	10	12,3	14	1,5	2,05	2,7
14	20	24,1	27	9	10,8	12	1,9	2,24	2,7
Moyennes:		22,1-31,9			10,8-14,0			1,85-2,29	

ORIGINE DES SPECIMENS

1 *Aphis rumicis* L. sur *Rumex acetosa*, Les Houches (Haute-Savoie, France) 21 VI 1976, Remaudière.
2 *Microlophium carnosum* Walker, sur *Urtica dioica*, Lac Vert (Haute-Savoie, France) 28 IX 1977, Remaudière.
3 *Wahlgreniella ossiannilssoni* Hille Ris Lambers, sur *Rosa alpina*, Lac Vert (Haute-Savoie, France) 28 VII 1977, Remaudière.
4 *Metopolophium dirhodum* Walker, sur *Triticum*, Coubert (Seine-et-Marne, France) 28 VII 1979, Remaudière.
5 *Metopolophium dirhodum* Walker, sur *Zea mays*, même localité.
6 *Microlophium carnosum* Walker, sur *Urtica dioica*, Quinéville (Manche, France) 27 XI 1977, Remaudière.
7 *Aphis ulicis* Walker, sur *Ulex europaeus*, Paimpol (Côtes-du-Nord, France) 26 VIII 1977, Remaudière.
8 *Macrosiphum gauraeWillia*, sur *Oenothera*, Chute-aux-Galets (Québec, Canada) 25 VIII 1976, Remaudière & Latgé.
9 *Nearctaphis bakeri* Cowen, sur *Trifolium*, Tuckerman's Ravine (New Hampshire, USA) 4 IX 1976, Remaudière & Latgé.
10 *Myzus persicae* Sulzer, sur ?, Xochimilco (Mexique, D.F.) 17 VIII 1978, Latgé.
11 Spécimen de même origine.
12 *Hyperomyzus lactucae* Mosley, sur *Sonchus*, Izmir (Turquie) 29 III 1979, Oncüer.
13 *Sitobion avenae* Fabricius, sur *Dactylis glomerata*, Tchalus (Iran)16 V 1977, Latgé.
14 *Aphis gossypii* Glover, sur *Ranunculus*, Pol-e-Karat (Iran) 19 V 1977, Latgé.

TABLEAU 5

Comparaison des dimensions moyennes (en µm) des conidies de "*E. aphidis*" sensu Nowak. et celles de notre matériel de *Erynia neoaphidis* sp. nov. (Tabl. 4), projetées d'insectes et de cultures (n = nombre de conidies mesurées) (les valeurs entre parenthèses correspondent à Lm/Dm estimé à partir des valeurs disponibles)

	LONGUEUR	DIAMETRE	L/Dmoy	n
ex INSECTES				
Nowakowski 1883	25,6	14,2	(1,8)	?
Thaxter 1888	25,0	12,0	(2,1)	?
Gustafsson 1965	21,0	11,0	(1,9)	?
Aruta & al. 1974	23,2	12,7	(1,8)	250
moyennes du Tabl. 4	22,1-31,9	10,8-14,0	1,85-2,29	14x50
moyennes générales	21,0-31,9	10,8-14,2	1,70-2,29	>1000
ex CULTURES				
5 souches Gustafsson	29,0-37,0	13,0-17,0	(1,6-2,2)	5x100
43 souches IPLB (orig.)	20,6-32,7	11,1-17,5	1,59-2,56	43x50
moyennes générales	20,6-37,0	11,1-17,5	1,59-2,56	2700

Remarques

Erynia neoaphidis correspond à l'espèce la plus fréquente dans les populations d'Aphides. A l'exception de *Entomophthora muscae* (Cohn) Fres. et peut-être de *E. grylli* Fres., Thaxter (1888) la considère comme la plus commune de toutes les Empusées. Pour chacune des 24 espèces d'*Entomophthora* qu'il a trouvées en Suède entre 1960 et 1963, Gustafsson (1965) donne le détail de ses récoltes; sa liste concernant "*E. aphidis*" est de loin la plus longue. Thoizon (1970) répertorie 95 espèces d'Aphides attaquées par cette Entomophthorale qu'elle a rencontrée dans 47 % de ses 191 lots de pucerons avec mycose provenant des diverses régions de France. Dans l'Est des USA et du Canada, Remaudière et al. (1978) constatent que "*E. aphidis*" est présent dans 82 % des échantillons comportant des cas de mycose et est responsable de la mort de 90 % des 696 pucerons dont l'agent de la mycose a été reconnu. Les prospections réalisées par Remaudière & Latgé en Iran et au Mexique (résultats non publiés) révèlent encore que *Erynia neoaphidis* est de très loin le principal pathogène des Aphides: l'espèce est représentée dans 81 % des échantillons avec mycose en Iran et 94 % au Mexique.

Erynia neoaphidis est l'une des espèces d'Entomophthorales les plus variables tant au point de vue morphologique que physiologique. La vitesse de croissance et les

exigences nutritionnelles diffèrent considérablement d'une souche à l'autre mais ces différences ne sont pas liées à des particularités morphologiques. Certaines souches se développent bien sur milieu de Sabouraud tandis que d'autres exigent un enrichissement de ce milieu par du jaune d'oeuf (4 parties de Sabouraud pour une partie de jaune d'oeuf).

La caractérisation de *Erynia neoaphidis* devient difficile dès que l'on fait abstraction de la famille hôte (*Hom. Aphididae*) car la ressemblance est grande entre *Erynia neoaphidis*, *Entomophthora delphacis* Hori 1906, espèce à statut mal défini qui attaque au Japon *Nilaparvata lugens* Stål (*Hom. Delphacidae*) et *Erynia dipterigena* (Thaxter) comb. nov. qui est un pathogène commun sur des Diptères de diverses familles. Selon Shimazu (1976) les trois espèces pourraient être distinguées par leur spectre d'hôte et par les caractères de croissance sur milieu artificiel. Vu les différences considérables que nous constatons, non seulement dans la vitesse de croissance, mais aussi dans l'aspect de la culture des quelques centaines de souches de *E. neoaphidis* que nous avons isolées depuis 10 ans, les critères proposés par Shimazu ne nous paraissent pas satisfaisants.

Morphologiquement, les 3 espèces considérées présentent des conidies très semblables mais *Erynia dipterigena* peut être séparé par la présence de spores durables hyalines à diamètre de 20 à 40 µm et de formation externe; chez *Erynia neoaphidis* et *Entomophthora delphacis* les spores durables ne sont pas connues; les dimensions données par Shimazu pour les conidies de *Entomophthora delphacis* projetées d'insectes, (29,2)32,7(35,6) x (13,0)14,8(17,5) sont supérieures à celles de *Erynia neoaphidis* obtenues de pucerons, toutefois Shimazu précise que les conidies de *Entomophthora delphacis* projetées de cultures mesurent (22,9)30,2(36,8) x (12,4)15,5(20,3) µm, valeurs qui correspondent bien à celles des conidies de culture de *Erynia neoaphidis*.

Une souche de *Entomophthora delphacis* reçue de Shimazu (F 33) (N° IPLB 918) nous a donné à trois époques différentes des conidies dont les mesures soulignent l'extrême variabilité:

1) (22)27,6(31) x (13)16,2(19) µm; L/D (1,5)1,70(1,9)
2) (20)24,7(28) x (12)14,8(18) µm; L/D (1,4)1,67(1,9)
3) (19)22,8(25) x (11)12,6(15) µm; L/D (1,4)1,81(2,0)

En l'absence de matériel original, nous ne pouvons décider d'une éventuelle identité entre *Entomophthora delphacis* et *Erynia neoaphidis* et préférons considérer *E. delphacis* comme *nomen dubium*.

D. DESCRIPTION DE *ERYNIA NOURYI* SP. NOV.

Erynia nouryi sp. nov.
(= "*Entomophthora aphidis*" sensu Petch 1939)
(= "*Entomophthora exitialis*" sensu Gustafsson 1965)

Diagnose (latine et française) (Fig. 26-28).

Fungus entomogeneus (Entomophthoraceae). Conidiophori *ramosi, in sporodochia ad hospitem aggregata.* Primaria conidia *uninucleata, hyalina, ovoidea, axialiter symetrica, sparsim asymetrica, in apice rotunda, cum lata, brevi, rotundata vel applanata, pauce prominente, pariete ad conidii corporem continuo, papilla, in insectis (12)15,0-16,6(20) x (7)8,0-10,5(12) µm, in cultura (Gustafsson) (16)18(21) x (9)11(12) µm (ultima et media dimensio).* Secondaria conidia *ignota.* Perdurantes sporae *hyalinae in maturitate, cum laevi et crasso (3-4 µm) pariete, in massa albae, basim brevi crassotunicato parietis conidiophori segmento post ejectionem ornatae, in insectis (20)24,9-30,4(36) µm, in cultura (Gustafsson) (23)30(33) µm.* Hyphalia corpora *hyalina, varia, 90-180 x 6-10 µm, rigida vel curvata vel sinuosa, simplicia vel ramosa, cum granuloso cytoplasmate et 4-6 µm crassis nucleis.* Rhizoidea, *ut singula hypha, in conidia ferentibus hospitibus, non vero in perdurantes sporas continentibus hospitibus.* Hospes: Pemphigus bursarius *L.*, Aphis fabae *Scop.*, Aphis umbrella *Börner. In Anglia, Francia, Suecia, Palestina.* Holotypus: *in* Pemphigus bursarius *ad Cichorii intybus radices, Buchy, Francia, 10 jan. 1957, E. Noury (G. Remaudière n° 4003).*

Conidiophores ramifiés, apparaissant en petits coussinets (sporodochies) à la surface de l'hôte. *Conidies primaires* uninucléées, ovoïdes, à sommet arrondi, hyalines à symétrie axiale, rarement asymétriques avec une papille assez large, peu marquée, courte, faiblement arrondie à presque aplatie, en continuité du corps de la conidie; dimensions ex insectes: (12)15,0-16,6(20) x (7)8,0-10,5(12) µm, ex culture (Gustafsson 1965): (16)18(21) x (9)11(12) µm (Tableau 6). *Conidies secondaires* non observées (sans doute semblables aux primaires). *Spores durables* hyalines à maturité, à paroi épaisse (3 à 4 µm) et lisse donnant un aspect blanc laiteux à l'hôte plein de spores; point d'attachement de la spore à l'hyphe dont elle est issue marqué par court segment à membrane épaissie; diamètre ex insectes (20)24,9-30,4(36) µm; ex culture (Gustafsson 1965) (23)30(39) µm (Tableau 6). *Corps hyphaux* incolores, variables, 90-180 x 6-10 µm, droits, courbés ou sinués, simples ou ramifiés, à cytoplasme granuleux, à noyaux assez volumineux de 4-6 µm de diamètre. *Cystides* rares cylindriques à apex obtus, un peu plus épaisses que les conidiophores et mesurant environ 70-140 x 8-11 µm. *Rhizoïdes* monohyphaux, observés sur hôte porteur de conidies; les hôtes présentant des spores durables sont habituellement dépourvus de conidies et de rhizoïdes et sont fixés à la plante par les stylets du rostre.

Hôtes connus: Pemphigus bursarius L. (deux cas: Petch en Angleterre, Noury en France), *Aphis fabae* Scop. (un cas: Gustafsson en Suède), *Aphis umbrella* Börner (un cas, Kenneth en Israël) (*Hom. Aphididae*).

Distribution géographique: Angleterre, France (Normandie), Suède, Israël.

Holotype: échantillon recueilli par E. Noury (N° 489) ex *Pemphigus bursarius* L. sur racines de *Cichorium intybus* (endives) à Buchy, Seine-Maritime, France, le 10 I 1957 et enregistré sous le N° 4003 dans la collection d'Aphides G. Remaudière, Institut Pasteur, Paris. L'échantillon comporte 2 larves et un adulte aptère porteurs de spores durables

TABLEAU 6

Mensurations (en µm) de conidies et de spores durables de *Erynia nouryi* sp. nov., projetées d'insectes et de cultures (n = nombre de conidies ou spores durables mesurées) (les valeurs entre parenthèses sont estimées à partir des données disponibles).

	LONGUEUR			DIAMETRE			L/D			n
	min	MOY	max	min	MOY	max	min	MOY	max	
CONIDIES ex INSECTES										
1 Petch 1939	12	(15)	18	9	(10,5)	12				?
3a Noury (orig.)	13	16,6	20	8	9,1	11	1,4	1,84	2,4	32
4a Kenneth (orig.)	13	16,5	20	7	8,4	11	1,5	1,97	2,6	50
4b Kenneth (orig.)	14	16,6	19	7	8,0	9	1,7	2,08	2,5	50
Moyennes		15,0-16,6			8,0-10,5			1,8-2,1		>150
CONIDIES ex CULTURES										
2 Gustafsson 1965	16	18	21	9	11	12		(1,6)		?
SPORES DURABLES ex INSECTES										
1 Petch 1939				23	(27,5)	32				?
3b Noury (orig.)				23	28,8	33				50
3c Noury (orig.)				26	30,4	36				50
3d Noury (orig.)				26	30,3	36				50
4a Kenneth (orig.)				20	24,9	30				50
Moyennes					24,9-30,4					>200
SPORES DURABLES ex CULTURES										
2 Gustafsson 1965				23	30	39				?

ORIGINE DES SPECIMENS

1 *Pemphigus bursarius* L.(= *P. lactucarius* Passerini) sur *Lactuca* (Angleterre) IX 1937 (in Petch 1939).

2 *Aphis fabae* Scopoli, sur *Beta vulgaris*, Arlöw (Skäne, Suède) 21 VII 1960 (in Gustafsson 1965).

3 *Pemphigus bursarius* L., sur *Cichorium intybus* (endive), Buchy (Seine-Maritime, France) 10 I 1957 (E. Noury leg. 489); a, b, c, d, spécimens isotypes.

4 *Aphis umbrella* Börner, sur *Malva* (Israël) 8 I 1979 (Shiller & Kenneth leg.); a, individu portant à la fois des conidies et des spores durables jeunes; b, individu portant seulement des conidies; la même collection comporte également des spécimens présentant des conidies de *Erynia neoaphidis*.

---

et une larve présentant des conidiophores et quelques conidies. Ces spécimens ont été conservés en alcool 22 ans et montés en 1979 dans le bleu trypan lactophénol. Une préparation isotype est déposée dans chacun des herbiers suivants: PC, K et FH.

Autres collections: Tableau 6.

Nous dédions cette espèce à la mémoire de E. Noury, naturaliste amateur qui a étudié avec passion les relations et les équilibres entre les peuplements végétaux et animaux de la Haute-Normandie.

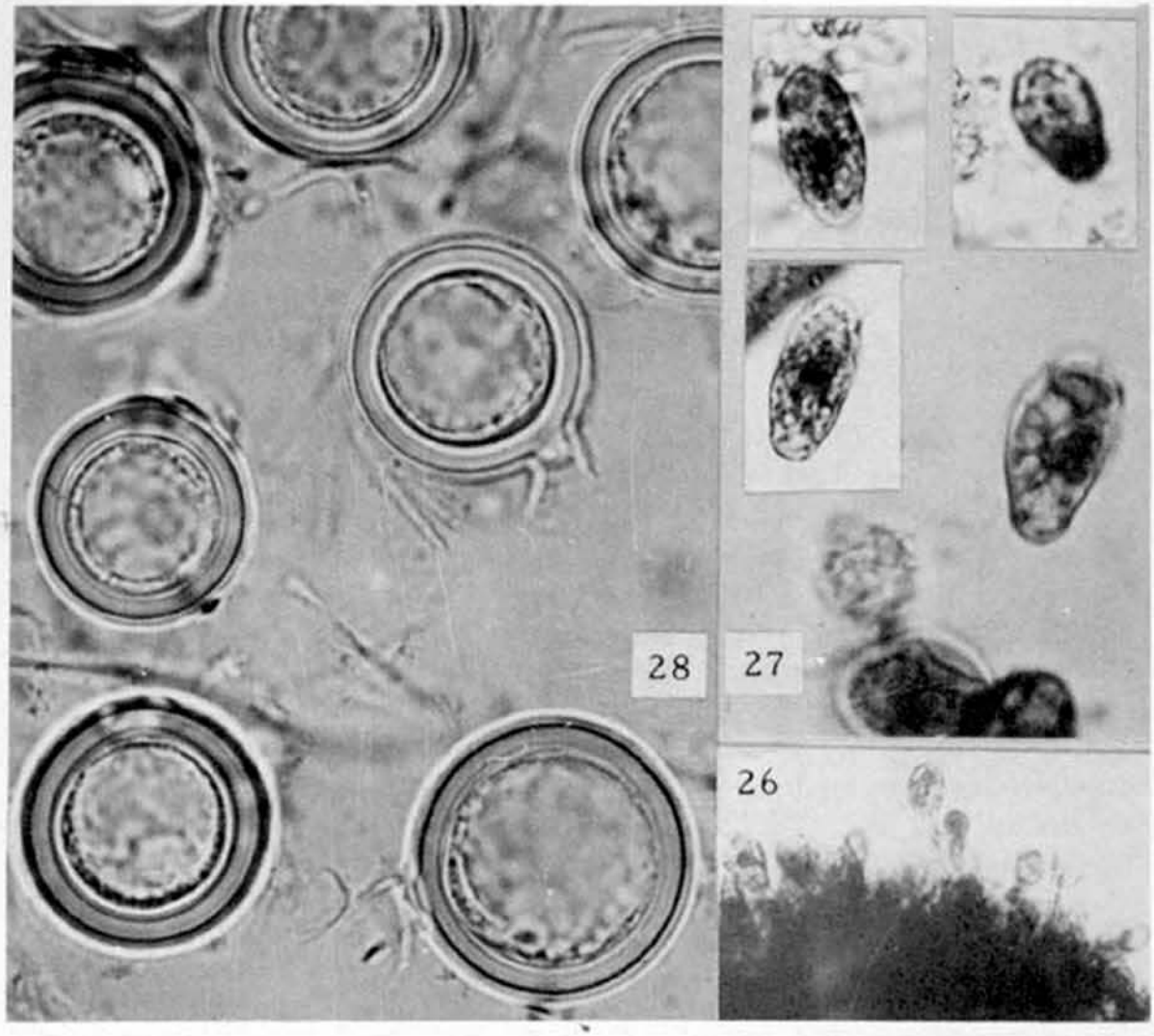


Fig. 26-28. *Erynia nouryi* sp. nov. ex *Pemphigus bursarius* L.; 26, conidiophores groupés en sporodochie portant de jeunes conidies; 27, conidies primaires; 28, spores durables mûres avec leur point d'attachement à l'hyphe.

Remarques:

Erynia nouryi est une espèce peu commune, surtout reconnaissable par ses conidies plus petites, à papille plus large et plus aplatie que celles de *E. neoaphidis* et par ses spores durables hyalines et lisses. La formation de ces spores durables n'a pas été observée. Il n'existe pas de culture de cette espèce qui a seulement été isolée une fois mais dont la souche a été détruite accidentellement (Gustafsson, 1965).

E. nouryi est une des rares espèces rencontrées dans les populations d'aphides radicicoles comme *Pemphigus bursarius* L.

Cette espèce est peut-être responsable des cas de mycose signalés sur *Pemphigus betae* Doane par Maxson (1916) au

Colorado, Charles (1941) en Californie et Harper (1958) en Alberta (Canada) et attribués à "*E. aphidis* Hoffm."

Aruta et al. (1974) ont signalé du Chili la présence de conidies et de spores durables de *Entomophthora aphidis* Hoffm. in Fres. dans les populations de 4 espèces de pucerons. Les dimensions données permettent de reconnaître les conidies de *Erynia neoaphidis*; en revanche les mensurations de spores durables, (25,8)29,4(33,1) µm, pourraient être celles de *E. nouryi* ou celles d'une autre espèce comme *Zoophthora radicans*.

Milner (1978), Milner & Teakle (1978) et Teakle (1978) ont observé en Australie sur 6 espèces d'Aphides (dont *Therioaphis trifolii* Monell, l'hôte original de *Entomophthora exitialis* Hall & Dunn) un agent de mycose qu'ils identifient provisoirement comme *Entomophthora* nr *exitialis*; occasionnellement, dans la nature, quelques individus ont été trouvés porteurs de spores durables petites (diamètre 20 µm). La souche EM 507 que ces auteurs ont isolée et nous ont transmise (IPLB 1172) représente typiquement *Erynia neoaphidis*; comme nos autres souches de cette espèce, elle ne donne pas de spores durables. Les spores durables constatées en Australie ne sont pas actuellement identifiables.

E. COMPARAISON DES TROIS ESPECES ETUDIEES

Le diagramme (Fig. 29) permet de comparer la forme et les dimensions des conidies primaires de *Zoophthora aphidis*, *Erynia neoaphidis* et *Erynia nouryi*, à la fois sur pucerons et en culture, sur la base des données déjà mentionnées pour chaque espèce.

Sur insectes, on constate la nette distinction des trois espèces: *Z. aphidis* présente les rapports L/D les plus élevés, *E. nouryi* présente les dimensions les plus faibles. En culture *E. neoaphidis* montre une grande variabilité.

En résumé nous reconnaissons:

Zoophthora aphidis (Hoffm. in Fres.) Batko, par la présence de capilloconidies, par des conidies primaires de longueur moyenne supérieure à 26 µm avec un rapport L/D moyen supérieur à 2,4 et par de grandes spores durables pigmentées; il est spécifique d'*Anoecia*.

Erynia neoaphidis sp. nov., par l'absence de capilloconidies, par des conidies primaires de longueur moyenne supérieure à 20 µm avec un rapport L/D moyen compris entre 1,7 et 2,6 et jusqu'à présent par l'absence de spores durables; il attaque la plupart des aphides.

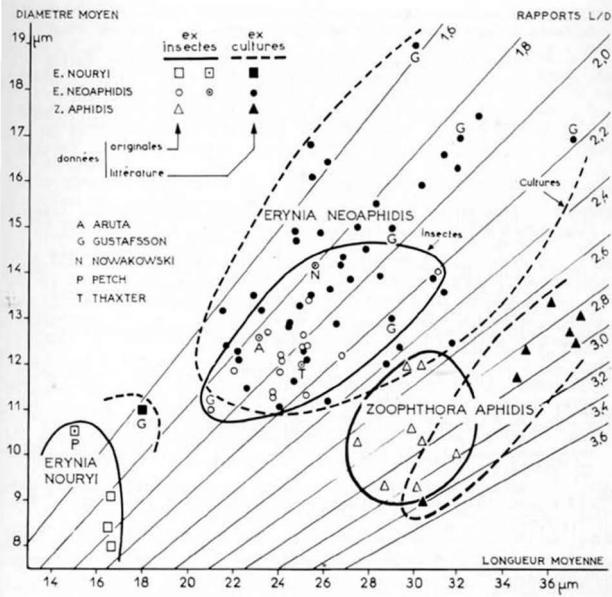


Fig. 29. Comparaison des dimensions conidiennes de *Zoophthora aphidis* (Hoffm. in Fres.) Batko, *Erynia neoaphidis* sp. nov. et *Erynia nouryi* sp. nov. (conidies de pucerons et de cultures).

Erynia nouryi sp. nov., par l'absence de capilloconidies, par des conidies primaires petites, de longueur moyenne inférieure à 18 µm et de rapport L/D moyen variant de 1,4 à 2,4 et par la présence de spores durables hyalines de dimension moyenne; il n'est connu que sur quelques aphides et en particulier sur les *Pemphigus* radicicoles.

REMERCIEMENTS

La présente étude n'aurait pu être réalisée sans la collaboration très appréciée des responsables des herbiers du Muséum de Paris, de Kew, d'Edinburgh, de Pavie et des collections de l'ATCC et du CBS.

Les auteurs remercient spécialement Mme R. Krejzova (Prague), le Dr S. Keller (Zurich), les Drs R. Kenneth et I. Ben Ze'ev (Rehovot, Israël) et le Dr M. Shimazu (Kyushu, Japon) pour la communication de souches et de spécimens de leur collection et pour leur permission de

faire état de ces matériaux. Ils sont reconnaissants aux Drs I.M. Hall et D. MacLeod pour leurs critiques et encouragements.

Les auteurs expriment leur vive gratitude à J.P. Latgé et B. Papierok (Unité de Lutte Biologique, Institut Pasteur) pour l'aide inestimable qu'ils ont apportée dans la mise au point de ce manuscrit ainsi qu'à M. G. Langlois et Mme J. Delabarre pour le soin avec lequel ils ont réalisé l'illustration et la préparation technique du présent mémoire.

BIBLIOGRAPHIE

ANDERSON, J.F. & RINGO, S.L. 1969. *Entomophthora aquatica* sp.n. infecting larvae and pupae of floodwater mosquitoes. *J. Invertebrate Pathol. 13*: 386-393.

ARUTA, C., CARILLO, R & GONZALES, S. 1974. Determinación para Chile de hongos entomopatógenos del género *Entomophthora* 1. *Agro Sur 2*: 62-70.

ARX, J.A. von 1970. The genera of fungi sporulating in pure culture. *J. Cramer Verlag*, 288 pp.

BATALIN 1881: N. SOROKIN, Zur Entwickelung der *Entomophthora*-Arten. *L. Just Bot. Jahresb. 9*: 291-292.

BATKO, A. 1964a. Remarks on the genus *Entomophthora* Fresenius 1856 non Nowakowski 1883 (*Phycomycetes: Entomophthoraceae*). *Bull. Acad. Polon. Sci., cl. II, Ser. Sci. biol. 12*: 319-321.

BATKO, A. 1964b. On the new genera : *Zoophthora* gen. nov., *Triplosporium* (Thaxter) gen. nov. and *Entomophaga* gen. nov. (*Phycomycetes: Entomophthoraceae*). *Bull. Acad. Polon. Sci., cl. II, Ser. Sci. biol. 12*: 323-326.

BATKO, A. 1964c. Remarks on the genus *Lamia* Nowakowski 1883 *vs.Culicicola* Nieuwland 1916 (*Phycomycetes: Entomophthoraceae*). *Bull. Acad. Polon. Sci., cl. II, Ser. Sci. biol. 12*: 399-402.

BATKO, A. 1964d. Some new combinations in the fungus family *Entomophthoraceae* (*Phycomycetes*). *Bull. Acad. Polon. Sci., cl. II, Ser. Sci. biol. 12*: 403-406.

BATKO, A. 1966a. A new aphidocolous fungus from Poland *Zoophthora phalloides* sp. nov. (*Entomophthoraceae*). *Acta Mycol. 2*: 7-13.

BATKO, A. 1966b. On the subgenera of the fungus genus *Zoophthora* Batko 1964 (*Entomophthoraceae*). *Acta Mycol. 2*: 15-21.

BEN ZE'EV, I. & KENNETH, R.G. 1979. *Zoophthora erinacea* sp.n. (*Zygomycetes: Entomophthoraceae*) a fungal parasite of Aphids. *Mycotaxon 10*: 219-232.

BEN ZE'EV, I. & KENNETH, R.G. 1980. *Zoophthora phytonomi* (Arthur) Batko and *Conidiobolus osmodes* Drechsler (*Zygomycetes: Entomophthoraceae*), two pathogens of *Hypera* species (*Coleoptera: Curculionidae*) coincidental in time and place. *Entomophaga 25*.

BOSE, S.K. & MEHTA, P.R. 1953. A new species of *Entomophthora* on beetles. *Trans. Brit. Myc. Soc. 36*: 52-56.

BREFELD, O. 1870. Entwicklungsgeschichte der *Empusa muscae* und *Empusa radicans*. *Bot. Zeitg. 28*: 161-166; 177-186.

BREFELD, O. 1877. Ueber die Entomophthoreen und ihre Verwandten. *Bot. Zeitg. 35*: 345-355; 368-372.

BROBYN, P.J. & WILDING, N. 1977. Invasive and developmental processes of *Entomophthora* species infecting aphids. *Trans. Brit. Mycol. Soc. 69*: 349-366.

BUCHER, G.E. & MACLEOD, D.M. 1974. Rediscovery of *Tarichium megaspermum* (*Entomophthoraceae*) in canadian cutworms (*Noctuidae*). *J. Invertebrate Pathol. 23*: 157-163.

CHARLES, V.K. 1941. A preliminary check list of entomogenous fungi in North America. *U.S. Dept. Agr., Insect Pest Survey Bull. 21*: 725.

COHN, F. 1855. *Empusa muscae* und die Krankheit der Stubenfliegen. *Verh. Keiserl. Leopold-Carol. Akad. Naturforsch. 25*: 299-360.

COHN, F. 1870a. Ueber Pilz-Epidemien bei den Insekten. *Jahresb. der Schles. Ges. vaterländ. Cultur 47*: 85-87.

COHN, F. 1870b. Ueber eine neue Pilzkrankheit der Erdraupen. *Beitr. z. Biol.d.Pflanzen 1*: 58-86.

FRESENIUS, G. 1856. Notiz, Insecten-Pilze betreffend. *Bot. Zeitg. 14*: 882-883.

FRESENIUS, G. 1858. Ueber die Pilzgattung *Entomophthora*. *Abhandl. Senckenberg. naturforsch. Ges. 2*: 201-210.

GIARD, A. 1879. Deux espèces d'*Entomophthora* nouvelles pour la flore française et présence de la forme *Tarichium* sur une Muscide. *Bull. Sci. France et Belg. 11*: 353-363.

GROBLER, J.H., MACLEOD, D.M. & DELYSER, A.J. 1962. The fungus *Empusa aphidis* Hoffmann parasitic on the woolly pine needle aphid, *Schizolachnus pini-radiatae* (Davidson). *Can. Entomologist 94*: 46-49.

GUSTAFSSON, M. 1965. On species of the genus *Entomophthora* Fres. in Sweden. I. Classification and distribution. *Landtbrukshögskolans Annaler 31*: 103-212.

HALL, I.M. & DUNN, P.H. 1957. Entomophthorous fungi parasitic on the spotted alfalfa aphid. *Hilgardia 27*: 159-181.

HARPER, A.M. 1958. Notes on behaviour of *Pemphigus betae* Doane (*Homoptera: Aphididae*) infected with *Entomophthora aphidis* Hoffm. *Can.Entomol. 90*: 439-440.

HAWKSWORTH, D.L. 1974. Mycologist's handbook. *Commonw. Mycol. Inst., Kew*, 231 pp.

HOUGHTON, W. & PHILLIPS, W. 1886. On *Aphis rumicis* Linn., as a pest on the mangel-wurzel crops in Shropshire in the autumn of 1885, and on a fungus destructive of the same *Aphis*. *Ann. Mag. nat. Hist. Ser.* 5, *18* (N° 103): 1-7.

HUMBER, R.A., SOPER, R.S., WILDING, N. & REMAUDIERE, G. 1977. The identification of certain widely studied strains of *Entomophthora* pathogenic for Aphids. *Mycotaxon 5*: 307-310.

KREJZOVA, R. 1973. The preparation of reproductive stages of *Entomophthora exitialis* Hall & Dunn. *Vestnik. Čs. spol. zool. 37*: 21-22.

KRENNER, J.A. 1961. Studies in the field of the microscopic fungi, III on *Entomophthora aphidis* H. Hoffm. with special regard to the family of the *Entomophthoraceae* in general. *Acta Bot. Acad. Sci. Hung. 7*: 345-376.

LAGERHEIM, G. 1898. Mycologische Studien. I. Beiträge zur Kenntnis der Parasitischen Pilze, 1-3. *Bihang Till K. Svenska Vet.-Akad. Handlingar 24*, Afd III: 3-21.

LAKON, G. 1919. Die Insektenfeinde ausder Familie Entomophthoraceen. *Z.f. angew. Ent. 5*: 161-216.

LAKON, G. 1935 (1934). Entomophthoraceen-Studien I-IV. *Z. f. angew. Ent. 21*: 89-95.

LATGE, J.P., KING, D.S. & PAPIEROK, B. 1980. Synonymie de *Entomophthora virulenta* Hall & Dunn et de *Conidiobolus thromboides* Drechsler. *Mycotaxon 11*: 255-268.

MACLEOD, D.M. & MÜLLER-KÖGLER, E. 1970. Insect pathogens: species originally described from their resting spores mostly as *Tarichium* species (Entomophthorales:*Entomophthoraceae*). *Mycologia 62*: 33-66.

MACLEOD, D.M., MÜLLER-KÖGLER, E. & WILDING, N. 1976. *Entomophthora* species with *muscae*-like conidia. *Mycologia 68*: 1-29.

MACLEOD, D.M., TYRRELL, D. & SOPER, R.S. 1979. *Entomophthora canadensis* sp. nov., a fungus pathogenic on the woolly pine-needle aphid, *Schizolachnus piniradiatae* (Davidson). *Can. J. Bot. 57*: 2663-2672.

MAXSON, A.C. 1916. Some unpublished notes on *Pemphigus betae* Doane. *J. econ. Ent. 6*: 500-505.

MILNER, R.J. 1978. The effects of disease on populations of Lucerne aphids. *Lucerne Aphid Workshop 27th-30th Nov. 1978. Dept. Agr. NSW.*: 105-108.

MILNER, R.J. & TEAKLE, R.E. 1978. An isolate of *Entomophthora* nr. *exitialis* from *Acyrthosiphon kondoi*. *Lucerne Aphid Workshop 27th-30th Nov. 1978. Dept. Agr. NSW*: 113-117.

NIEUWLAND, J.A. 1916. Critical notes of new and old genera of plants VII. *The Amer. Midl. Nat. 4*: 374-378.

NOWAKOWSKI, L. 1877. Die Copulation bei einigen Entomophthoreen. *Bot. Zeitg. 35*: 217-222.

NOWAKOWSKI, L. 1881. O grupie owadomorków (*Empusaceae*). *Dzienn. III Zjazdu Lek. Przyr. Polak. Krakow, Sekc. Bot. 6*: 67-68.

NOWAKOWSKI, L. 1882. Ueber die Entomophthoreen. *Bot. Zeitg. 40*: 560-561.

NOWAKOWSKI, L. 1883. *Entomophthoreae*. Przyczynek do znajomości pasorzytnych grzybków sprawiających pomór owadów. *Pamietn. Wydz. Akad. Umiej. w. Kraków 8*: 153-183.

PETCH, T. 1937. Notes on entomogenous fungi. *Trans. Brit. Mycol. Soc. 21*: 34-67.

PETCH, T. 1939. Notes on entomogenous fungi. *Trans. Brit. Mycol. Soc. 23*: 127-148.

PETCH, T. 1948. A revised list of british entomogenous fungi. *Trans. Brit. Mycol. Soc. 31*: 286-304.

POVAH, A.H.W. 1935. The fungi of Isle Royale, Lake Superior. *Pap. Mich. Acad. Sci. Arts Lett. 20*: 113-156.

RABENHORST, G.L. 1858. Klotzschii herbarium vivum mycologicum sistens fungurum per totam Germaniam crescentium collectionem perfectam. *Editio nova II Dresden, Cent. VIII*, N° 768.

REMAUDIERE, G., KELLER, S., PAPIEROK, B. & LATGE, J.P. 1976. Considérations systématiques et biologiques sur quelques espèces d'*Entomophthora* du groupe *sphaerosperma* pathogènes d'insectes (*Phycomycètes: Entomophthoraceae*). *Entomophaga 21*, 163-177.

REMAUDIERE, G., LATGE, J.P. & PAPIEROK, B. 1979. Reconsidération taxonomique de *Entomophthora obscura* Hall & Dunn. *Ann. Microbiol. (Inst. Past.), 130A*: 151-162.

REMAUDIERE, G., LATGE, J.P. & SMIRNOFF, W.A. 1978. Considérations écologiques sur quelques Entomophthorales pathogènes d'aphides communes dans l'Est des USA et du Canada. *Phytoprotection 59*: 150-156.

ROZSYPAL, J. 1966. A new fungal parasite of calyptrate flies from Europe *Zoophthora vomitoriae* sp. nov. (*Entomophthoraceae*). *Acta Mycol. 2*: 23-24.

SCHNEIDER, W.S. 1873. Die in und an Insekten schmarotzenden Pilze. *Jahresber. Schles. Gesellsch. vaterl. Kultur 1872, Breslau 1873*: 176-182.

SHIMAZU, M. 1976. *Entomophthora delphacis* isolated from the brown planthopper, *Nilaparvata lugens* (Stål). *Jap. J. appl. Ent. Zool. 20*:144-150.

SOROKIN, N. 1880. Zur Entwickelung der *Entomophthora*-Arten. In: Über einige Krankheiten der Insecten. *Schrift. Kaiserl. Akad. Wiss. St. Petersburg*: 58-69.

STAFLEU, F.A. et al. 1972. Code International de la Nomenclature Botanique. Utrecht 1972: 1-426.

TEAKLE, R.E. 1978. Pathogens of Lucerne aphids in Queensland. *Lucerne Aphid Workshop 27th-30th Nov. 1978. Dept. Agr. NSW*: 109-112.

THAXTER, R. 1888. The *Entomophthoreae* of the United States. *Mem. Boston Soc. nat. Hist. 4*: 133-201.

THOIZON, G. 1970. Spécificité du parasitisme des Aphides par les Entomophthorales. *Ann. Soc. Entomol. France, N.S. 6*, 517-562.

TURIAN, G. & WUEST, J. 1969. Mycoses à Entomophthoracées frappant des populations de Fourmis et de Drosophiles. *Bull. Soc. ent. Suisse 42*: 197-201.

TURIAN, G. & WUEST, J. 1977. Description complémentaire de *Zoophthora* (*Entomophthora*) *myrmecophaga* Turian & Wuest, agent d'une mycose chez *Serviformica fusca* L. *Bull. Soc. ent. Suisse 50*: 285-289.

TYRRELL, D. & MACLEOD, D.M. 1975. In vitro germination of *Entomophthora aphidis* resting spores. *Can. J. Bot. 53*, 1188-1191.

VUILLEMIN, P. 1886. Etudes biologiques sur les champignons. *Bull. Soc. Sci. Nancy, Ser. 2, 19*: 33-172.

WEISER, J. 1965. Notes on two new species of the genus *Tarichium* Cohn (*Entomophthoraceae*). *Česka. Mycol. 19*: 201-204.

WINTER, G. 1881. Zwei neue Entomophthoreen-Formen. *Bot. Centralbl.*, 5: 62-64.

WINTER, G. 1884. Die Pilze Deutschlands, Oesterreichs und der Schweiz. *In* L. Rabenhorst's Kryptogamen Flora zweite Aufl. Erster Bd., *Verl. E. Kummer Leipzig* (*Entomophthoreae*: 74-79).

YEN, D.F. 1962. An *Entomophthora* infection in the larva of the tiger moth, *Creatonotus gangis* (Linnaeus). *J. Insect Pathol. 4*: 88-94.

ZIMMERMANN, G. 1978. *Entomophthora blunckii* an Kohlschaben (*Plutella maculipennis*) Isolierung und neue Beschreibung. *Entomophaga 23*: 181-187.

MYCOTAXON

Vol. XI, No. 1, p. 322 April-June 1980

N O T I C E

SOLHEIM MYCOLOGICAL HERBARIUM ESTABLISHED

A new mycological herbarium has been established within the Department of Botany at the University of Wyoming. The Wilhelm G. Solheim Mycological Herbarium, consisting of over 50,000 fungal specimens, commemorates 50 years of work by the late Professor Emeritus of Botany and his wife, Ranghild.

The herbarium is rich in material collected throughout the Rocky Mountain region and contains, as well, considerable exchange material acquired from elsewhere in North and South America, Europe, and Asia. Parasitic fungi are especially well-represented.

Housed in the Aven Nelson Memorial Building, along with Dr. Solheim's personal mycological library, the collection is available for study by qualified students and researchers. Specimens may be borrowed by recognized institutions for one year. Additionally, some duplicates from Centa IV - XVII of **Mycoflora Saximontanensis Exsiccata** are available for exchange.

To encourage graduate studies in mycology, a memorial scholarship has also been established at the University in honor of Dr. Solheim.

Inquiries concerning the herbarium should be addressed to: The Curator, W. G. Solheim Mycological Herbarium, Department of Botany, University of Wyoming, Laramie, WY 82071 U.S.A.

MYCOTAXON

Vol. XI, No. 1, pp. 323-338 April-June 1980

REVISION SYSTEMATIQUE DES GENRES D'ENTOMOPHTHORACEAE A POTENTIALITE ENTOMOPATHOGENE

G. REMAUDIERE

Unité de Lutte biologique contre les Insectes
Institut Pasteur
25 rue du Dr Roux 75724 Paris Cedex 15, France

S. KELLER

Station fédérale de Recherches agronomiques
Reckenholzstrasse 191/211 8046 Zurich, Suisse

RESUME

Les défauts de la classification de MacLeod (1963) et de celle proposée par Batko (1964-1966) pour les *Entomophthoraceae* entomopathogènes sont discutés, ainsi que le poids relatif qu'il convient d'attacher aux différents caractères. Les changements apportés par rapport à la classification de Batko sont les suivants: inclusion de *Entomophaga* Batko dans le genre *Conidiobolus* Bref., inclusion de *Culicicola* Nieuwl. dans le genre *Entomophthora* Fres., remplacement de *Triplosporium* (Thaxter) Batko par *Neozygites* Witl., prioritaire, acceptation des genres *Zoophthora* Batko et *Erynia* Nowak. dans le sens de Remaudière & Hennebert (1980), classement de *Strongwellsea* Batko & Weiser comme synonyme de *Erynia* Nowak., traitement de *Tarichium* Cohn comme *genus incertae sedis*. Une diagnose des genres est donnée, ainsi que les nouvelles combinaisons impliquées par les modifications proposées.

ZUSAMMENFASSUNG

Die Klassifikationen der insektenpathogenen *Entomophthoraceae*, wie die von MacLeod (1963) und von Batko (1964-1966) vorgeschlagen werden, beinhalten Mängel, auf die hingewiesen wird. Nach einer Diskussion der Eignung verschiedener Merkmale als Gattungskriterien werden folgende Änderungen der Klassifikation von Batko vorgeschlagen: Eingliederung von *Entomophaga* Batko in die Gattung *Conidiobolus* Bref., Eingliederung von *Culicicola* Nieuwl. in die Gattung *Entomophthora* Fres., Ersetzung von *Triplosporium* (Thaxter) Batko durch *Neozygites* Witl. aus Prioritätsgründen, Anerkennung der Gattungen *Zoophthora* Batko und *Erynia* Nowak.im Sinne von Remaudière & Hennebert (1980), Betrachtung von

Strongwellsea Batko & Weiser als Synonym von *Erynia* Nowak., sowie Behandlung von *Tarichium* Cohn als *genus incertae sedis*. Die Gattungsdiagnosen werden angeführt wie auch die Neukombinationen, die sich aus den vorgeschlagenen Modifikationen ergeben.

A B S T R A C T

The deficiencies in the classification of MacLeod (1963) and that proposed by Batko (1964-1966) for the entomopathogenic *Entomophthoraceae* are discussed, along with the suitable relative weights attached to different characters. The changes brought to bear on the classification of Batko are the following: the inclusion of *Entomophaga* Batko into the genus *Conidiobolus* Bref.; the inclusion of *Culicicola* Nieuwl. into the genus *Entomophthora* Fres.; the replacement of *Triplosporium* (Thaxter) Batko with the genus *Neozygites* Witl., by priority; the acceptance of the genera *Zoophthora* Batko and *Erynia* Nowak. in the view of Remaudière & Hennebert (1980); the classing of *Strongwellsea* Batko & Weiser as synonym of *Erynia* Nowak.; the treatment of *Tarichium* Cohn as *genus incertae sedis*. A diagnosis of these genera is given along with new combinations implicated by the proposed modifications.

1. INTRODUCTION

La famille des *Entomophthoraceae* est remarquable par la diversité écologique de ses représentants: à côté d'espèces saprophytes, on trouve en effet des pathogènes d'algues, de fougères, de nématodes, de tardigrades, d'arachnides, d'insectes et, occasionnellement, de vertébrés.

Nous limitons la présente révision aux seuls genres qui comprennent des espèces entomopathogènes.

Depuis la création, en 1855, du premier genre de la famille, *Empusa* Cohn, la classification a subi beaucoup d'aléas et demeure controversée. Deux tendances s'opposent aujourd'hui: MacLeod (1963), suivi par de nombreux auteurs, réunit dans le genre *Entomophthora* Fres. la plupart des espèces entomopathogènes, tandis que Batko (1964a,b,c,d et 1966) répartit ces espèces dans 5 genres et 4 sous-genres.

Le défaut majeur de chacune de ces positions est de ne pas tenir compte du genre *Conidiobolus* Bref. qui était appliqué à des espèces de *Entomophthoraceae* saprophytes. La reconnaissance des potentialités entomopathogènes de certains *Conidiobolus* comme *C. osmodes* Drechsler (Remaudière & al. 1976), le transfert dans *Conidiobolus* d'espèces classées auparavant dans *Entomophthora* comme *C. coronatus* (Cost.)Batko, *C. pseudococci* (Speare) Tyrr. & MacLeod, la démonstration de la synonymie *C. thromboides* Drechsler = *E. virulenta* Hall & Dunn (Latgé et al. 1980) montrent l'inconsistance du critère biologique "saprophyte/pathogène" utilisé auparavant pour séparer *Conidiobolus* et *Entomophthora* sensu lato. La classification de Batko n'a pas levé cette difficulté, la frontière entre les genres *Entomophaga* Batko et *Conidiobolus* n'étant pas délimitée.

Si la tentative méritoire de clarification de la systématique des Entomophthoracées entomopathogènes entreprise par Batko a été fort peu suivie par les auteurs, nous estimons

que cela est dû essentiellement aux deux raisons suivantes:
- l'absence de critères morphologiques sur lesquels pourrait être fondée la séparation des genres *Conidiobolus* et *Entomophaga*
- le poids, à notre avis excessif, donné à certains caractères comme les rhizoïdes et les cystides, qui a conduit Batko à réunir dans certains genres des espèces dépourvues d'affinités et à séparer 4 sous-genres sur des bases fragiles.

Le genre *Zoophthora* Batko ayant été révisé par Remaudière & Hennebert (1980), nous proposons, après une brève analyse historique, une classification plus cohérente des autres genres de *Entomophthoraceae* à potentialité entomopathogène.

2. APERÇU HISTORIQUE

L'histoire de la classification des *Entomophthoraceae* a été retracée par différents auteurs (MacLeod 1963, Gustafsson 1965, Remaudière & Hennebert 1980). Une confusion nomenclaturale a été créée par la persistance de l'utilisation du nom *Empusa* Cohn 1855, pourtant reconnu illégitime par Fresenius et remplacé par *Entomophthora* Fres. 1856.

Cette confusion a été aggravée lorsque Nowakowski (1883) a donné une application différente à ces deux noms synonymes. Cet auteur admet alors 4 genres caractérisés de la façon suivante:
- *Empusa* Cohn 1855, à conidiophores simples et dépourvu de rhizoïdes,
- "*Entomophthora* Fres. 1856" sensu Nowak., à conidiophores ramifiés et pourvu de rhizoïdes,
- *Lamia* Nowak. 1883, à conidiophores simples et rhizoïdes,
- *Tarichium* Cohn 1870 qui réunit les espèces dont seules les spores durables sont connues.

Nowakowski rejette son genre *Erynia* Nowak. 1881 comme synonyme de "*Entomophthora*"

Thaxter (1888) retient *Empusa* avec *Lamia* comme synonyme, "*Entomophthora*" comme sous-genre et crée un deuxième sous-genre, *Triplosporium* Thaxter 1888 caractérisé par des conidies primaires subhyalines ou fuligineuses, un type particulier de capilloconidies et la formation de zygospores par isogamie. Il cite aussi le genre *Massospora* Peck 1879.

En 1916, Nieuwland remplace *Lamia* Nowak., préoccupé, par le nouveau nom *Culicicola* Nieuwl. 1916.

Après Hall & Bell (1962), MacLeod (1963) confirme l'illégitimité de *Empusa* Cohn et ne reconnaît que deux genres entomopathogènes: *Entomophthora* et *Massospora*. Il est suivi par la majorité des auteurs postérieurs et en particulier par Waterhouse (1973) qui rejette les genres retenus ou créés par Batko au rang de synonymes de *Entomophthora* Fres.

La classification élaborée par Batko (1964a,b,c,d) représentait pourtant une tentative intéressante de clarification. La clé suivante indique schématiquement les caractères permettant de séparer les 5 genres considérés par

Batko: *Entomophthora* Fres. 1856, *Triplosporium* (Thaxter 1888) Batko 1964, *Culicicola* Nieuwl. 1916 (= *Lamia* Nowak. 1883), *Zoophthora* Batko 1964, *Entomophaga* Batko 1964.

1- Conidiophores simples, conidies plurinucléées, à paroi simple. 2
- Conidiophores ramifiés, conidies uninucléées, à paroi double, rhizoïdes toujours présents . . . . *Zoophthora*

2- Rhizoïdes présents. . . . . *Culicicola*
- Rhizoïdes absents 3

3- Conidies primaires à 4 noyaux, à papille tronquée, présence de capilloconidies, zygospores formées par isogamie . . . . . *Triplosporium*
- Conidies primaires ayant au moins une dizaine de noyaux, capilloconidies absentes. 4

4- Conidies primaires campanulées, à apex pointu, à base tronquée, comportant 10-12 noyaux. . . . . *Entomophthora*
- Conidies primaires sphériques à pyriformes, à apex arrondi, à papille arrondie, à très nombreux petits noyaux . . . . . *Entomophaga*

Batko & Weiser (1965) créent le nouveau genre *Strongwellsea*, proche de *Zoophthora* mais dépourvu de rhizoïdes et à conidiophores seulement exceptionnellement ramifiés. Le genre est surtout remarquable par le mode d'adaptation à son hôte qui survit à l'infection et participe activement à la dispersion des conidies projetées de son abdomen.

En 1966, Batko scinde son genre *Zoophthora* en 4 sous-genres (*Zoophthora* Batko 1964 sensu stricto, *Erynia* Nowak. 1881, *Pandora* Batko 1966 et *Furia* Batko 1966) qu'il caractérise sur des bases subtiles telles que l'aspect des conidies primaires, des cystides, des rhizoïdes et sur l'aptitude à donner des capilloconidies.

Ayant redécouvert *Entomophthora aphidis* Hoffm. in Fres. 1858, espèce proche de *Zoophthora radicans* (Bref.) Batko (type de *Zoophthora* Batko 1964), Remaudière & Hennebert (1980) ont montré que la diagnose du sous-genre *Pandora* Batko 1966 ne correspond pas à *Entomophthora aphidis* Hoffm. in Fres., son espèce type, mais à une espèce bien différente "*Entomophthora aphidis*" sensu Nowak. 1883. Ils limitent l'application du genre *Zoophthora* Batko à son seul sous-genre *Zoophthora*, avec *Pandora* comme synonyme et rétablissant *Erynia* Nowak. 1881 au rang de genre avec *Furia* comme synonyme.

Un dernier genre, *Tarichium* Cohn 1870, dans lequel sont rassemblées les espèces dont seules les spores durables sont connues, est considéré par Lakon (1915) comme "Hilfsgattung". Il est encore rencontré dans la littérature récente; MacLeod & Müller-Kögler (1970) utilisent le terme *Entomophthora (Tarichium)* pour ces espèces, sans lui donner la signification d'une division subgénérique au sens du Code international de Nomenclature Botanique (Lanjouw et al. 1966).

En 1970, von Arx propose une classification très particulière des Entomophthoracées; à côté du genre *Conidiobolus*

qu'il sépare comme non entomopathogène, il retient deux genres (1) *Entomophthora* Fres. 1856 qu'il typifie par *E. sphaerosperma* Fres. et caractérise par des conidies pyriformes ou ellipsoïdales (2) *Myiophyton* Lebert 1856 (!) avec pour basionyme *Empusa muscae* Cohn dans lequel il réunit les espèces à conidies campanulées.

3. CRITIQUE DES CLASSIFICATIONS ANTERIEURES

Rejoignant les conceptions des anciens auteurs qui ont tenté de séparer les *Entomophthoraceae* entomopathogènes en plusieurs groupes de rang générique ou subgénérique (Nowakowski 1881, 1883, Thaxter 1888), nous considérons que le genre *Entomophthora* pris dans le sens que lui appliquent MacLeod (1963), Gustafsson (1965) et Waterhouse (1973) est beaucoup trop hétérogène pour être conservé indivis.

La classification proposée par Batko (1964a,b,c, 1966) et Batko & Weiser (1965), compte tenu des modifications déjà apportées par Remaudière & Hennebert (1980), pour le genre *Zoophthora*, comporte encore un certain nombre d'imperfections:

1- Les espèces à conidies campanulées sont réparties dans 2 genres, *Entomophthora* et *Culicicola*, sur le seul critère absence ou présence de rhizoïdes.

2- De même les espèces à conidies sphériques multinucléées sont réparties dans les genres *Entomophaga* et *Culicicola* sur la base du même critère.

3- Conséquemment, le genre *Culicicola* réunit d'une façon artificielle des espèces à conidies campanulées, paucinucléées et à papille aplatie, et des espèces à conidies sphériques, multinucléées et à papille arrondie, ceci sur la base de l'unique caractère commun à ces deux groupes, la présence de rhizoïdes. Batko & Weiser (1965, tableau 1) ont tenté de corriger cette anomalie en adjoignant au genre *Entomophaga* le sous-genre nouveau "*Lichia* Weiser & Batko 1965", caractérisé par l'existence de rhizoïdes et de conidies à plus de 20 noyaux et en précisant que *Culicicola* a des conidies à 1-4 noyaux. Comme le sous-genre "*Lichia*" n'a jamais été décrit ni typifié, nous devons le rejeter comme *nomen nudum*.

4- La frontière entre *Entomophaga* et *Conidiobolus* n'est pas délimitée bien qu'une tentative de distinction des 2 genres soit esquissée dans le tableau 1 de Batko & Weiser (1965) mais non explicitée dans le texte: "resting spores in rel. to sporangium" internes chez *Conidiobolus*, externes chez *Entomophaga*, comme chez les autres genres entomopathogènes. L'utilisation d'un tel critère, s'il était justifié aurait l'inconvénient d'impliquer la création d'un nouveau groupe à position incertaine pour l'ensemble des espèces de *Conidiobolus* et d' *Entomophaga* dont les spores durables ne sont pas connues.

5- Le genre *Strongwellsea* Batko & Weiser est séparable de *Zoophthora* sensu Batko (= *Zoophthora* + *Erynia* sensu

Remaud. & Henn.) seulement par des caractères de faible poids: le caractère conidiophores ramifiés n'est pas toujours évident, le caractère rhizoïdes et cystides n'est pas constaté chez certaines espèces de *Zoophthora* et de *Erynia*. La particularité essentielle du genre, selon ses auteurs, est de représenter un cas d'adaptation d'un degré inhabituellement élevé du parasite à son insecte hôte, beaucoup plus élevé que dans le genre *Massospora* Peck, au point de représenter l'unique *Entomophthoraceae* non létale. Le genre *Strongwellsea* semble donc établi davantage sur une base clinique, symptomatique et écopathologique que sur une base morphologique classique. En réalité, hormis les *Massospora*, des comportements semblables ont été signalés chez au moins quatre espèces appartenant à deux genres bien distincts: *Entomophthora erupta* Dustan, *E. thripidum* Samson et al., *E. weberi* Lakon ex Samson et *Entomophaga kansana* (Hutchison) Batko. Keller (non publié) observant récemment une épizootie de *E. erupta* sur le *Miridae Notostira elongata* constate que, contrairement aux observations de Dustan (1924), les hôtes meurent avant l'apparition des conidies. Ces différents types de comportement sont l'expression de l'interaction hôte/parasite et non une propriété intrinsèque du champignon. A notre avis, ils ne peuvent être retenus comme critères de distinction générique.

La classification proposée par von Arx (1970) est inacceptable: (1) *Entomophthora* Fres. 1856 nom. nov. pour *Empusa* Cohn 1855, illégitime, a obligatoirement pour type *Empusa muscae* Cohn; la désignation de *Entomophthora sphaerosperma* Fres. comme type de *Entomophthora* Fres. doit être rejetée car contraire à l'article 7 du Code International de Nomenclature Botanique (Stafleu, 1972). (2) *Myiophyton* Lebert a été publié en 1857 et non en 1856 et est un synonyme postérieur de *Entomophthora* Fres. 1856.

4. MODIFICATIONS TAXONOMIQUES ET NOMENCLATURALES PROPOSEES

a) REMARQUES SUR LE POIDS RELATIF ATTACHE A DIFFERENTS CARACTERES

Une classification doit être basée sur un ensemble de critères morphologiques stables et bien définis, indépendants des conditions de l'environnement. Les caractères de comportement ne peuvent être retenus que dans la mesure où ils sont liés à des structures particulières de l'organisme à classer et non pas à des réactions particulières de son hôte.

Suivant Nowakowski (1883) et Lakon (1919, 1962), Batko a accordé un poids excessif au caractère présence/absence de rhizoïdes. Le développement des rhizoïdes, chez certaines espèces, est en effet lié à une série de facteurs écologiques (nécessité de la présence d'eau liquide en contact de l'hôte, chez *Zoophthora aphidis* (Hoffm. in Fres.) Batko par exemple) ou de facteurs physiologiques (constance des rhizoïdes chez les cadavres d'aphides projetant des conidies de *Entomophthora planchoniana* Cornu, inconstance des

rhizoïdes chez ceux contenant les spores durables de la même espèce). L'aptitude à développer des rhizoïdes ne peut être retenue comme caractère d'importance générique car elle obligerait à classer dans des genres distincts des espèces très voisines.

La nature et le mode de formation des spores durables ne peut pas non plus être retenu comme critère primordial d'une classification des *Entomophthoraceae*. Indépendemment du fait que les spores durables ne sont pas connues (ou n'existent pas) chez une série d'espèces et que les conditions de formation des spores durables demeurent inconnues dans beaucoup de cas, les connaissances acquises à ce jour indiquent que différents modes de reproduction sexuée ou asexuée coexistent dans les groupes d'espèces les plus homogènes.

Ainsi les caractères fondamentaux qui peuvent être retenus aujourd'hui sont la morphologie des conidies primaires et secondaires, le mode de leur formation et de leur libération. C'est d'ailleurs sur ces bases que Gustafsson (1965), Waterhouse (1975) et Zimmerman (1978) ont déjà distingué des groupes d'espèces dans le genre *Entomophthora* Fres. pris au sens large.

b) MODIFICATIONS PROPOSEES

Les modifications que nous proposons ont essentiellement pour objet de remédier aux principales imperfections relevées dans la classification de Batko. Compte tenu de la récente révision des genres *Zoophthora* Batko et *Erynia* Nowak. par Remaudière & Hennebert (1980), il nous paraît nécessaire:

(1) d'inclure dans le genre *Conidiobolus* Bref. les espèces du genre *Entomophaga* Batko ainsi que les espèces à conidies sphériques et multinucléées classées par Batko dans *Culicicola* Nieuwl.;

(2) de réunir dans le genre *Entomophthora* toutes les espèces à conidies campanulées, paucinucléées, y compris *Culicicola culicis* (A. Braun) Nieuwl.; ainsi *Culicicola* Nieuwl. devient synonyme de *Entomophthora* Fres., vu l'inclusion de son espèce type *C. culicis*;

(3) de traiter le genre *Strongwellsea* Batko & Weiser comme synonyme de *Erynia* Nowak.

Du point de vue nomenclatural, il convient de remplacer le nom générique *Triplosporium* Thaxter 1888 par *Neozygites* Witlaczil 1885. Giard (1889) a montré que *Neozygites aphidis* Witl., décrit comme une Grégarine, était en fait une Entomophthorée; en comparant les figures 128-140 de Thaxter illustrant la formation des zygospores de *Triplosporium fresenii* Nowak., avec les figures 1 à 13 de Witlaczil, il conclut à l'identité générique du *Triplosporium* et du *Neozygites*. Comme *T. fresenii* Nowak. 1883 est la seule espèce du genre fréquente sur Aphides (*T. lageniformis* Thaxter a été rarement observé, ses spores ne sont pas connues), nous devons reconnaître que *Neozygites aphidis*, découvert sur *Hyalopterus pruni* Geoff. (= *H. arundinis* auctt.), est un synonyme

de *T. fresenii*. Gustafsson (1965) avait adopté la même position qui est d'ailleurs rappelée par Waterhouse (1973).

Le genre *Tarichium* Cohn 1870 (espèce type *T. megaspermum* Cohn 1870) est un genre basé sur une espèce incomplètement connue donc de position incertaine. Comme il n'est pas possible de rattacher *Tarichium* à l'un des genres de *Entomophthoraceae* que nous acceptons aujourd'hui, il convient de traiter *Tarichium* comme *genus incertae sedis* et toutes les espèces qui y sont habituellement classées, comme *species incertae sedis*.

En conclusion nous retenons les 6 genres suivants: *Conidiobolus* Bref. 1884, *Neozygites* Witl. 1885, *Entomophthora* Fres. 1856, *Erynia* Nowak. 1881, *Zoophthora* Batko 1964, *Massospora* Peck 1879.

5. CARACTERISATION DES GENRES RETENUS

Genre *CONIDIOBOLUS* Brefeld 1884 (*Untersuch. aus d. Gesammtgeb. d. Mykol. Leipzig, H6*: 35-78).
Espèce type: *Conidiobolus utriculosus* Bref. 1884 (*loc. cit.* p. 37)
= *Entomophaga* Batko 1964, syn. nov. (*Bull. Acad. Polon. Sci., cl. II, ser. Sci. Biol. 12*: 325-326); espèce type: *Entomophthora grylli* Fres. 1856 (*Bot. Zeitg. 14*: 883) ≡ *Conidiobolus grylli*.

Diagnose:

Conidiophores simples, renflés ou non. *Conidies primaires* sphériques, subsphériques à pyriformes, à symétrie axiale, apex toujours arrondi; papille basale conique à arrondie, parfois pointue ou apiculée, sans épaulement; paroi unituniquée, lisse; noyaux souvent très nombreux (5)25-50(100) et petits; éjectées par projection violente à 1-3 cm. *Conidies secondaires* pouvant correspondre à certains des 4 types suivants (a) semblables aux primaires (b) microconidies en couronne autour des primaires (c) conidies fusiformes ou ellipsoïdales éjectées comme les primaires (d) capilloconidies allongées à symétrie axiale; à apex arrondi, détachables passivement. *Spores durables* pouvant correspondre à l'un des trois types suivants: zygospores formées par anisogamie, azygospores, spores villeuses, inconnues chez certaines espèces; sphériques, hyalines ou plus ou moins brunes, à épispore lisse ondulée ou cannelée. *Cystides* rarement présentes. *Rhizoïdes* parfois présents.

Espèces saprophytes ou/et pathogènes d'insectes et arachnides, occasionnellement de vertébrés. Culture généralement peu exigeante à croissance rapide.

Nouvelles espèces incluses dans le genre:

C. apiculatus (Thaxter 1888) comb. nov. ≡ *Empusa apiculata* Thaxter 1888 (*Mem. Boston Soc. nat. Hist. 4*: 163-164, fig. 62-75).
C. batkoi (Bałazy 1978) comb. nov. ≡ *Entomophthora batkoi* Bałazy 1978 (*J. Invertebrate Pathol. 31*: 278-279, fig. 1-3).
C. carpentieri (Giard 1888) comb. nov. ≡ *Entomophthora carpentieri* Giard 1888 (*Bull. Sci. Fr. Belg. 19*: 303-304).
C. conglomeratus (Sorokin 1877) comb. nov. ≡ *Entomophthora conglomerata* Sorokin 1877 (*Cohn Beitr. Biol. Pflanz. 2*: 388-393, fig. 1-11).

C. giganteus (Keller 1978) comb. nov. ≡ *Entomophthora gigantea* Keller 1978 (*Sydowia, Ann. Mycol. Ser II, 31*: 89-92, fig. 6-19).
C. grylli (Fresenius 1856) comb. nov. (*loc. cit.*).
C. major (Thaxter 1888) comb. nov. ≡ *Empusa apiculata* var. *major* Thaxter 1888 (*Mem. Boston Soc. nat. Hist. 4*: 164-165, fig. 71-73).
C. obscurus (Hall & Dunn 1957) comb. nov. ≡ *Entomophthora obscura* Hall & Dunn 1957 (*Hilgardia 27*: 162-163, fig. 4-5).
C. papillatus (Thaxter 1888) comb. nov. ≡ *Empusa papillata* Thaxter 1888 (*Mem. Boston Soc. nat. Hist. 4*: 166-167, fig. 82-90).
C. tenthredinis (Fresenius 1858) comb. nov. ≡ *Entomophthora tenthredinis* Fresenius 1858 (*Abhandl. Senckenb. Naturf. Ges. Frankfurt a.M. 2*: 205, fig. 51-58).
C. tipulae (Fresenius 1858) comb. nov. ≡ *Entomophthora tipulae* Fresenius 1858 (*Abhandl. Senckenb. Naturf. Ges. Frankfurt a.M. 2*: 206, fig. 46-50).

27 autres espèces de ce genre sont citées et redécrites par King (1977).

Genre *NEOZYGITES* Witlaczil 1885 (*Arch. f. Mikr. Anat. 24*: 599-603).
Espèce type: *Neozygites aphidis* Witl. 1885 (*loc. cit.*) = *Neozygites fresenii*.
= *Empusa* subg. *Triplosporium* Thaxter 1888 syn. nov. (*Mem. Boston Soc. nat. Hist. 4*: 152); espèce type: *Empusa fresenii* Nowak. 1883 (*Pamietn. Wydz. Akad. Umiej. w. Krakŏw 8*: 17-172) ≡ *Neozygites fresenii*.
≡ *Triplosporium* (Thaxter) Batko 1964 syn. nov. (*Bull. Acad. Polon. Sci., cl II, Ser. Biol. 12*: 324-325); espèce type: *Empusa fresenii* Nowak. 1883 (*loc. cit.*) ≡ *Neozygites fresenii*.

Diagnose

Conidiophores simples. *Conidies primaires* en forme de montgolfière, sphériques à pyriformes, à symétrie axiale, apex toujours arrondi; papille basale courtement cylindrique tronquée, sans épaulement; paroi unituniquée, lisse, un peu sombre; généralement 4 noyaux; éjectées par projection à faible distance. *Conidies secondaires* pouvant correspondre aux deux types suivants (a) semblables aux primaires (b) capilloconidies amygdaliformes à symétrie bilatérale, avec une partie basale largement arrondie et une partie apicale subconique surmontée d'un disque ou d'une gouttelette adhésive, à paroi un peu épaissie, légèrement pigmentée, détachables passivement. *Spores durables* correspondant à l'un des deux types suivants: soit zygospores formées par isogamie, soit azygospores; inconnues chez certaines espèces; ovoïdes à subsphériques avec point d'attachement généralement marqué par un fragment hyphal; brunes à noires, à épispore lisse ou ridée. *Cystides* et *rhizoïdes* toujours absents.

Espèces pathogènes d'acariens et d'insectes *Homoptera* et *Thysanoptera*. Apparemment jamais cultivé.

Principales espèces du genre:

N. adjarica (Tsintsadze & Vartapetov 1976) comb. nov. ≡ *Entomophthora adjarica* Tsintsadze & Vartapetov 1976 (*Bull. Acad. Sci. Georgian SSR 83*: 465-468).
N. floridana (Weiser & Muma 1966) comb. nov. ≡ *Entomophthora floridana* Weiser & Muma 1966 (*Florida Ent. 49*: 155-157, fig. 1-3).

N. fresenii (Nowak. 1883) comb. nov. (*loc. cit*).
N. fumosa (Speare 1922) comb. nov. ≡ *Empusa fumosa* Speare 1922 (*U.S. Dept. Agr. Bull. 1117*: 1-18).
N. lageniformis (Thaxter 1888) comb. nov. ≡ *Empusa lageniformis* Thaxter 1888 (*Mem. Boston Soc. Nat. Hist. 4*: 169, fig. 141-160).
N. parvispora (MacLeod & Carl in MacLeod et al. 1976) comb. nov. ≡ *Entomophthora parvispora* MacLeod & Carl in MacLeod et al. 1976 (*Entomophaga 21*: 307-312, fig. 1-19).
N. tetranychi (Weiser 1968) comb. nov. ≡ *Triplosporium tetranychi* Weiser 1968 (*Fol. parasitol. Praha 15*: 117-121, fig. 1-3).
N. turbinata (Kenneth 1977) comb. nov. ≡ *Entomophthora turbinata* Kenneth 1977 (*Mycotaxon 6*: 388, fig. 1-8).

Genre *ENTOMOPHTHORA* Fresenius 1856 (*Bot. Zeitg. 14*: 883).
Espèce type: *Empusa muscae* Cohn 1855 (*Hedwigia 1*: 60) ≡ *Entomophthora muscae*.
≡ *Empusa* Cohn 1855 (*loc. cit.*) non Lindley 1824 (*Orchidaceae*); espèce type: *Empusa muscae* Cohn 1855 (*loc. cit.*) ≡ *Entomophthora muscae*.
≡ *Myiophyton* Lebert 1857 (*Neue Denkschr. allg. Schweiz. Ges. gesammt. Naturwiss. 15*: 26); espèce type: *Myiophyton cohni* Lebert 1857 (*loc. cit.*) ≡ *Empusa muscae* Cohn 1855 ≡ *Entomophthora muscae*.
= *Lamia* Nowak. 1883 (*Pamietn. Wydz. Akad. Umiej. w. Kraków 8*: 173-174) non Endlicher 1841, non *Lamium* Linn. (*Labiatae*); espèce type: *Lamia culicis* A. Braun 1855 (*Alg. unicell. gen. nov. et min. cogn. praem. obs. de algis unicell. in gen., W. Engelmann, Lipsiae*: 105) ≡ *Entomophthora culicis*.
≡ *Culicicola* Niewl. 1916 (*The Amer. Midl. Nat. 4*: 378); espèce type: *Culicicola culicis* A. Braun 1855 (*loc. cit.*) ≡ *Entomophthora culicis*.

Diagnose:

Conidiophores simples, renflés sous l'apex. *Conidies primaires* campanulées, à symétrie axiale, apex pointu ou portant une pointe émoussée; papille basale large très courte tronquée, plate à faiblement convexe, sans épaulement; paroi unituniquée lisse; 2 à 20 noyaux; éjection par projection violente à 1-2 cm, la conidie étant, chez certaines espèces, éjectée avec le contenu cytoplasmique du conidiophore. *Conidies secondaires* d'un seul type, semblables aux primaires ou à apex arrondi. *Spores durables*, azygospores, sphériques, à épispore hyaline à brune, lisse ou avec quelques cannelures. *Cystides* absentes. *Rhizoïdes* absents ou présents.

Espèces pathogènes d'insectes. Quelques espèces cultivées, à croissance lente.

Principales espèces du genre:

E. culicis (A. Braun) Fres.
E. erupta (Dustan) Hall
E. muscae (Cohn) Fres.
E. planchoniana Cornu
E. thripidum Samson et al.
E. weberi Lakon ex Samson in Samson et al.

Genre *ERYNIA* Nowakowski 1881 (*Dzienn. III Zjazdu Lek. i Przyr. Pol. w. Kraków 6*: 67).
Espèces originales: *Erynia ovispora* Nowak., *E. curvispora* Nowak. et *E. conica* (*nomen nudum* en 1881).

Espèce lectotype: *Entomophthora ovispora* Nowak. 1877 (*Bot. Zeitg. 14*: 220) ≡ *Erynia ovispora*.
≡ *Zoophthora* subg. *Erynia* (Nowak. 1881) Batko 1966 (*Acta Mycol. 2*: 18); espèce type: *Entomophthora ovispora* Nowak. 1877 (*loc. cit.*) ≡ *Erynia ovispora*.
= *Zoophthora* subg. *Furia* Batko 1966 (*loc. cit.* p. 20); espèce type du sous-genre: *Empusa virescens* Thaxter 1888 (*Mem. Boston Soc. nat. Hist. 4*: 178) ≡ *Erynia virescens*.
= *Strongwellsea* Batko & Weiser 1965, syn. nov. (*J. Invertebrate Pathol. 7*: 460-463, fig. 1-4); espèce type: *Strongwellsea castrans* Batko & Weiser 1965 (*loc. cit.*) ≡ *Erynia castrans*.

Diagnose:

Conidiophores généralement ramifiés, non renflés. *Conidies primaires* ovoïdes à longuement fusiformes, courbées ou non, généralement à symétrie bilatérale, apex arrondi ou pointu; papille basale arrondie à presque aplatie, parfois indistincte, jamais apiculée, non séparée du corps de la conidie par un épaulement; paroi bituniquée, lisse, adhésive; généralement uninucléées; éjectées par projection à faible distance, 1 cm. *Conidies secondaires* pouvant correspondre à 3 types (a) semblables aux primaires ou un peu plus larges (b) subsphériques avec papille arrondie, à symétrie axiale, parfois indistinctement apiculées au sommet (c) subcylindriques à apex arrondi ou conique, à papille basale indistincte à symétrie axiale, formées sur un conidiophore court et large; conidies des types (a) et (b) éjectées comme les primaires, celles du type (c) probablement détachables passivement; souvent 2 types de conidies secondaires par espèce; capilloconidies toujours absentes. *Spores durables* variables, zygospores formées par anisogamie, azygospores ou inconnues; sphériques, hyalines, jaunes ou brunes, lisses, ridées ou échinulées ou à excroissances bulliformes, parfois formées à l'extérieur de l'hôte. Cystides et rhizoïdes presque toujours présents.

Espèces pathogènes d'insectes, occasionnellement d'arachnides. Culture possible pour beaucoup d'espèces, vitesse de croissance très variable.

Quelques espèces du genre:

Erynia castrans (Batko & Weiser 1965) comb. nov. (*loc. cit.*).
Erynia magna (Humber 1976) comb. nov. ≡ *Strongwellsea magna* Humber 1976 (*Mycologia 68*: 1057-1058, fig. 1-9).
Erynia ovispora (Nowak. 1877) Nowak. 1881.
Erynia virescens (Thaxter 1888) Remaudière & Hennebert 1980.

23 autres espèces sont citées dans ce genre par Remaudière & Hennebert (1980).

Genre ZOOPHTHORA Batko 1964 (*Bull. Acad. Polon. Sci. cl II, Ser. Sci. Biol. 12*: 323-324).
Espèce type: *Empusa radicans* Bref. 1870 (*Bot. Zeitg. 28*: 161-166, 177-186) ≡ *Zoophthora radicans* (= "*Empusa sphaerosperma* Fres." sensu Thaxter 1888).
≡ *Zoophthora* subg. *Zoophthora* Batko 1966 (*Acta Mycol. 2*: 16-18); espèce type: *Empusa radicans* Bref. 1870 (*loc. cit.*) ≡ *Zoophthora radicans*.
= *Zoophthora* subg. *Pandora* Batko 1966 (*loc. cit.* p. 18-19); espèce type: *Entomophthora aphidis* Hoffm. in Fres. 1858

(*Abhandl. Senckenb. Naturf. Ges. Frankfurt a.M.* 2: 208-209, fig. 59-67) ≡ *Zoophthora aphidis*.

Diagnose:

Conidiophores ramifiés non renflés. *Conidies primaires* cylindriques, cylindro-coniques à fusiformes, à symétrie axiale, apex arrondi ou conique émoussé; papille basale conique, avec pointe ou apicule, ou arrondie, séparée du corps de la conidie par un petit épaulement; paroi bituniquée, lisse adhésive; uninucléées; éjectées par projection à faible distance, moins de 1 cm. *Conidies secondaires* de deux types, (a) semblables aux primaires ou un peu élargie au centre ou à l'apex leur donnant un aspect faiblement pyriforme, (b) capilloconidies amygdaliformes à falciformes, à symétrie bilatérale, parfois arquées à l'apex qui est émoussé ou pointu mais toujours dépourvu de dispositif adhésif, paroi très peu épaissie, hyaline, lisse, détachables passivement. *Spores durables* azygospores? sphériques, hyalines à brunes, lisses ou à reliefs; non observées chez une espèce. *Cystides* rarement présentes. *Rhizoïdes* presque toujours présents et en général multihyphaux.

Espèces pathogènes d'insectes. Culture souvent possible, croissance lente, parfois rapide.

Quelques espèces du genre:

Zoophthora aphidis (Hoffm. in Fres.) Batko
Z. radicans (Bref.) Batko

6 autres espèces sont citées par Remaudière & Hennebert (1980).

Genre *MASSOSPORA* Peck 1879 (*31st Ann. Rept. N.Y.St. Mus. Nat. Hist.*: 44).
Espèce type: *Massospora cicadina* Peck 1879 (*loc. cit.*).

Diagnose:

Conidiophores probablement simples. *Conidies primaires* ovoïdes à naviculaires à apex arrondi ou aigu, à courte papille arrondie ou dépourvue de papille et tronquée à la base; à paroi épaisse (peut-être bituniquée) lisse ou verruqueuse, crénelée; 1 à 6 noyaux, le plus souvent 2 en position bipolaire; non éjectées, produites à l'intérieur de l'abdomen de l'hôte, souvent crèmes à brunâtres en masse, libérées par la désintégration de la cuticule de l'hôte. *Conidies secondaires* mal connues ou absentes. *Spores durables*, peut-être azygospores, sphériques à reliefs élevés formant un réticulum diversement ornementé et délimitant des pores profonds, généralement brunâtres en masse. *Cystides* et *rhizoïdes* absents.

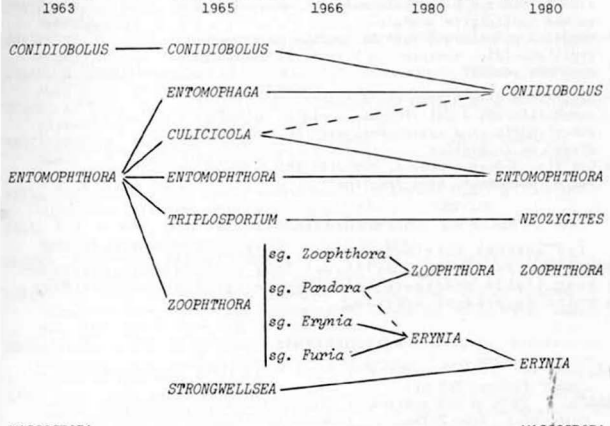
Pathogène hautement spécifique sur *Hom. Cicadidae*. Jamais cultivé.

Onze espèces du genre sont citées et décrites par Soper (1974).

6. CONCLUSION

Parmi les six genres d'Entomophthoracées à potentialité entomopathogène que nous avons retenus, quatre correspondent à des groupes d'espèces très homogènes: *Entomophthora*, *Neozygites*, *Zoophthora* et *Massospora*. Il n'en est pas de même pour les genres *Conidiobolus* et *Erynia*, toutefois les

EQUIVALENCE TAXONOMIQUE DES CLASSIFICATIONS



connaissances acquises à ce jour sur la morphologie et la cytologie des nombreuses espèces classées dans ces genres sont insuffisantes pour permettre un affinement de la classification.

Le tableau ci-dessus permet de comparer notre conception de la classification des genres d'*Entomophthoraceae* à celle des auteurs antérieurs.

Les genres à potentialité entomopathogène que nous avons retenus peuvent être séparés par la clé suivante:

1- Conidies souvent à paroi verruqueuse, jamais éjectées . . . . . *Massospora*
- Conidies primaires à paroi lisse, toujours éjectées 2

2- Conidies primaires campanulées, avec pointe apicale . . . . . *Entomophthora*
- Conidies primaires jamais campanulées 3

3- Conidies primaires subsphériques à pyriformes, unituniquées, conidiophores simples. 4

- Conidies primaires allongées, ovoïdes à cylindriques ou fusiformes, bituniquées, conidiophores plus ou moins ramifiés. 5

4- Conidies primaires à papille tronquée, capilloconidies à symétrie bilatérale avec à l'apex un disque ou une gouttelette adhésive. . . . . *Neozygites*
- Conidies primaires à papille conique ou arrondie, capilloconidies absentes ou à symétrie axiale et apex non adhésif . . . . . *Conidiobolus*

5- Capilloconidies présentes, à symétrie bilatérale, amygdaliformes à falciformes; conidies primaires subcylindriques à fusiformes, avec un épaulement au niveau de la papille . . . . . *Zoophthora*
- Capilloconidies absentes, conidies primaires ovoïdes à fusiformes, sans épaulement. . . . . *Erynia*

REMERCIEMENTS

Les auteurs expriment au Pr G.L. Hennebert (Université catholique de Louvain, Belgique) leur profonde reconnaissance pour l'aide précieuse qu'il leur a apportée dans la mise au point du présent article.

BIBLIOGRAPHIE

ARX, J.A. von 1970. The genera of fungi sporulating in pure culture. *J. Cramer Verlag*, 288 pp.

BAŁAZY, S. 1978. A new species of *Entomophthoraceae (Mycophyta: Entomophthorales)* from Poland. *J. Invertebrate Pathol. 31*: 275-279.

BATKO, A. 1964a. Remarks on the genus *Entomophthora* Fresenius 1856 non Nowakowski 1883 *(Phycomycetes: Entomophthoraceae). Bull. Acad. Polon. Sci., cl. II, Ser. Sci. Biol. 12*: 319-321.

BATKO, A. 1964b. On the new genera: *Zoophthora* gen. nov., *Triplosporium* (Thaxter) gen. nov. and *Entomophaga* gen. nov. *(Phycomycetes: Entomophthoraceae). Bull. Acad. Polon. Sci., cl. II, Ser. Sci. Biol. 12*: 323-326.

BATKO, A. 1964c. Remarks on the genus *Lamia* Nowakowski 1883 *vs. Culicicola* Nieuwland 1916 *(Phycomycetes: Entomophthoraceae). Bull. Acad. Polon. Sci., cl. II, Ser. Sci. Biol. 12*: 399-402.

BATKO, A. 1964d. Some new combinations in the fungus family *Entomophthoraceae (Phycomycetes). Bull. Acad. Polon. Sci., cl. II, Ser. Sci. Biol. 12*: 403-406.

BATKO, A. 1966. On the subgenera of the fungus genus *Zoophthora* Batko 1964 *(Entomophthoraceae). Acta Mycol. 2*: 15-21.

BATKO, A. & WEISER, J. 1965. On the taxonomic position of the fungus discovered by Strong, Wells and Apple: *Strongwellsea castrans* gen. nov. et sp. nov. *(Phycomycetes: Entomophthoraceae). J. Invertebrate Pathol. 7*: 455-463.

BRAUN, A. 1855. Algarum unicellularum genera nova et minus cognita. *Engelmann, Lipsiae*: 111 pp.

BREFELD, O. 1870. Entwiclungsgeschichte der *Empusa muscae* und *Empusa radicans. Bot. Zeitg. 28*: 161-166, 177-186.

BREFELD, O. 1884. *Conidiobolus utriculosus* und *minor. Untersuch. Gesamt. Mycol. VI. Heft*: 35-72.

COHN, F. 1855. *Empusa muscae* und die Krankheit der Stubenfliegen. *Hedwigia (1852-1857) 1*: 57-61.

COHN, F. 1870. Ueber eine neue Pilzkrankheit der Erdraupen. *Beitr. z. Biol. d. Pflanzen 1*: 58-86.

DUSTAN, A.G. 1924. Studies on a new species of *Empusa* parasitic on the green apple bug (*Lygus communis* var. *novascottiensis* Knight). *Proc. Acadian Ent. Soc. (1923) 9*: 14-36.

FRESENIUS, G. 1856. Notiz, Insekten-Pilze betreffend. *Bot. Zeitg. 14*: 882-883.

FRESENIUS, G. 1858. Ueber die Pilzgattung *Entomophthora*. *Abhandl. Senckenb. naturf. Ges. 2*: 201-210.

GIARD, A. 1888. Fragments biologiques XI. Sur quelques Entomophthorées. *Bull. Sci. Fr. Belg. 19*: 298-309.

GIARD, A. 1889. Sur quelques types remarquables de champignons entomophytes. *Bull. Sci. Fr. Belg. 1889*: 197-224.

GUSTAFSSON, M. 1965. On species of the genus *Entomophthora* Fres. in Sweden. I. Classification and distribution. *Lantbrukshögskolans Annaler 31*: 103-212.

HALL, I.M. & BELL, J.V. 1962. Nomenclature of *Empusa* Cohn 1855 *vs Entomophthora* Fresenius 1856. *J. Insect Pathol. 4*: 224-228.

HALL, I.M. & DUNN, P.H. 1957. Entomophthorous fungi parasitic on the spotted alfalfa aphid. *Hilgardia 27*: 159-181.

HUMBER, R.A. 1976. The systematics of the genus *Strongwellsea (Zygomycetes: Entomophthorales)*. *Mycologia 68*: 1042-1060.

KELLER, S. 1978. *Entomophthora gigantea* sp. nov. and *E. caroliniana* (Thaxter) comb. nov., two pathogens of *Tipula paludosa* Meig. *Sydowia, Ann. Mycol. Ser. II, 31*: 87-93.

KENNETH, R.G. 1977. *Entomophthora turbinata* sp. n. a fungal parasite of the peach trunck aphid *Pterochloroides persicae (Lachnidae)*. *Mycotaxon 6*: 381-390.

KING, D.S. 1977. Systematics of *Conidiobolus (Entomophthorales)* using numerical taxonomy. III. Descriptions of recognized species. *Can. J. Bot. 55*: 718-729.

LAKON, G. 1915. Zur Systematik der Entomophthoreen Gattung *Tarichium*. *Z. f. Pflanzenkrankh. 25*: 257-272.

LAKON, G. 1919. Die Insektenfeinde aus der Familie Entomophthoraceen. *Z. f. angew. Ent. 5*: 161-216.

LAKON, G. 1962. *Entomophthoraceae. Nova Hedwigia 5*: 7-26.

LANJOUW, J. et al. 1956. International Code of Botanical Nomenclature. *Int. Assoc. for Plant Taxon, Utrecht*: 338 pp.

LATGE, J.P., KING, D.S. & PAPIEROK, B. 1980. Synonymie de *Entomophthora virulenta* Hall & Dunn et de *Conidiobolus thromboides* Drechsler. *Mycotaxon 11*: 255-268.

LEBERT, H. 1957. Ueber die Pilzkrankheit der Fliegen nebst Bemerkungen über andere pflanzlichparasitische Krankheiten der Insekten. *Neue Denkschr. d. allgem. Schweiz. Ges. gesammt. Naturwiss. 15*: 1-48.

MACLEOD, D.M. 1963. Entomophthorales infections. In Steinhaus, E.A.: Insect Pathology II: 189-231.

MACLEOD, D.M. & MÜLLER-KÖGLER, E. 1970. Insect pathogens: species originally described from their resting spores mostly as *Tarichium* species (Entomophthorales: *Entomophthoraceae*). *Mycologia 62*: 33-66.

MACLEOD, D.M., MÜLLER-KÖGLER, E. & WILDING, N. 1976. *Entomophthora* species with *E. muscae*-like conidia. *Mycologia 68*: 1-29.

MACLEOD, D.M., TYRRELL, D. & CARL, K.P. 1976. *Entomophthora parvispora* sp. nov., a pathogen of *Thrips tabaci*. *Entomophaga 21*: 307-312.

NIEUWLAND, J.A. 1916. Critical notes of new and old genera of plants VII *The Amer. Midl. Nat. 4*: 374-378.

NOWAKOWSKI, L. 1877. Die Copulation bei einigen Entomophthoreen. *Bot. Zeitg. 35*: 217-222.

NOWAKOWSKI, L. 1881. O grupie owadomorków *(Empusaceae). Dzienn. III Zjazdu Lek. Przyr. Polak. Kraków, Sekc. bot. 6*: 67.

NOWAKOWSKI, L. 1883. *Entomophthoreae*. Przyczynek do znajomości pasorzytnych grzybków sprawiajacych pomór owadów. *Pamietn. Wydz. Akad. Umiej. w. Krakòw 8*: 153-183.

PECK, C.H. 1879. Report of the botanist. *N.Y. State Mus. Nat. 31st Ann. Rep.*: 19-44.

REMAUDIERE, G. & HENNEBERT, G.L. 1980. Révision systématique de *Entomophthora aphidis* Hoffm. in Fres. description de deux nouveaux pathogènes d'Aphides. *Mycotaxon 11:* 269-321.

REMAUDIERE, G., LATGE, J.P., PAPIEROK, B. & COREMANS-PELSENEER, J. 1976. Sur le pouvoir pathogène de quatre espèces d'Entomophthorales occasionnellement isolées d'Aphides en France. *C.R. Acad. Sci., Ser. D. 283*: 1065-1068.

SAMSON, R.A., RAMAKERS, P.M.J. & OSWALD, T. 1979. *Entomophthora thripidum* a new fungal pathogen of *Thrips tabaci*. *Can. J. Bot. 57*: 1317-1323.

SOPER, R.S. 1974. The genus *Massospora*, entomopathogenic for Cicadas, part I, taxonomy of the genus. *Mycotaxon 1*: 13-40.

SOROKIN, N. 1877. Ueber zwei neuè *Entomophthora*-Arten. *Beitr. Biol. Pflanz. 2*: 387-398.

SPEARE, A.T. 1922. Natural control of the citrus mealy-bug in Florida. *U.S. Dept. Agr. Bull. 1117*: 1-19.

STAFLEU, F.A. et al. 1972. Code International de la Nomenclature Botanique. *Utrecht*: 426 pp.

THAXTER, R. 1888. The *Entomophthoreae* of the United States. *Mem. Boston Soc. nat. Hist. 4*: 133-201.

TSINTSADZE, K.V. & VARTAPETOV, S.G. 1976. A new fungus *Entomophthora adjarica* sp. n. *(Phycomycete Entomophthoraceae)* affecting *Tetranychus urticae* Koch. *Bull. Acad. Sci. Georgian SSR 83*: 465-468.

WATERHOUSE, G.M. 1973. Entomophthorales In: Ainsworth, G.C., Sparrow, F.K. & Sussman, A.S. *The fungi, an advanced treatise, Acad. Press, vol. IVb, ch. 12*: 219-229.

WATERHOUSE, G.M. 1975. Key to the species *Entomophthora* Fres. *Bull. British Mycol. Soc. 9*: 15-41.

WEISER, J. 1968. *Triplosporium tetranychi* sp.n. *(Phycomycetes, Entomophthoraceae)*, a fungus infecting the red mite *Tetranychus althaeae* Hanst. *Folia Parasitol. (Praha) 15*: 115-122.

WEISER, J. & BATKO, A. 1966. A new parasite of *Culex pipiens* L., *Entomophthora destruens* sp. nov. *(Phycomycetes Entomophthoraceae). Folia Parasitol. (Praha) 13*: 144-149.

WEISER, J. & MUMA, M.H. 1966. *Entomophthora floridana* n.sp. *(Phycomycetes: Entomophthoraceae)* a parasite of the Texas citrus mite, *Eutetranychus banksi*. *Florida Ent. 49*: 155-159.

WITLACZIL, E. 1885. *Neozygites aphidis*, eine neue Gregarine. *Arch. f. Mikr. Anat. 24*: 599-603.

ZIMMERMANN, G. 1978. Zur Biologie, Untersuchungsmethodik und Bestimmung von Entomophthoraceen *(Phycomycetes: Entomophthorales)* an Blattläusen. *Z. f. angew. Ent. 85*: 241-252.

MYCOTAXON

Vol. XI, No. 1, pp. 339-364 April-June 1980

THE GENERIC CONCEPT IN HYPHOMYCETES - A REAPPRAISAL

BRYCE KENDRICK

Department of Biology
University of Waterloo, Waterloo, Ontario,
Canada N2L 3GI

ABSTRACT

It is postulated that there are now too many genera of Hyphomycetes. The characters used to define them are often inadequate, poorly defined or purely monothetic, and the construction of workable keys has become impossible. The condensation of many groups of genera is suggested, and several possible strategies proposed. Several genera centered on *Beltrania* are analyzed in detail; four other groups of genera are also discussed. Finally, the dangers of ignoring convergent evolution are stressed.

INTRODUCTION

As one of the prime movers in the production of two illustrated compendia of hyphomycete anamorph-genera (Kendrick & Carmichael 1973, Carmichael et al. 1980) I have noted with some despondency the enormously variable amount of confidence we can place in the different descriptions and illustrations scattered through the literature. What a motley assemblage the genera of hyphomycetes are. How could they be anything else, conceived as they have been over a

span of two centuries, and in the minds of hundreds of different authors? But the task of compilation was such that we had to focus all our energies on the main objective, rein in our critical faculties (to some extent), and postpone the issue of revision and rationalization.*

Yet these compilations surely allow us, for the first time, to survey our generic patrimony as a whole. I hope that from this ability will spring a dialogue among mycologists about the anamorph-generic concept, and the usefulness of existing genera. This paper is intended as a contribution to such a dialogue.

We deplore the lack of a fossil or genetic base for our classification, and generally agree that anamorph-taxa are mainly matters of convenience. It is my thesis that the number of anamorph-genera of hyphomycetes has already risen to a point where it is no longer convenient. Not only that, but new genera are being proposed in increasing numbers. In 1973 Kendrick & Carmichael recognised about 600 'good' genera. This number has now risen to nearly 900 (Carmichael et al. 1980). It seems inevitable that we will be confronted by well over one thousand such genera long before the end of the century.

Why does this matter? It matters because, having decided that an unknown fungus belongs to the anamorph-class hyphomycetes, the seeker-after-identification (the consumer) must immediately choose among this excessively large, and growing, number, and may encounter two serious, and worsening, difficulties. The first involves the characters used in delimiting genera. As the number of genera grows, the taxonomic gaps which should help to define them are being filled in, or are at least narrowing, sometimes to the point of imperceptibility. New genera are being erected on smaller and smaller bases, and existing genera are being carved up by the recognition of segregate genera. Sometimes these activities are justified by

---

* I use this word in the sense of making rational rather than in its frequent interpretation as explaining away irrationality.

differences which, though small, are fundamental (e.g. dolipore septa vs. simple septa - an example of this is cited later in this paper). And, of course, as any experienced taxonomist knows, distinctive segments of the anamorph spectrum remain to be described. But fairly frequently the description of new genera is merely an exercise in splitting hairs. Such exercises serve only to confuse and frustrate the consumer. Here is a powerful reason for a selective but significant reduction in the rate of description of new genera and in the number of genera currently accepted.

The second difficulty involves the mechanics of the system of information storage and retrieval which the consumer must use when trying to identify an unknown. None of the traditional systems can cope properly with 900 genera. Anyone who has picked their way through an extended dichotomous key to hyphomycetes knows that the chance of error increases with each choice made. After encountering a hundred or so couplets, the seeker will usually come up with a name, but may well feel that they have compromised and guessed their way into error. Synoptic keys (Korf 1972, Michaelides et al. 1979) sidestep the endless choosing and allow entry at any point, but are unsuited for use with large numbers of taxa.

If the hyphomycetes could be reasonably classified in a hierarchical manner by means of acceptable orders and families, the monolithic dichotomous key, such as that in Ellis (1971), could be replaced by a number of shorter, more manageable keys: one to the orders; then perhaps one to the families within each order, then one to the genera within each family.

Unfortunately, and probably for the reasons given in detail by Kendrick (1980), hyphomycete taxonomists have largely rejected families and orders for their organisms. Those suprageneric categories erected by Saccardo have fallen into disuse, and those proposed by several more recent authors simply have not caught on, because they ultimately lack credibility. What I wrote about hyphomycetologists in 1971 still holds true: "I often liken a hyphomycete specialist to someone

holding a large bunch of balloons (the better the specialist, the larger the bunch of balloons!) Each balloon is a hyphomycete [genus] and each has a separate, independent string leading to it". The balloons are in danger of becoming unmanageable.

Since we cannot bring ourselves to adopt supragenetic categories, it seems to me that a reasonable alternative would be to attempt some condensation of genera, and shift some of the load from the 'generic key' to the 'species keys' that can easily be constructed for even fairly large genera.

One of the aims of this paper will be to show, by means of selected examples, that such a shift could be implemented.

PROPOSED PHASES IN CONDENSATION OF GENERA

I envisage several phases of the condensation process.

1. The first, with which this paper is chiefly concerned, involves the fusion of groups of very similar and, in all probability, truly related genera. The genera in many of these related groups are in fact readily separable in a monothetic way - often by single but well marked characters. Nevertheless, their relatedness enables us to adopt a polythetic generic concept, so that a single larger genus can embrace several extant but narrow genera.

2. A second phase could involve groups of genera in which the very morphological simplicity of the organisms makes one wonder about the convenience and validity of the existing generic delimitations. One such group produces rounded, dark, amerosporous chlamydospores - *Humicola* Traaen, *Gilmaniella* Barron, *Thermomyces* Tsiklinskaya, *Acremoniula* Ciferri, *Desertella* Mouchacca, *Botryoderma* Papendorf & Upadhyay -- and if we extend consideration to dark amerosporous chlamydospores of other shapes, the genera *Rhinocladium* Saccardo & Marchal, *Mammaria* Cesati and *Echinobotryum* Corda can be added.

3. A third phase could involve genera which are morphologically very similar but have different modes of conidiation. Although the fashion in recent years has been to separate such anamorphic fungi, there may be good reasons for reconsidering this position.

For many years von Arx among others has maintained that if the differences between two 'genera' were too inconspicuous to be readily recognised then those genera should not, for all practical purposes, be maintained as separate. His position was well stated by Hennebert (in Kendrick 1971: 115). "Dr. von Arx does not make any distinction between phialides and annellophores. His keys to genera of Hyphomycetes are based on the assumption that for all practical purposes there are no distinguishing characters. He will assert that, since the conidiogenous cell of *Cryptosporiopsis* looks like a phialide in ordinary light microscopy, and has long been called a phialide, he will maintain that usage. Remember also that we may in future decide that poroconidia are really only blastoconidia, and that many phialides are really annellides when we look at their internal arrangements. So von Arx may have some reason to ignore the fine differences between phialides and annellides. We must be careful in making keys. They are only tools, not classifications. They must be practical. Not everyone can look at fungi with an electron microscope to identify them."

For years, caught up as many of us were in the search for features of conidium development, we rejected von Arx's thesis, and called upon each other to push the light microscope to the limits of resolution, and even bring the electron microscope to bear, in order to distinguish between such annellidic, phialidic and sympodial 'genera' as *Leptographium* Lagerberg & Melin, *Phialocephala* Kendrick and *Verticicladiella* Hughes. But now we have come to realise that ontogeny is often much less conservative, and much more plastic, than we had hoped (Madelin 1979, Kendrick 1978) and it is being relegated to the status of just another character, rather than the character. It also appears that the differences between phialides and annellides are more in their externals than in their inner workings.

In his recent revision of *Cladobotryum* Nees ex Steudel, de Hoog (1978) states that "Although markedly different types of conidiation are present in this group of fungi, these characters alone are not sufficient for the delimitation of the genera. They are used here only in combination with other criteria". And indeed, evidence from anamorph-teleomorph connections often runs counter to that from conidium ontogeny. (See Kendrick & DiCosmo 1979, Madelin 1979). So it seems reasonable, when both morphology and relationship point in the same direction, to reconsider some of the ontogenetically based generic segregations made in recent years. Since *Leptographium*, *Verticicladiella* and *Phialocephala* have very similar, complex conidiophores, and in some cases are associated with teleomorphs in *Ceratocystis* Ellis & Halst., it might be reasonable, as well as convenient, to group them within a single anamorph-genus.

4. A fourth phase might concern itself with recognizing morphological and developmental similarities between some mononematous, synnematous, and possibly even sporodochial and acervular genera, e.g. *Leptographium-Graphium* Corda, *Verticicladiella-Pesotum* Crane & Schoknecht, *Gamsia* Morelet - *Gymnodochium* Massee & Salmon. This phase could explore our growing conviction (Kendrick & Nag Raj 1979) that the gap apparently separating hyphomycetes and coelomycetes is largely illusory. Certainly there seem to be series in which the sporodochial conidioma passes by imperceptible gradations into the acervular conidioma. Genera now placed on opposite sides of this dichotomy might eventually be united. Dr Nag Raj (pers. comm.) is currently exploring this possibility.

In our long search for a more natural basis on which to classify fungi, we must use our growing knowledge of anamorph-teleomorph connections to detect similarities that may underlie and supersede the old categories 'mononematous-synnematous-sporodochial-acervular.' Eventually we may perceive in the ascomycetes and basidiomycetes as a whole a beautifully regular pattern like that found among the anamorphs of the rust fungi, and we must keep such possibilities in mind. This fourth phase might well serve more than one purpose: a glance at the synnematal 'genera' compiled

by Carmichael et al. (1980) shows that a lot of them seem virtually indistinguishable, e.g. *Crinula* Fries - *Dendrostilbella* Höhnel - *Phialographium* Upadhyay & Kendrick. This is a sure sign that many such genera need to be critically re-examined. Taxonomists please note.

5. A fifth phase could bring about the final and long overdue extirpation of those anamorph-genera obligately based on the co-occurrence of two different anamorphs on the same mycelium, e.g. *Thielaviopsis* Went, *Chalaropsis* Peyronel, *Dimorphospora* Tubaki, *Duosporium* Thind & Rawla, *Diheterospora* Kamyschko, *Dwayabeeja* Subramanian, *Triadelphia* Shearer & Crane, *Mycochlamys* Marchand & Cabral. In most cases generic names already exist for the individual anamorphs of which these composite genera are made up. For example, *Chalaropsis* is an unnecessary name for a *Chalara* (Corda) Rabenhorst and a *Humicola*. *Mycochlamys* comprises a *Humicola* and a *Scytalidium* Pesante.

Other phases may emerge during the debate, but it is time to return to the main theme of this paper - what I have called phase one.

PROPOSED AMALGAMATION OF CONTIGUOUS GENERA

Perusing the 129 plates in Carmichael et al. (1980) and the fine illustrations in Ellis (1971, 1976) one is occasionally struck by groups of 'genera' whose members exhibit what might be called a 'family likeness'. These are the first candidates for a more detailed scrutiny. The following 26 groupings will exemplify the idea.

(Chalara - Chaetochalara Sutton & Pirozynski*)*
(Catenularia Grove ex Saccardo - *Chloridium* Link - *Dischloridium* Sutton - *Bisporomyces* van Beyma*)*
(Clonostachys Corda - *Mariannaea* Arnaud*)*
(Selenosporella Arnaud ex McGarvie - *Umbellidion* Sutton & Hodges*)*
(Beltrania Penzig - *Beltraniopsis* Batista & Bezerra *Ellisiopsis* Batista - *Beltraniella* Subramanian - *Pseudobeltrania* P. Hennings*)*
(Rhinocladiella Nannfeldt - *Ramichloridium* Stahel ex de Hoog*)*

(*Phymatotrichopsis* Hennebert - *Amphobotrys* Hennebert - *Dichobotrys* Hennebert - *Glischroderma* Fuckel - *Pulchromyces* Hennebert - *Chromelosporium* Corda - *Streptobotrys* Hennebert - *Verrucobotrys* Hennebert - *Botrytis* Persoon ex Fries)
(*Haplobasidion* Eriksson - *Echinocatena* Campbell & Sutton - *Lacellinopsis* Subramanian)
(*Fulvia* Ciferri - *Alysidiopsis* Sutton - *Cladosporium* Link ex Fries - *Sorocybe* Fries)
(*Ovulariopsis* Patouillard & Hariot - *Oidium* Saccardo)
(*Staheliella* van Emden - *Botryomonilia* Goos & Pirozynski - *Oidiodendron* Robak)
(*Antromycopsis* Patouillard & Trabut - *Sclerostilbum* Povah)
(*Arthrinium* Kunze ex Fries - *Cordella* Spegazzini-*Pteroconium* Saccardo ex Grove)
(*Mycosylva* Tulloch - *Pachnodium* Upadhyay & Kendrick)
(*Circinotrichum* Nees ex Persoon - *Gyrothrix* (Corda) Corda - *Ceratocladium* Patouillard)
(*Hyphodiscosia* Lodha & Chandra Reddy - *Leptodiscella* Papendorf)
(*Cylindrotrichum* Bonorden - *Chaetopsis* Greville)
(*Cyphellophora* de Vries - *Phialogeniculata* Matsushima - *Phialophora* Medlar)
(*Myrothecium* Tode ex Fries - *Septomyrothecium* Matsushima)
(*Torula* Persoon ex Fries - *Dwayabeeja* Subramanian - *Bahusaganda* Subramanian)
(*Septonema* Corda - *Lylea* Morgan-Jones)
(*Varicosporium* Kegel - *Dendrospora* Ingold - *Dendrosporomyces* Nawawi, Webster & Davey)
(*Scorpiosporium* Iqbal - *Tricladium* Ingold)
(*Heliscus* Saccardo - *Clavatospora* Nilsson)

Such groups have both morphological and developmental similarities, and many are also cemented by our knowledge of the respective teleomorphs. It would obviously take far too long to discuss all of them, so I have selected five examples for further consideration. The first of these may be regarded as a test case and has been set forth in considerable detail.

1) *Beltrania-Beltraniopsis-Ellisiopsis-Beltraniella-Pseudobeltrania*

The anamorph-genus *Beltrania* Penzig 1882 was erected for the single species *B.rhombica* Penzig. *B.querna* Harkness was added two years later. In 1886 Penzig and Saccardo thought the conidia were didymosporous, and although Penzig's type specimen has been lost, a clearly recognizable concept had been established, and by 1963, when Pirozynski's beautifully illustrated account of the tribe appeared, it had grown to six anamorph-genera with 11 species in all. This despite Pirozynski's recognition of a very broad 'neoconcept' for *B.rhombica*, and his synonymization of *B.indica* Subramanian and *B.multispora* Swart with it.

In the intervening seventeen years the number of species in the tribe has doubled, reflecting the sharply increased concern of mycologists with conidial fungi. Perhaps surprisingly, the number of 'genera' involved has remained constant. My question is whether that number should in fact be reduced. The quotation which follows is from Kendrick & Carmichael (1973) " ... the recently recognized form-genera *Beltraniella*, *Ellisiopsis* and *Beltraniopsis* are differentiated from the classical *Beltrania* by characters which could easily be regarded as valid only at the species level ... [the species of these genera] are so similar that they should probably be treated as congeneric in any practical, working classification". These genera are indeed separable by single characters, but they probably represent a luxury we can no longer afford, if our system is to be manageable, so this seems an appropriate place to take up and extend the earlier discussion. The species of the genera *Beltrania*, *Beltraniopsis*, *Beltraniella* and *Ellisiopsis*, as well as those of two other genera, *Pseudobeltrania* and *Hemibeltrania* Pirozynski, which are relevant to the discussion, are all illustrated in Ellis (1971:237-235, 1976:200-207).

Let us first analyze the constellation of characters that make *Beltrania* distinctive. Almost unique among hyphomycetes are the striking biconic conidia which are lightly pigmented but have a narrow hyaline band at the conjunction of upper and lower cones. This

strangely shaped conidium also has a tubular apical appendage and often a basal 'separating cell', swollen in the middle, but narrowly truncate at each end. The separating cells arise from denticles clustered at the apex of unbranched, multiseptate conidiophores which spring from around the radially lobed, rosette-like bases of long, dark, pointed setae.

There is a strong tendency for anamorph-genera to be monothetic; that is, for them to be based on the possession by all member species of a unique feature or features. Among the *Beltrania*-like hyphomycetes this means that an all-or-nothing reliance on one or two characters has led to the recognition of several numerically small genera. The salient features of these genera are analyzed in Table 1. I have tried to rate these features in terms of their frequency of occurrence over the whole spectrum of hyphomycetes. My categories range from: ' * = unique', through '** = very rare', to '*** = unusual', to '**** = common'. From the point of view of their value as characters delimiting monothetic genera, we can surely discount the four-star features completely. For example, anamorph-genera with '(1) Conidia amerosporous' fill no fewer than 55 of the 129 plates in Carmichael et al. (1980). '(3) Conidia lightly pigmented' and '(4) Conidia limoniform or obovoid' are less common, but can still be found in scores of genera. '(5) Conidiophores arising from substrate' must describe the majority of all hyphomycetes and is only included as a foil for those arising along the setae.

Let us pass on, then, to the remaining characters. Three (#6-8) are rated as "unusual". '(6) Dark setae' can be found in about 30 anamorph-genera (e.g. *Chaetochalara*, *Codinaea* Maire, *Cordella*, *Lacellina* Saccardo, *Lacellinopsis*, *Mahabalella* Sutton & Patil, *Minimidochium* Sutton, *Septosporium* Corda). This total does not include genera with setiform conidiophores. An interesting situation arises with the publication of *Beltrania mundkurii* and *B.santapaui*, whose setae are often branched, since it is on branched vs. unbranched setae that the genera *Gyrothrix* and *Circinotrichum* are differentiated - see below '(7) Conidiophores

Table 1

Salient Features of the *Beltrania* group and other selected genera

	Frequency rating of characters	Beltrania	Beltraniopsis	Beltraniella	Ellisiopsis	Pseudobeltrania	Hemibeltrania	Rhombostilbella	Chaetendophragmia	Subulispora
1. Conidia amerosporous	****	✓	✓	✓	✓	✓	✓	✓	x	x
2. Conidia phragmosporous	****	x	x	x	x	x	x	x	✓	✓
3. Conidia lightly pigmented	****	✓	✓	✓	✓	✓	✓	x	✓	✓
4. Conidia limoniform or obovoid	****	x	x	x	x	x	✓	x	x	x
5. Conidiophores arising from substrate	****	✓	✓	✓	✓	✓	✓	✓	✓	✓
6. Dark setae present	***	✓	✓	✓	✓	x	x	x	x	x
7. Conidiophores arising along setae	***	x	✓	✓	✓	x	x	x	x	x
8. Conidia beaked or apiculate	***	x	✓	x	x	✓	(✓)	✓	✓	✓
9. Conidia with hyaline equatorial band	**	✓	✓	✓	✓	✓	x	x	x	x
10. Bases of setae or conidiophores radially lobed	**	✓	✓	✓	✓	✓	✓	x	✓	✓
11. Conidia biconic	**	✓	✓	(✓)	x	✓	x	✓	x	x
12. Conidia turbinate	*	x	x	✓	✓	x	x	x	x	x
13. Conidia with apical, tubular, non-septate appendage	*	✓	x	x	x	x	x	x	x	x
14. Swollen separating cell often present	*	✓	✓	(✓)	(✓)	x	x	x	x	x

Weighting used in Table 4

**** = 1, *** = 3, ** = 7, * = 10

No character is included in the key unless it is present in at least two of the fungi and therefore contributes to similarity.

(or conidiogenous cells) arising along setae.' This condition is about as frequent as that described above (#6); examples are *Chaetopsina* Rambelli, *Chaetopsis* Greville, *Conoplea* Persoon, *Cryptophiale* Pirozynski, *Gonytrichum* Nees & Nees, *Hansfordia* Hughes, *Kumanasamuha* Rao & Rao, and *Zanclospora* Hughes & Kendrick. '(8) Conidia beaked or apiculate' Depending on just how it is interpreted, this feature occurs in at least 40 anamorph-genera of hyphomycetes (excluding staurosporous and scolecosporous forms). Examples are: *Echinobotryum*, *Hansfordiella* Hughes, *Hansfordiellopsis* Deighton, *Sessiliospora* Hawksworth, *Sporidesmium* Link, *Toxosporium* Vuillemin, *Walkeromyces* Thaung).

It is apparent that the last six features (#9-14) carry the real taxonomic weight. '(9) Conidia with hyaline equatorial band'. Darker central bands are found in a number of genera, and longitudinal germ slits are not uncommon, but a hyaline band around the body of the conidium is rare. I am aware of such a feature only in *Arthrinium*, *Pteroconium* and *Cordella* (three very similar genera) outside the *Beltrania* group, in which five of the six 'genera' share this character. One species of *Beltraniella*, *B.porosa* Pirozynski & Patil, has several equatorial hyaline pores in place of the continuous band. This configuration is unique, and were the fungus not so obviously a member of the *Beltrania* group, could easily have led to its segregation at the generic level.

'(10) Bases of setae or conidiophores radially lobed' The bases of setae and conidiophores in many genera are swollen (e.g. *Cacumisporium* Preuss, *Sporoschismopsis* Holubová-Jechová & Hennebert, *Circinotrichum*, *Periconia* Tode ex Persoon), but I am aware of the existence of radial lobes in only two genera -- *Chaetendophragmia* Matsushima and *Subulispora* Tubaki -- outside the *Beltrania* group. Within the group, species of all six 'genera' possess this feature. Because of its rarity, common possession of this character must raise questions about the possible relationships among the genera concerned. It is difficult to be dogmatic in a group so poorly known genetically and palaeontologically, yet neither *Chaetendophragmia* nor *Subulispora* resembles the

Beltrania group in most ways: a comparison is given in Table 2. This suggests that the lobing may have arisen separately on at least three occasions as a solution to the common problem of obtaining stability for tall structures.

Table 2

A comparison of anamorph-genera with radially lobed conidiophore bases.

	Beltrania group	Subulispora	Chaetendophragmia
conidiophore bases radially lobed	✓	✓	✓
conidia pigmented	✓	x	✓
conidia with apical appendages	(✓)	x	✓
conidia with lateral appendages	x	x	✓
conidiophore proliferating	x	x	✓
conidiophore proliferating sympodially	x	✓	x
separating cells present	✓	x	x
conidia phragmosporous	x	✓	✓
conidia arising on denticles	✓	x	x

'(11) Conidia biconic. Of the six genera in the *Beltrania* group, four share this feature. Only two other hyphomycete genera produce conidia of this shape: the hyaline, synnematous, fungicolous *Rhombostilbella* Zimmermann, and the hyaline, sporodochial *Fusisporella* anamorph of *Nectria pallidula* Cooke. It seems most probable that the similarity in conidium shape is

coincidental, and that neither of these fungi is related to *Beltrania*. As Pirozynski (1963) pointed out, biconic spores are found among the Sphaeriales, Microthyriales and Helotiales, so this shape is not necessarily good evidence for close relationship.

'(12) Conidia turbinate.' This means 'shaped like a child's whipping top.' Such conidia have a rounded or rather flattened apex, and a pointed base. Yet the word turbinate specifies an over-all shape rather than simply those of base and apex. So although it is not hard to find genera whose conidia have a rounded or flattened apex and a tapered base, these usually have little resemblance to *Beltraniella* or *Ellisiopsis*. I think it is fair to suggest that, were the shape of the conidia in these two genera to be fully specified (as in a drawing, rather than as an oversimplified verbal description) it would be essentially unique: the *Exosporiella fungorum* (Fries) Karsten conidium is about the only example I can think of that bears it much resemblance.

'(13) Conidia with one apical, tubular, nonseptate appendage.' Apical appendages are common among coelomycetes, but found in relatively few genera of hyphomycetes, especially if one excludes forms with a simple apical extension like that of some species of *Alternaria* Nees or *Hansfordiella*, and discriminates between the fine non-cellular setulae of such genera as *Codinaea*, *Mahabalella*, *Menispora* Persoon, *Menosporopsis* Hughes, *Minimidochium* and *Mycoleptodiscus* Ostazeski, and the tubular kind that lack cytoplasmic content at maturity. *Camposporium* may have 0-several appendages, sometimes septate; *Chaetendophragmia* has one or two lateral appendages in addition to the apical; *Pleiochaeta* (Saccardo) Hughes usually has two or three apical appendages. If one can exclude the 'beaks' of e.g., *Phaeotrichoconis crotalariae* (Salam & Rao) Subramanian and *Blastodictys hibisci* (Hansford) Ellis (which are very appendage-like, and suggest that the word 'appendage' needs some attention), only *Monotrichum* Gaeumann is seen to possess anything comparable to the appendage found in some species of *Beltrania*.

'(14) Swollen separating cell often present.' Separating cells are found in more than twenty anamorph-genera of hyphomycetes. Sometimes they are nothing more than a denticle which has a septum laid down across the base. The denticle may be very short, as in *Dematophora* Hartig, *Conoplea* or *Hansfordia*, and the separating cell therefore disc-like. In other genera the denticle is larger (*Nakataea* Hara, *Pyricularia* Saccardo, *Parapyricularia* Ellis) and in yet others it may be very long in proportion to its width (*Brachysporium* Saccardo, *Paratrichoconis* Deighton & Pirozynski, *Rhombostilbella*). The separating cells of these genera differ from those of the *Beltrania* group in three significant ways. First, they are all cylindrical or tubular - none is swollen in the manner typical of those in *Beltrania*, *Beltraniopsis*, *Beltraniella** or *Ellisiopsis*. Second, the cylindrical kind of separating cell usually ruptures when the single conidium it bears secedes, part of the cell going with the conidium, part remaining attached to the conidiogenous cell. In the *Beltrania* group, the swollen separating cell does not usually rupture, but either remains on the conidiophore in its entirety or secedes with the conidium. Third, it is fairly common for a separating cell of the *Beltrania* group to bear more than one conidium: I am not aware of such behaviour among cylindrical separating cells. So, although several other genera have separating cells, those of the *Beltrania* group are unique.

Even a cursory examination of the ratings in Table 1 will convince the reader that the *Beltrania* group occupies a fairly well-defined region of the fungal spectrum. If we look only at the six most unusual features, we find that only one, radially lobed setae or conidiophore base, is present in all six pseudotaxa, though another, the hyaline equatorial band, is found on the conidia of five of the six, and two more (biconic conidia and swollen separating cells) are found in four of the six 'genera'.

---

* Separating cells of *Beltraniella nilagirica* Pirozynski & Patil may be cylindrical, but they are much wider than the denticles from which they arise, and each commonly bear several conidia, as in other *Beltraniella* species.

Table 3 shows the results of cross-matching the various features present in each 'genus' in an unweighted manner. However, in the normal taxonomic approach some features are always given more 'weight' than others. I thought it would be salutary to visualize this usually cerebral process, and assigned weightings of 10, 7, 3 and 1 to the four degrees of rarity recognized earlier. Although this scheme is doubly arbitrary, it produces similarities (Table 4) that do not seem unrealistic when one makes the usual mental comparisons.

I admit that this comparison is made on a limited sample of data, but I am fairly sure that it was upon just these characters that the original 'generic' delimitations were based.

Table 4 makes it clear that *Hemibeltrania* is peripheral or even external to the *Beltrania* group. Although it shares four or five features with each of the other genera in the group, three of these are of the common or garden variety, and only feature 11, the radially lobed conidiophore base, a seven-point character, gives it any semblance of credibility as a member of the group. To drive this point home further, I have compared *Chaetendophragmia triangularia* Matsushima and *Subulispora procurvata* Tubaki with the 'genera' of the *Beltrania* group, extending Table 1 as necessary to include all the main features, and found that each of them was, in fact, just as 'close' to the other members of the *Beltrania* group as is *Hemibeltrania*. Note that this degree of similarity is essentially based on two features, the '3-point' apiculate conidia and the '7-point' radially lobed conidiophore base.

In the conidial fungi we are, as I have recently pointed out at some length (Kendrick 1980), at a considerable disadvantage when speaking about conservatism in characters because we have so little fossil record on which to base conclusions. Yet if we can attach some importance to 'shared rarity' (and how else can we taxonomize organisms) we could suggest that *Chaetendophragmia triangularia* and *Subulispora procurvata*, no less than species of *Hemibeltrania*, may be related in some way to the otherwise closely knit *Beltrania* group. But although there is, as I have tried to demonstrate, a

strong case for condensing the five *Beltrania* genera into one (as their weighted resemblances in Table 4 suggest), there can be little justification for including *Hemibeltrania*, *Chaetendophragmia* or *Subulispora* in this expanded generic concept.

Table 3

Positive resemblances between genera (unweighted - out of 10)

	Beltraniopsis	Beltraniella	Ellisiopsis	Pseudobeltrania	Hemibeltrania	Rhombostilbella
Beltrania	8	8	7	6	4	3
Beltraniopsis		9	8	7	5	4
Beltraniella			9	6	4	3
Ellisiopsis				5	4	3
Pseudobeltrania					5	4
Hemibeltrania						3

Table 4

Positive resemblances between genera.
(Weighted - out of 47).

	Beltraniopsis	Beltraniella	Ellisiopsis	Pseudobeltrania	Hemibeltrania	Rhombostilbella	Chaetendophragmia	Subulispora
Beltrania	37	37	30	24	10	9	9	8
Beltraniopsis		40	33	27	13	12	12	11
Beltraniella			43	27	10	9	9	8
Ellisiopsis				17	10	2	9	9
Pseudobeltrania					13	12	12	11
Hemibeltrania						5	12	11
Rhombostilbella							4	5
Chaetendophragmia								12

The five core 'genera' in what I have called the *Beltrania* group contain in all only about 20 species. I suggest that even were the number of species to double (which it well may, as the hyphomycetes of the tropics are more fully enumerated) it would be easier to track down any of them initially under a single generic heading (largely on the basis of qualitative features) then run it down to species by using the remaining qualitative features for subgeneric groupings (which might correspond to the genera now recognized), and finally by means of quantitative differences.

If we adopt the traditional monothetic stance, we can define the *Beltrania* group as producing biconic, or sometimes turbinate, pigmented conidia which have a hyaline equatorial band. But that gives a very inadequate account of the group as a whole, and since other very unusual or even unique characters are also found in the majority of species within the group, it seems more reasonable to include those in the generic constellation, adopting a more polythetic approach.

Among the unusual, rare, or unique features already enumerated, no less than five are present in at least four of the five genera. These five features (# 6,9, 10,11,14 in Table 1) are present in *Beltrania*, *Beltraniopsis* and *Beltraniella;* four of them in *Ellisiopsis*, and three in *Pseudobeltrania*. Only one of the five is found in *Hemibeltrania*. I propose, then, that membership in the expanded, slightly polythetic genus *Beltrania* sensu lato be granted to fungi possessing any three of the five features listed below: (1) dark setae, (2) setae or conidiophores with radially lobed bases, (3) swollen separating cells, (4) biconic conidia (5) conidia with hyaline equatorial band.

Using this polythetic concept, I believe that all species thus far described in *Beltrania*, *Beltraniopsis*, *Beltraniella*, *Ellisiopsis* and *Pseudobeltrania* fall within the limits of the single expanded anamorph-genus. *Hemibeltrania* is clearly excluded.

It is encouraging to note that Pirozynski & Patil (1970) foreshadowed the present paper by reducing *Ellisiopsis* to synonymy with *Beltraniella*.

I have deliberately delayed until this point any consideration of the species most recently described in *Hemibeltrania*, *H. navicularis* Sutton. Sutton (1976) reports that his collections of the new taxon "have not only shown characteristics of *Hemibeltrania* but also extraneous features [sic] not hitherto reported in the family [sic]." Sutton notes that the new species is "similar in morphology and ontogeny of conidia ..... to *Hemibeltrania* species but in addition to solitary conidia it produces short chains of up to 3 conidia. Were it not for this feature there would be no hesitation in placing the species in *Hemibeltrania*, but, if a strict interpretation of the generic limits is imposed, there would be no alternative to the introduction of a new generic name to accommodate it."

I consider that the inclusion of this species in *Hemibeltrania* involves an excessive extension of the generic concept. Not only are the conidia of the two extant species of *Hemibeltrania* obovoid or limoniform and not at all 'navicular' or spindle-shaped, but they never form in chains, and completely lack the swollen separating cells which Sutton invokes as a derivative of the chains found in his fungus. If we can extend the generic limits of *Hemibeltrania* to include an additional shape of conidia, and conidia in chains, how much easier it would be to extend the limits of *Beltrania* to incorporate the other four genera already mentioned, which already have so much in common with the original genus. Sutton's new fungus, even if it can be postulated as having some relationship with the *Beltrania* group - and perhaps it can - must surely be regarded as distinct both from *Beltrania* sensu lato and from *Hemibeltrania*. It possesses none of the constellation of five features that characterize *Beltrania* sensu lato, and is not much more similar to *Hemibeltrania*, as that genus has generally been understood. It could, in fact, be considered more closely allied to *Spondylocladiopsis* M.B. Ellis, or to *Haplariopsis* Oudemans (see Ellis 1971: 293-294).

Since this is the beginning of the debate, I am deliberately refraining from making the suggested transfers, not wishing to prejudge the outcome, or to clutter the literature with combinations that may, if the argument goes against them, be rendered superfluous.

(2) *Chalara* - *Chaetochalara*

As Nag Raj & Kendrick (1975) showed, *Chalara* is unique in its production of cylindrical, phialidic, amerosporous or didymosporous conidia from a conidiogenous locus lying at the base of an extended cylindrical collarette. Unique, that is, except for the contiguous genus *Chaetochalara*, which has exactly the same characteristics, with one addition, that of dark setae. Although Nag Raj & Kendrick were conservative and retained both genera, it seems to me that there is now very little reason to do so. *Chaetochalara* has only six species (Nag Raj & Kendrick 1975) and could be absorbed into *Chalara* with virtually no loss of information, since the six species would constitute a small subgeneric group that could be quickly keyed out on their possession of setae ... (Remember that some members of *Beltrania* sensu lato have setae, while some do not). I propose, therefore, that the concept of the genus *Chalara* be expanded to admit species with setae, *Chaetochalara* becoming a facultative synonym of *Chalara*

(3) *Circinotrichum* - *Gyrothrix* - *Ceratocladium*

The only feature separating *Circinotrichum*, with six species, from *Gyrothrix*, with twelve, is the unbranched setae of the former vs. the branched setae of the latter (See Pirozynski 1962). Species of these two genera are remarkably similar in every other respect. Referring back to the *Beltrania* discussion, we may note that two species of *Beltrania*, *B. mundkurii* Pirozynski & Patil and *B. santapaui* Pirozynski & Patil have recently been described as having branched setae, while the other members of *Beltrania* sensu stricto all have unbranched setae. Although I know it is not always safe to transfer taxonomic conclusions from one situation to another, this is surely a case in which what makes sense in *Beltrania* does so also in *Circinotrichum* - *Gyrothrix*. I therefore suggest unification of the two genera, with *Gyrothrix* becoming a facultative synonym of *Circinotrichum*.

Ceratocladium Corda 1839, with one species, *C. microspermum* Corda, has branched setae like *Gyrothrix*, but while the conidiogenous cells in *Gyrothrix* arise from the substrate, the almost identical cells of

Ceratocladium arise along the lower part of the setae. This might seem like a reasonable generic distrinction, but for the fact that the conidiogenous cells of a recently described *Circinotrichum, C. pseudocladum* Pirozynski & Patil, also develop along the lower portion of the setae. Thus *Ceratocladium microspermum* is to *Gyrothrix* what *Circinotrichum pseudocladum* is to the rest of *Circinotrichum*. If *C. pseudocladum* can be accepted as a good species of *Circinotrichum* (and I do not see why it should not be), then *Ceratocladium microspermum* can now be logically and comfortably disposed in *Gyrothrix* - and hence in *Circinotrichum* sensu lato. Once again it is encouraging to note that Pirozynski & Patil (1970) having described *Circinotrichum pseudocladum*, drew attention to the same logical redisposition of *Ceratocladium microspermum*, though they did not go as far as to propose the second step.

(4) *Antromycopsis - Sclerostilbum*

Sclerostilbum septentrionale Povah has recently been revealed as the synnematal anamorph of *Collybia racemosa* (Persoon ex Fries) Quelet (Watling & Kendrick 1977). Its conidia are formed by the arthric disarticulation of closely clamped hyphae in the head of the synnematal conidioma. Quite independently, it has also been shown that *Antromycopsis broussonetiae* Patouillard & Trabut is the synnematal anamorph of *Pleurotus cystidiosus* O.K. Miller (Jong & Peng 1975, Pollack & Miller 1976). Its conidia form in exactly the same manner as those of *Sclerostilbum*, though the *Pleurotus* also produces an anamorph on the monokaryotic mycelium: this is, of course, not clamped and the arthric conidia are not as distinctive as those of the dikaryon. The literatures of these two basidiomycetous anamorphs have followed separate, if parallel, paths, and the actual comparison between them has been made only very recently (Watling & Kendrick 1977, Kendrick & Watling 1979). It seems that there is little reason to maintain them as separate anamorph-genera, and I propose that *Sclerostilbum* should become a facultative synonym of *Antromycopsis*.

(5) *Heliscus* - *Clavatospora*

Heliscus lugdunensis Saccardo & Therry, the type species of *Heliscus* Saccardo, has tetraradiate, amerosporous, phialidic conidia in which the three upwardly directed arms are comparatively short (Carmichael et al. 1980, Fig. 117D). Because those of *H. longibrachiatus* Ingold were much longer, Nilsson established the segregate genus *Clavatospora* Nilsson ex Marvanova & Nilsson for it. The only significant difference between *H. lugdunensis* and *C. longibrachiata* (Ingold) Nilsson (Carmichael et al. 1980, Fig. 119A) lies in the respective lengths of the three upper arms of their conidia. Since both species are amphibious, and the conidia of both are basically amero-staurosporous and phialidic, I consider their segregation to have been unnecessary. I therefore suggest that *Clavatospora* should become a facultative synonym of *Heliscus*.

EXCEPTIONS DUE TO CONVERGENCE

I must now sound a note of warning. The staurosporous conidia of *Varicosporium*, *Dendrospora* and *Dendrosporomyces* share a basic pattern of construction even to the constrictions at the base of each branch or arm of the conidium. Yet Nawawi et al. (1977) showed unequivocally that *Dendrosporomyces prolifer* Nawawi, Webster & Davey has dolipore septa, and must therefore be a basidiomycetous anamorph. *Dendrospora erecta* Ingold, on the other hand, has simple septal pores, and is therefore assumed to be an ascomycetous anamorph. The status of *Varicosporium* has not yet been resolved.

Spiniger Stalpers was erected for basidiomycetous anamorphs that in most ways resemble *Oedocephalum* Preuss. We may expect to encounter other unclamped basidiomycetous anamorphs which may well display similar parallelism or convergence with ascomycetous anamorphs. But these cases will be the exception rather than the rule. I do not think that arguments of possible polyphyly can reasonably be advanced to defend many of the segregate genera produced in recent years.

REFERENCES

Carmichael, J.W., Kendrick, B., Conners, I.L. & Sigler, L (1980). The Genera of Hyphomycetes. Univ. of Alberta Press, Edmonton.

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

Ellis, M.B. (1971) Dematiaceous hyphomycetes. Commonw. Mycol. Inst., Kew. 608 pp.

Ellis, M.B. (1976) More dematiaceous hyphomycetes. Commonw. Mycol. Inst, Kew. 507 pp.

Jong, S.C. & Peng, J.T. (1975) Identity and cultivation of a new commercial mushroom in Taiwan. Mycologia 67: 1235-1238

Kendrick, B. (Ed.) 1971. Taxonomy of fungi imperfecti. Univ. of Toronto Press, Toronto. 309 pp.

Kendrick, B. (1978) Recent developments in the systematics of pathogenic fungi. pp. 119-137 (In) Biosystematics in Agriculture (Eds.) Romberger, J.A., Foote, R.H., Knutson L.W. & Lentz P.L. Beltsville Symposia in Agricultural Research, Vol. 2. Allanheld, Osmun, Montclair.

Kendrick, B. (1980) The Systematics of Hyphomycetes (In) Biology of Conidial Fungi (Eds.) Cole G.T. & Kendrick B. Academic Press, New York.

Kendrick, B. & Carmichael J.W. (1973). Hyphomycetes, pp. 323-509 (In) The Fungi, Vol. IVA. (Eds.) Ainsworth, G.C., Sparrow F.K. & Sussman A.S. Academic Press, New York.

Kendrick, B. & Di Cosmo, F. (1979). Teleomorph-anamorph connections in Ascomycetes. pp. 283-359 (In) The Whole Fungus. Vol. 1 (Ed.) Kendrick, B. Nat. Mus. Canada, Ottawa.

Kendrick, B. & Nag Raj, T.R. (1979) Morphological terms in Fungi Imperfecti pp. 43-61 (In) The Whole Fungus, Vol. 1 (Ed.) Kendrick, B. Nat. Mus. Canada, Ottawa.

Kendrick, B. & Watling R. (1979) Mitospores in Basidiomycetes. pp. 473-545 (In) The whole Fungus, Vol. 2. (Ed.) Kendrick, B. Nat. Mus. Canada, Ottawa.

Korf, R.P. (1972) Synoptic key to the genera of the Pezizales. Mycologis 64: 937-955.

Madelin, M.F. (1979) An appraisal of the taxonomic significance of some different modes of producing blastic conidia. pp. 63-80 (In) The Whole Fungus, Vol. 1 (Ed.) Kendrick, B. Nat. Mus. Canada, Ottawa.

Michaelides, J., Hunter L., Kendrick B. & Nag Raj T.R. (1979) Synoptic key to 200 genera of coelomycetes. Icones generum coelomycetum supplement. Univ. of Waterloo Biol. Ser. 20: 42 pp.

Nag Raj, T.R. & Kendrick B. (1975) A monograph of *Chalara* and allied genera. Wilfrid Laurier University Press, Waterloo. 200 pp.

Nawawi, A., Webster, J. & Davey, R.A. (1977) *Dendrosporomyces prolifer* gen. et sp. nov., a basidiomycete with branched conidia. Trans. Brit. Mycol. Soc. 68: 59-63.

Pirozynski, K.A. (1962) *Circinotrichum* and *Gyrothrix* Mycol. Pap. 84: 28 pp.

Pirozynski, K.A. (1963) *Beltrania* and related genera. Mycol. Pap. 90: 37 pp.

Pirozynski, K.A. & Patil, S.D. (1970) Some setose hyphomycetes of leaf litter in south India. Can. J. Botany 48: 567-581.

Pollack, F.G. & Miller, O.K. (1976) *Antromycopsis broussonetiae* found to be the name of the imperfect state of *Pleurotus cystidiosus*. Mem. N.Y. Bot. Gard. 28: 174-178

Sutton, B.C. (1976) Species of *Hemibeltrania* Piroz. and *Dischloridium* gen. nov. Kavaka 4: 43-50.

Watling, R. & Kendrick, B. (1977) Dimorphism in *Collybia racemosa*. Mich. Bot. 16: 65-72.

ACKNOWLEDGEMENT

I thank Dr G.J. Samuels and Miss Joan Dingley for many stimulating discussions during the preparation of this paper, which was written while I was Visiting Scientist at the Plant Diseases Division, D.S.I.R., Auckland, New Zealand.

I gratefully acknowledge the award of a Guggenheim Fellowship which made my visit to the antipodes possible, and the granting of sabbatical leave by the University of Waterloo.

MYCOTAXON

Vol. XI, No. 1, pp. 365-368 April-June 1980

SOME TAXONOMICAL CONSIDERATIONS ON *CANDIDA* AND ALLIED GENERA

ONORATO VERONA

Istitute of Agricultural Microbiology
of the University of Pisa (Italy)

GINO FLORENZANO

Istitute of Agricultural Microbiology
of the University of Florence (Italy)

SUMMARY

The authors discuss the taxonomy of *Candida*, *Torulopsis* and *Cryptococcus*. According to a previous proposal the Aa. still retein valid the idea of unify these genera. However it seems necessary that two genera are created from the resulting larg grouping: this to separate the species related to hemiascomycetes from those related to basidiomycetes.

During a meeting on the genus *Candida*, held in Pisa in December 1977, the systematic status of the genus was discussed (1). The idea of joining together *Candida* and *Torulopsis*, so far regarded as being separate genera, was considered worthy of attention. The validity of this proposal was warranted by several arguments, the most convincing of which was the recognition of the fact that the main differentiating character, i.e. the ability to form mycelial filaments, is valueless.

We ourselves mentioned some species which originally known to be filamentous, subsequently lost this property. On the other hand there are some tipically not filamentous species that under the influence of particular stimuli, show filament production. Moreover, structural, biochemical and taxonomic similarities between *Candida* and *Torulopsis* were mentioned.

In this comunication we intend to confirm our previous statements and to add some additional considerations.

Our discourse starts from the genus *Cryptococcus*. As

it has been pointed out by Phaff and Spencer (2), it is more and more difficult to maintain the distinctions among *Cryptococcus, Torulopsis* and *Rhodotorula*. Capsule formation, absence of myceliar filaments and inability to produce carotenoids have lost much of their validity as discriminating characters. Perhaps the ability to assimilate inositol is the only discriminating character. Not much indead! Moreover the validity of this character is questionable, because some species included in the genus *Candida* are able to utilize inositol.

Moreover, till a short while ago it was assumed that none of the *Cryptococcus* species produces spores. The diagnosis of the genus prepared by Phaff and Spencer says: "ascospores, teliospores, ballistospores are not produced". Now the situation has changed. It has been shown that also the type species *Cryptococcus neoformans* has a sporogenous stage, characterised by filament formation and by the production of heterobasidious like structures, for this phase the genus *Filobasidiella* Kwon-Chung was established. Subsequently, two additional species have been found to be sporogenous: *Cr. cereanus* Phaff et al. and *C. lactativorus* Fell et Phaff. But these species are related at one ascogenous genus: *Sporopachidermia* Rodrigues de Miranda. Hence in the *Cryptococcus* the situation of *Torulopsis* and *Candida* exists.

As far as *Torulopsis* and *Candida* are concerned, van Uden and Buckley (3) have really pointed out that the separation of the two genera was based upon arbitrary standards.

In 1977 we proposed the unification of *Candida* and *Torulopsis* on the basis of several arguments (1).

In october 1978 Yarrow and Meyer (4) advanced the same proposal, suggesting simply the suppression of the genus *Torulopsis* through the transfer of its species into *Candida*. To do this, they introduce the following amendment in the *Candida* diagnosis: "pseudoyphae absent, rudimentary or well developed".

The Yarrow and Meyer amendment leaves the problem of the characterization of the genus unsolved since characterization of the genus unsolved since filamentation, withe the other characters, is no longer valed. The only attribute remaining in this large group of asporogenous yeasts is cell-shape, although variable. In one sense it is a return to the past.

We believe that the right approach to the taxonomic revision of the yeast including *Candida, Torulopsis* and,

eventually, *Cryptococcus*, must start from the basic consideration, already advanced by us in 1977, that within each genus there are taxa belonging to hemiascomycetes and taxa belonging to the heterobasidiomycetes.

It is evident that yeast species showing such a great taxonomic diversity cannot be grouped under the same genus. It is well known that the different taxonomic position entails peculiar properties: i.e. the value of G + C%, the structure of the cell wall, the structure of hyphal septa when hyphae or pseudohyphae are produced, etc.

It must be stressed that within Deuteromycetes (Hyphomycetes) this distinction is usually made. For example, *Spiniger* Stalpers has been segregated from *Oedocephalum* because its sexual stage shows basidiomicetous characters (5). Idem for *Moniliophthora* Evans et al. segregated from *Monilia* for identical reasons (6).

We suggest that the *Candida-Torulopsis-Cryptococcus* group might well be divided into two genera on the basis of their phylogeny.

The introduction in the diagnosis of the sentence "DBB positive" for one genus and "DBB negative" for the other is sufficient:(·)

"Cells globose, oval, elliptical or elongate; never apiculate, trigone or flash-shaped. A rudimentary or a more or less developed pseudomycelium may be present. Some species produce a capsule. Multiplication by budding.
Nitrate assimilation: variable.
Fermentation: positive or negative
DBB: positive
For some species a sexual stage referable to the heterobasidiomycetes is known".
"Cells globose etc.....
DBB: negative
For some species a sexual stage referable to the hemiascomycetes is known".

The biochemical characters maintain their taxonomic importance in the definition of the single species and variety.

The denomination of the two genera is irrelevant question.

Finally, since the new taxonomic attachment will lead to an increased amount of species, it would be desirable to arrange them into groups, by analogy with the situation of other large genera (i.e. *Aspergillus*, *Penicillium*, *Fusa-*

(·) For DBB test see van der Walt and Hopsu-Havu (7).

rium, etc.).

LITERATURE CITED

1. VERONA O. AND FLORENZANO G. (1977). Considerazioni di ordine sistematico e proposte di revisione del genere *Candida*. Convegno specializzato sul genere *Candida* (Soc. Italiana di Microbiologia), Pisa.

2. PHAFF H.J., SPENCER: see Phaff and Fell, in J. Lodder: The yeast, Amsterdam 1970, p. 1090.

3. VAN UDEN N., BUCKLEY H., in J. Lodder: The yeast, Amsterdam 1970, p. 893.

4. YARROW D., MEYER S.A. (1978). Proposal for amendment of the diagnosis of the genus *Candida* Berkhout nom. cons. Int. J. Systematic Bact. 28, 611-615.

5. STALPERS J.A. (1974). *Spiniger*, a new genus for imperfect states of Basidiomycetes. Koninkl. Nederl. Akademic van Wetenschappen, ser. C., p. 402-407.

6. EVANS H.C. AND STALPERS J.A., SAMSON R.A., BENNY G.L. (1978). On the taxonomy of *Monilia rorei*, an important pathogen of *Teobroma cacao* in South America. Can. Journal Botany, 56, 2528-2532.

7. VAN DER WALT J.P. AND HOPSU-HAVU V.K. (1976). A colour reaction for the differentiation of ascomycetous and hemibasidiomycetous yeasts. Ant. van Leeuwenh, 42, 157-163.

MYCOTAXON

Vol. XI, No. 1, pp. 369-375 April-June 1980

TRICHOPHAEA CONTRADICTA: A NEW COMBINATION AND AN EMENDED DESCRIPTION FOR PATELLA CONTRADICTA SEAVER[1]

HAROLD J. LARSEN[2]

Department of Botany and Plant Pathology, Oregon State University, Corvallis, OR 97331

SUMMARY

A culture derived from a British Columbia collection of "Patella" contradicta produced both the teleomorphic state and a Dichobotrys anamorphic state when grown on several media. The teleomorphic state characteristics are intermediate between those of Trichophaea s. str. and Sphaerosporella. The anamorphic state has 8-9 µm diameter subglobose to globose conidia with a 1 µm broad pedicel and typically produces three to five conidia per conidiogenous cell. The isolate has a rosy buff to salmon pink colonial and conidial color when grown on PDA under 12 hr diurnal fluorescent illumination, and mature apothecia are present 18-21 days after inoculation onto CM or CMMY agar. The combination Trichophaea contradicta (Seaver) comb. nov. is proposed and an emended description is given.

A small, lenticular, dark brown discomycete was collected in British Columbia during June 1971. Its distinctive features were: the smooth, broadly ellipsoidal ascospores; the short, light-colored marginal hairs, each with a subglobose basal cell; and the long, brown, flexuous hairs scattered over the undersurface of the receptacle. Culture attempts with 2% water agar (WA) and corn meal-malt extract-yeast extract agar (CMMY) succeeded, and the fungus was subsequently grown on these and on corn meal agar (CM) and potato-dextrose agar (PDA) after Lacey and Bridgmon (9). The isolate produced both a Dichobotrys anamorphic state and a teleomorphic state with dark brown apothecia which, when grown under room conditions, were identical to those of the parent collection. The collection and culture are similar to the sphaerical-spored Trichophaea brunnea (Alb. & Schw. ex Fr.) Batra & Batra and to the dark variant of T. abundans

[1]Based in part on a dissertation submitted to the Graduate School of Oregon State University in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

[2]Present address: Tree Fruit Research Center, 1100 N. Western Ave., Wenatchee, WA 98801.

(Karst.) Boudier (1,5,10), but the British Columbia collection differs from both these species in the greater breadth of its ascospores and in the blunt tips of its lower excipular hairs. A long-neglected species, Patella contradicta Seaver, closely matches the characteristics of the BC collection (15). Comparison of the BC collection with Seaver's type confirmed the identification, and the BC collection was reported as P. contradicta in the Pezizales Checklist (11).

The generic name Patella Weber in Wigg. ex Seaver is, however, a synonym of the older genus Scutellinia (Cke.) Lambotte (4). Species formerly assigned to Patella have thus been reassigned to other genera such as Anthracobia Boudier, Cheilymenia Boudier, Humaria Fuckel, Leucoscypha Boudier, Scutellinia, Tricharina Eckblad, and Trichophaea Boudier (7); however, Seaver's P. contradicta has not been reassigned. In my judgment, it should be transferred to the genus Trichophaea. The following new combination and emended description are therefore proposed:

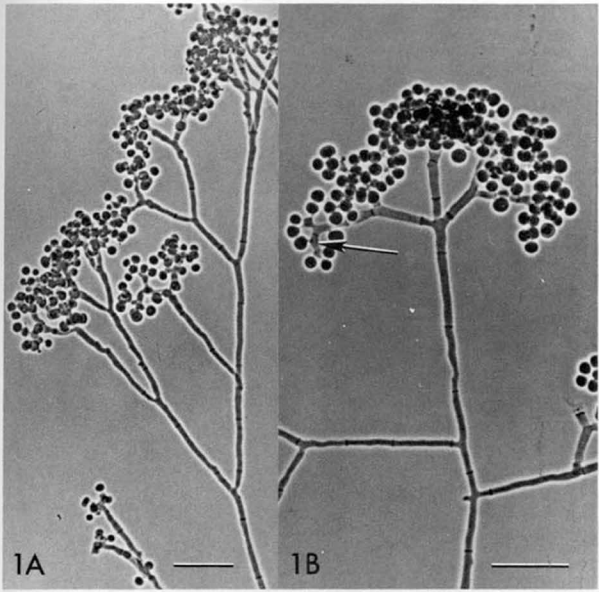
TRICHOPHAEA CONTRADICTA (Seaver) H. J. Larsen, comb. nov.
≡Patella contradicta Seaver, Mycologia 32:567. 1940.
Figs. 1,2.

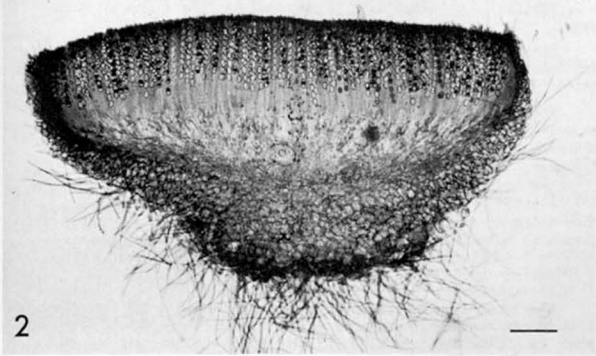
Apothecia gregarious to crowded, sessile, early becoming slightly concave but flattened at maturity, 1-2.5 mm diam; hymenium "Isabelline" (19'i)[1] to "Sepia" (13"m) brown with the apothecial margin darker, elevated, and clothed with an inconspicuous fringe of hairs; lower margin and flank clothed with scattered longer and darker hairs.

Excipular hairs of the upper margin typically single but occasionally grouped in small fascicles, very short, 20-45(-65) X 4-6 µm, hyaline to very light brown, thin-walled, (1-)2-4 celled, narrowing quickly above the 8-10 µm diam swollen basal cell and terminating in a narrowly obtuse to acuminate tip; excipular hairs of the lower margin and flank longer, 80-115(-140) X 5-7 µm, 3-5 celled, "Umber" (15m) brown, more flexuous, also arising from a swollen outer excipular basal cell but more gradually tapering to a narrowly obtuse tip. Ectal excipulum 180-230 µm thick at the base, narrowing to 60 µm thick toward the margin of the apothecium, composed of texture globulosa toward the base of the apothecium with cells (10-)25-60 µm diam and the outermost cells brownish walled; grading into texture angularis for the upper half of the ectal excipulum, with the 15-40 X (5-)10-15(-20) µm cells oriented with their long axis perpendicular to the outer surface. Medullary

[1]Colors after Rayner (12) with Ridgeway (13) equivalents in parentheses.

Figures 1-2. Trichophaea contradicta. Fig. 1. Dichobotrys anamorphic state by phase contrast microscopy. Bar=50 µm. (A) Typical dichotomously branched conidiophores with conidia. (b) Atypical trichotomously branched conidiophore with catenulate ampullae (arrow). Fig. 2. Teleomorphic state cross-section by brightfield microscopy showing the duplex excipulum. Bar=100 µm.


1A
1B


2

excipulum 60-100 µm thick, composed of textura intricata with cells 5-8 µm diam.

Asci cylindrical, operculate, J-, eight-spored, 150-170 X 11-14 µm. Ascospores uniseriate, smooth, broadly ellipsoidal to occasionally subsphaerical, (12-)14.5-16(-18) X (8.5-)9.0-10.5(-11) µm, mode 15 X 10 µm, containing one or usually two oil drops and a large DeBary bubble when mounted in lactic acid, lactophenol, or Melzer's reagent; nuclei carminophobic. Paraphyses slender, septate, unbranched, 150-170 X 1.5-2.5 µm; apices enlarged to 5-8 µm diam, usually clavate to spatulate, with the apical cell brownish and containing numerous small oil droplets.

Anamorphic state assigned to Dichobotrys Hennebert. Colonies on CM agar effuse, spreading rapidly, initially white becoming cream-white with age and conidial production, hyphae hyaline, prostrate, septate. Conidiophores erect, 4-6 µm diam, dichotomously (rarely trichotomously) branched 2-5 times beginning at one-half to two-thirds their 180-1000 µm total height, primary branches (15-)30-80(-100) µm long, secondary and subsequent branches 15-25 µm long, the branch length decreasing with each furcation, terminal branches bearing paired, inflated, cylindrical to claviform or sphaerical (rarely catenulate-sphaerical) ampullae which develop 3-5(-8) simultaneous conidial buds and collapse at maturity. Conidia holoblastic, single celled, smooth subglobose to globose, 8-9 µm diam, cream-white to pale ochraceous en masse, with a 1 X 1 µm cylindrical pedicel attached to the conidia at maturity and remaining from the 2-4 µm high X 1(-2) µm diam denticle; cell wall uniformly thickened. Homothallic, with mature apothecia produced 18-21 days after inoculation on CM and CMMY agar.

Colonies on PDA more floccose and with more abundant aerial mycelium, initially white but becoming "Rosy Buff" (13"D) and finally "Flesh" pink (5'd) when grown under daylight fluorescent lights with a 12 hr diurnal off/on cycle. Conidiophores and conidia similar to those on CM agar, but much more abundant and the conidia "Salmon" (11'd) en masse. Few or no apothecia produced on PDA.

Habitat: On burned soil or charcoal in late spring or early summer.

Distribution: Known only from the type locality at the New York Botanic Garden and from Glacier National Park, British Columbia, Canada.

Materials examined: Canada: on burned soil and litter at the edge of a forest fire site, beside Transcanada Highway No. 1 in Glacier National Park, British Columbia, col. H. J. Larsen, 26 June 1971 (HJL F-204; OSC 33,351); United States: on burnt ground, New York Botanic Garden, Bronx, New York City, col. F. J. Seaver, 27 June 1916 (NY) (HOLOTYPE).

Culture: H. J. Larsen 62-I, derived from collection HJL F-204. Culture to be submitted to the American Type Culture Collection.

DISCUSSION

The transfer of Seaver's P. contradicta to Trichophaea is based upon the presence of brown hairs arising from the outer cells of the ectal excipulum, the presence of oil

droplets in the ascospores, the lenticular apothecia which lack carotenoid pigments, and the Dichobotrys anamorphic state (Fig. 1) (6,7). The genus Sphaerosporella (Svrček) Svrček & Kubička shares these characteristics and differs only in having sphaerical spores (3,4,7,14). Korf (7,8) has advocated the merger of Trichophaea and Sphaerosporella on the basis that the difference in ascospore shape is insufficient to separate these genera. T. contradicta supports this tenet since its broadly ellipsoidal ascospores (L:W 1.5) are nicely intermediate between those of species with sphaerical spores (L:W 1.0) and those of species with elliptical ascospores (L:W 1.7-2.9). Korf's view is therefore accepted here and the species is assigned to Trichophaea since it has priority if the two genera are merged (7).

The species most closely related to T. contradicta appear to be T. brunnea and the dark apothecial variant of T. abundans. Both of these pyrophilic species are dark brown and have a duplex excipulum and a Dichobotrys anamorphic state (1,10,14). Ascospore shape and excipular hair morphology and distribution are the primary differences separating the three species. T. brunnea has sphaerical ascospores and excipular hairs which are often fasciculate near the apothecial margin and which lack enlarged basal cells. The holotype of T. contradicta has a few small fascicles of excipular hairs at the apothecial margin, but the fasciculation is neither as common nor as obvious as in T. brunnea. T. abundans has narrower ascospores (L:W 1.8) and longer excipular hairs at the margin (50-80 µm long) and on the lower exterior (80-150 µm long); the basal cell of the excipular hairs of T. abundans is also less enlarged than those of T. contradicta.

The anamorphic state of T. contradicta differs in several respects from the four Dichobotrys species described by Hennebert (5). As seen in Table I, the most distinctive characteristic separating the species is the number of conidia produced per ampulla. The conidial sizes and shapes for D. abundans Henneb. and D. sessilispora Henneb. overlap those for the T. contradicta anamorph, but D. sessilispora is readily distinguished by its broader pedicel. The degree of conidiophore branching has only limited value as a diagnostic character since it varies with the richness of the medium for D. abundans (2); similarly, many conidiophores of the T. contradicta anamorph tend to have four to five dichotomies when grown on PDA but only two to three dichotomies when grown on WA. Trichotomously branched conidiophores and catenulate ampullae, like those occasionally observed in the T. contradicta anamorph (Fig. 1-B), are reported only for D. sessilispora (2) and neither feature is typical for either species. The "Rosy Buff" to "Flesh" pink colonial and "Salmon" pink conidial coloration, observed when the T. contradicta anamorph is grown on PDA under 12 hr diurnal fluorescent illumination, contrasts with the ochraceous colors reported for the other species (2,5).

Table I. Characteristics of the anamorphic state of T. contradicta and known Dichobotrys species.

Dichobotrys species	Conidia per ampulla	Conidial size	Conidial shape	Pedicel width	No. of Conidiophore branches
T. contradicta anamorph	3-5(-8)	8-9 µm	subglobose to globose	1(-2) µm	2-5
D. abundans	10-15	8-11 X 7-9 µm	napiform to subglobose	1 µm	3-7
D. brunnea	6-12	12-15 µm diam.	globose	?	2-3
D. parvispora	"numerous"	4-6 X 4-8 µm	napiform to subglobose	1 µm	1-4
D. sessilispora	1-4	(6-)9-10(-14) µm diam.	subglobose to globose	3-4(-7) µm	1-3

I thank the New York Botanical Garden for lending me the type collection of P. contradicta. Support during the intial stage of this study was provided by NSF Graduate Traineeship GX 1697.

LITERATURE CITED

1. BINYAMINI, N. 1972. Trichophaea abundans (Karst.) Boud.= Anthracobia humillima Malençon. Bot. Tidskr. 67:154-158.
2. CAIN, R. F., and N. A. HASTINGS. 1956. Studies of soil fungi. II. A new species of Sphaerospora with a Botrytis-like stage. Can. J. Bot. 34:360-376.
3. DENNIS, R. W. G. 1968. British Ascomycetes. J. Cramer. Lehre. 455 p.
4. ECKBLAD, F.-E. 1968. The genera of the operculate Discomycetes. A re-evaluation of their taxonomy, phylogeny and nomenclature. Nytt Mag. Bot. 15:1-191.
5. HENNEBERT, G. L. 1973. Botrytis and Botrytis-like genera. Persoonia 7:183-206.
6. KANOUSE, B. B. 1958. Some species of the genus Trichophaea. Mycologia 50:121-140.
7. KORF, R. P. 1972. Synoptic key to the genera of the Pezizales. Mycologia 64:937-994.
8. KORF, R. P. 1973. Discomycetes and Tuberales. In Ainsworth, G. C., F. K. Sparrow, and A. S. Sussman (eds.), The Fungi: an advanced treatise 4A:249-319. Academic Press, New York.
9. LACEY, M. L., and G. H. BRIDGMON. 1962. Potato-Dextrose agar prepared from dehydrated mashed potatoes. Phytopathology 52:173.
10. LARSEN, H. J., Jr. 1975. A note concerning the synonymy of Anthracobia humillima with Trichophaea abundans. Mycologia 67:1058-1061.

11. LARSEN, H. J., Jr., and W. C. DENISON. 1978. A checklist of the operculate cup-fungi (Pezizales) of North America west of the Great Plains. Mycotaxon 7:68-90.
12. RAYNER, R. W. 1970. A mycological colour chart. Commonwealth Mycological Institute, Kew. 34 p.
13. RIDGEWAY, R. 1912. Color standards and color nomenclature. Ridgeway, Washington. 43 p.
14. RIFAI, M. A. 1968. The Australasian Pezizales in the herbarium of the Royal Botanic Gardens Kew. Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk., Tweede Sect., 57(3):1-295.
15. SEAVER, F. J. 1940. Photographs and descriptions of cup-fungi. XXXV. A new species of Patella. Mycologia 32:567-569.

MYCOTAXON

Vol. XI, No. 1, pp. 376-380 April-June 1980

A NEW SPHERICAL SPORED SPECIES OF COPROTUS (PEZIZALES)[1]

JACK L. GIBSON AND JAMES W. KIMBROUGH

Department of Botany
University of Florida
Gainesville, Florida 32611

The genus *Coprotus* (Kimbrough and Korf, 1967) includes those species of coprophilous discomycetes with eight or multispored, nonamyloid asci and smooth ascospores with characteristic gaseous inclusions referred to as deBary bubbles. *Coprotus* was placed in the tribe Theleboleae of the Pezizaceae, and a total of six speciew were transferred to the genus. In recent studies of the Pezizales, *Coprotus* is recognized and the tribe Theleboleae is raised to familial rank (Rifai 1968; Eckblad, 1968). However, cytological and developmental studies by Kish (1974) suggest that the genus shows much closer affinities with the Pyronemataceae than with the Thelebolaceae. Morphological and cytochemical similarities between the apical apparatuses of asci in *Pyronema* and *Coprotus* shown by Samuelson (1978) support this view.

According to Eckblad (1968), van Brummelen studied the type of *Leporina multispora* Velenovsky and found it to be identical with *Ascobolus sexdecimsporus* Crouan, the holotype of *Coprotus* Korf and Kimbr. This implied to Eckblad that *Leporina* should be the correct name for *Coprotus*. Kimbrough (1970) discussed the nomenclatural problem in greater detail and pointed out that, in view of the multiplicity of organisms that existed on the type of *Leporina*, the genus was perhaps based on a type consisting of two or more entirely disconcordant elements. He concluded that the unambiguous taxon *Coprotus* should be retained.

---

[1] Florida Agricultural Experiment Station Jour. Ser. No. 2363

In a monograph of the North American species of *Coprotus*, Kimbrough, Luck-Allen, and Cain (1972) transferred five more species to the genus and described six new ones. Taking into account observations on these species, they further modified the original generic diagnosis of *Coprotus*. Subsequent to this monograph, the following species have been described, *C. trichosurus* Bell and Kimbrough (1973), *C. baeosporus* Jeng and Krug (1977), and *C. sarengparensis* Thind and Kaushal (1978). These differed largely from previously described species in ascospore size and shape.

During a study of coprophilous fungi on dung samples from California, a species of *Coprotus* was discovered which could not be identified as any of the currently accepted species. This fungus is, therefore, described as a new species.

Coprotus sphaerosporus Gibson and Kimbrough, sp. nov.

(Figs. 1-7)

Apothecia dispersa vel gregaria, sessile, 0.2-0.7 mm in diametro, alba vel fere pellucida, primo globosa demum discoidea, superficies asperita per asci protrudens. Excipulum basalis e textura globosa, e 2-3 strata cellulis compositis, cellulae 5.0-6.5 µm in diametro, cellulae marginales elongatae, 6.0-8.5 x 2.0-3.5 µm. Asci 8-spori, cylindracei vel clavati, e basi attenuati, tholiformis vel aliquanto truncati, 76-89 x 13-19 µm. Ascosporae uniseriatae minus saepe biseriate, globosae vel subglobosae, 8.0-8.5 x 5.5-6.0 µm, unusquisque "deBary bubble" conspicuus praeditae. Paraphyses filiformes, septatae, simplex vel prope basi ramosi, guttulatae, interdum superne leviter inflatae. In fimo equinum.

Holotype: On horse dung from San Bernardino Co., California, N. side of Granite Mts., el. 4200 ft., T. C. Emel, 3/27/75, FLAS F 52105.

Apothecia scattered to gregarious, sessile, 0.2-0.7 mm in diam, white to almost translucent, at first globose, then becoming discoid, surface roughened by protruding asci; basal excipulum of a *textura globosa*, in 2-3 cell layers with cells 5.0-6.5 um in diam; marginal excipulum with cells elongated, 6.0-8.5 x 2.0-3.5 um; asci eight-spored, cylindric to clavate, attenuate at the base, dome-shaped to somewhat truncate, 76-89 x 13-19 um; ascospores uniseriate, less frequently biseriate, globose to subglobose, 8.0-8.5 x 5.5-6.0 um, each with a conspicuous deBary bubble; paraphyses filiform, septate, simple or branched near the bases, guttulate, sometimes slightly inflated at the apices. On horse dung.

COMMENTS

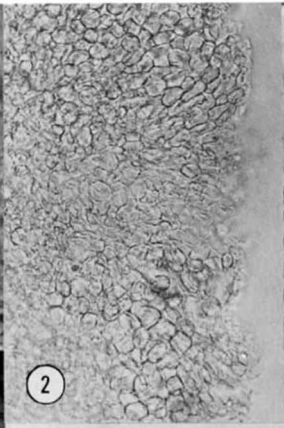
Coprotus sphaerosporus differs from all other species described in the genus in having spherical spores. All previously known species have ellipsoidal spores. Apothecia of *C. sphaerosporus* (Fig. 4) are similar to those of *C. albidus* (Boud.) Kimbr. and *C. winteri* (Marchal) Kimbr. in that they are white to translucent throughout development. The cells of the medullary excipulum (Fig. 2) are very similar to those of *C. glaucellus* (Rehm) Kimbr. and *C. breviascus* (Vel.) Kimbr., Luck-Allen, and Cain. However, the marginal cells of the ectal excipulum (Fig. 3) are more like those of *C. duplus* Kimbr. and *C. nivius* (Fckl.) Kimbr., Luck-Allen, and Cain. The uniseriate to sometimes biseriate, 8-spored asci (Figs. 1 and 5) are typical of several species, including *C. glaucellus*, *C. leucopocillum* Kimbr., and *C. ochraceus* (Cr. and Cr.) Larsen. The septate, filiform, basally branched paraphyses (Fig. 7) are similar to those of *C. dextrinoideus* Kimbr. Although it shares many common features with other species of the genus, when spores are examined, *C. sphaerosporus* is not likely to be mistaken for any of the known species.

ACKNOWLEDGEMENTS

We would like to thank Dr. Dana Griffin, III for assisting with the Latin diagnosis and Dr. Gerald Benny for reviewing the manuscript and assisting in preparing the photographic plate. We also appreciate Dr. Don Pfister's willingness to review the manuscript.

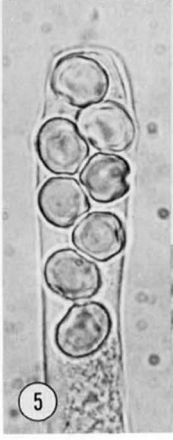
Figs. 1-7. *Coprotus sphaerosporus*. (1) A mature ascus with spherical ascospores showing conspicuous deBary bubbles, X 1000. (2) Section of apothecium showing cells of the medullary excipulum, X 400. (3) Apothecial section with elongated marginal cells of the ectal excipulum, X 400. (4) A mature apothecium on dung, X 30. (5) An ascus with plasmolyzed, immature spores, X 1000. (6) An empty ascus with attached operculum, X 1000. (7) Septate, filimorm paraphyses, X 1000.


1


2


3


4


5


6

7

LITERATURE CITED

Bell, Ann and J. W. Kimbrough. 1973. *Coprotus trichosurus* sp. nov. from New Zealand. Trans. Brit. Mycol. Soc. 61: 190-193.

Eckblad, F.-E. 1968. The genera of operculate Discomycetes. A re-evaluation of their taxonomy, phylogeny and nomenclature. Nytt Mag. Bot. 15: 1-191.

Jeng, R. S. and J. C. Krug. 1977. New records and new species of coprophilous Pezizales from Argentina and Venezuela. Canad. J. Bot. 55: 2987-3000.

Kimbrough, J. W. 1970. A segregate of *Ascophanus*, *Coprotus* vs. *Leporina*. (Thelebolaceae, Pezizales) Taxon 19: 779-781.

_____ and R. P. Korf. 1967. A synopsis of the genera and species of the tribe Theleboleae (=Pseudoascobolaceae_. Amer. J. Bot. 54: 9-23.

_____, E. R. Luck-Allen, and R. F. Cain. 1972. North American species of *Coprotus* (Thelebolaceae: Pezizales). Canad. J. Bot. 50: 957-971.

Kish, L. P. 1974. Culture and cytological development of *Coprotus lacteus* (Pezizales). Mycologia 66: 422-435.

Rifai, M. A. 1968. The Australasian Pezizales in the herbarium of the Royal Botanic Gardens Kew. Verh. K. Ned. Akad. Wetensch. Afd. Natuurk. Tweede Reeks, 57: 1-295.

Samuelson, D. A. 1978. Asci of the Pezizales III: The apical apparatus of eugymnohymenial representatives. Amer. J. Bot. 65: 748-758.

Thind, K. S., S. C. Kaushal, and R. Kaushal. 1978. The genus *Coprotus* in India. J. Indian Bot. Soc. 57: 63-67.

MYCOTAXON

Vol. XI, No. 1, pp. 381-395 April-June 1980

LATER STARTING POINT BLUES. II. DUMONTINIA TUBEROSA: THE THORNY THICKETS OF SYNONYMY AND SOME EXAMPLES OF NOMENCLATORIALISM*

RICHARD P. KORF

Plant Pathology Herbarium, Cornell University
Ithaca, NY 14853

and

LINDA M. KOHN

Department of Botany, Clemson University, Clemson SC 29631

SUMMARY

Six examples derived from a study of the synonymy of Dumontinia tuberosa are used to illustrate that "learning to live with later starting points" yields only frustration for the conscientious mycologist. Later starting points not only fail to avoid pre-starting-point bibliographic work, but create an additional, intolerable bibliographic load, and perniciously create new names (legal fictions). Adoption of a favored status for the "basic books" of Persoon and Fries, coupled with a change of the starting point to 1753, offers great hope for nomenclatural stability.

"Some have plunged into the thorny thickets of synonymy, floundering amid the multitudinous meticulosities of Nomenclatorialism,[2] from which they rarely emerge unscathed; ....

[2] NOMENCLATORIALISM. An intricate, esoteric art which strives to affix to every living creature (plant or animal) a definite unchangeable Latin label in strict accordance with the very latest views about Scientific Nomenclature. The object of the art was to reach finality; but it has not attained that end, nor can it, so long as the multiplicity of nature is rivalled by the variety of men's minds. A naturalist should take heed lest he become too nomenclatorialistically minded." – W. B. Grove, **British Stem- and Leaf-Fungi**, vol. 2, p. 637. 1937.

INTRODUCTION

Later starting points were introduced for certain groups of plants, including the fungi, for the purposes of bringing order and simplicity to the citation of names in those groups that Linnaeus (1753) had not adequately treated. Our attempts to follow the later starting-point provisions of the International Code of Botanical Nomenclature (ICBN) (Stafleu, 1978) have demonstrated consistently that rather than reduce the work of taxonomists, these provisions inordinately increase the work load and yield often completely arbitrary results. A single synonymy is considered here in some detail, that of Dumontinia tuberosa (TABLE 1), a species treated by the junior author in her monographic studies of Sclerotinia (Kohn, 1979). Citation of the authorities for the dozen names in synonymy is unnecessarily complex and required untold hours of bibliographic research, most of which was directly the result of later starting-point provisions. We cannot even claim, after our exhaustive search of the literature, that we have correctly cited the names in that Table.

Two early-described fungi have usually been synonymized, Octospora tuberosa Hedwig 1789 (TABLE 1: Rank 1) and Peziza tuberosa Bulliard 1791 (Rank 3). The two epithets happen to be the same, but the names rest on different type specimens. A year after Hedwig published his name, Dickson transferred it to Peziza (Rank 2). Bulliard's name, published still a year later, would be a later homonym of P. tuberosa (Hedw.) Dicks. were it not for the provisions of a later starting point, which devalidate all three names. Because these are Ascomycetes [part of the Fungi caeteri cited in ICBN, Art. 13.1 (f)], special status is given to the names used by Fries in the Systema mycologicum 1821-1832. Fries recognized Bulliard as the author of the name he accepted, Peziza tuberosa, and he considered Octospora tuberosa Hedw. to be a taxonomic synonym of it. We may consider that under the ICBN Fries thereby sanctioned the use of Bulliard's name.

TABLE 1: THE SYNONYMY

Rank by date	
12	Dumontinia tuberosa (Bull. ex Mérat) Kohn, Mycotaxon **9:** 433. 1979.
3	≡ [Peziza tuberosa Bull., Hist. champ. France p. 266, pl. 485, III. 1791 (pre-starting point; not validly published [ICBN, Art. 13.1 (f)], "later homonym" of P. tuberosa (Hedw.) Dickson 1790).]
4	≡ Peziza tuberosa Bull. ex Mérat, Nouv. fl. envir. Paris ed. 2, **1**: 24. 1821 (**sanctioned** [ICBN, Art. 13.1 (f)] by Fries, Syst. mycol. **2**(1): 58. 1822, 2(2): 612. 1823).
8	≡ Rutstroemia tuberosa (Bull. ex Mérat) Karst., Bidrag Kännedom Finlands Natur Folk **19:** 105. 1871.
10	≡ Hymenoscyphus tuberosus (Bull. ex Mérat) Phill. (ut "Hymenoscypha tuberosa"), Man. Brit. discomyc. p. 113. 1887.
11	≡ Whetzelinia tuberosa (Bull. ex Mérat) Korf & Dumont [ut "(Hedw. ex Mérat)"], Mycologia **64:** 250. 1972.
1	= [Octospora tuberosa Hedw., Descr. micr.-anal. musc. frond. **2:** 33. 1789 (pre-starting point; not validly published [ICBN, Art. 13.1 (f)]).]
2	≡ [Peziza tuberosa (Hedw.) Dickson, Fasc. pl. crypt. brit. **2:** 25. 1790 (pre-starting point; not validly published [ICBN, Art. 13.1 (f)]).]
6	≡ Peziza tuberosa (Hedw.) Dickson ex Ficinus & Schubert (ut "Diks."), Fl. Dresden Ed. 2, **2:** 456. 1823 (validly published later homonym, **illegitimate**), not P. tuberosa Bull. ex Mérat 1821.
7	≡ Sclerotinia tuberosa Fuckel [ut "(Hedw.)"], Jahrb. Nassauischen Vereins Naturk. **23-24:** 331. 1870 (a **new name** [ICBN, Art. 72.1 Note 1]).
9	≡ Phialea tuberosa Gillet (ut "Hedw."), Champ. France discomyc. p. 97. 1881 (1882?) (a **new name** [ICBN, Art. 72.1 Note 1]).
5	= Macroscyphus tuberosus [Hedw.? Bull.?] S.F. Gray, Nat. arr. Brit. pl. **1:** 672. 1821.

NOTES ON THE TABLE: The synonymy is essentially a revised arrangement of the early taxonomic synonyms and the later nomenclatural synonyms from Kohn (**1979**); later taxonomic synonyms given there, of no nomenclatural significance, are intentionally omitted here.

An examination of the literature will show the reader that in almost no instance have **any** of the post-1820 names appearing in TABLE 1 been given the author citations attributed to them there, simply because the provisions of later starting points are too complicated for even the best-intentioned workers to follow. Not a single textbook, not a single flora, not a single monograph (save that of the junior author) uses what we consider to be the "correct" authorities under ICBN. Any claim that later starting points lead to stability in names and author citations is wholly inconsistent with these results.

By a series of "examples," we hope to lead the reader to a better understanding of how later starting points have caused and will cause havoc in nomenclature. W. B. Grove, to whom we fondly dedicate this paper, had it right: there are indeed "thorny thickets of synonymy" and "multitudinous meticulosities of Nomenclatorialism" (Grove, 1937: 637).

AN HISTORICAL PERSPECTIVE: THE 1753 STARTING POINT

When the International Botanical Congress of 1867 adopted its first Code, the Lois de la Nomenclature Botanique prepared by Alphonse L. P. P. de Candolle, the Linnean binomial system was adopted, but no "starting point" was established. Nomenclature was not to be seriously discussed again at an International Botanical Congress until the Paris Congress of 1900 moved that the subject of nomenclature be given careful consideration at the Vienna Congress of 1905. The next five years saw a flurry of activity, including publication of the unfortunate "American Code" in 1904, which was proposed for complete substitution for the laws of 1867. At the Vienna Congress the American Code gained few adherents, and the new set of laws retained practically the original form, with some alterations and additions. The rules were seen to apply principally to vascular plants, and the special problems in connection with cryptogams were placed in the hands of committees, to be given further consideration at the Brussels Congress in 1910. A starting point for vascular plants was designated at the 1905 Congress: Linnaeus's Species Plantarum ed. 1 (1753).

MORE HISTORY: THE LATER STARTING-POINT CONCEPT AND THE SLIDING DATE

It was at the Brussels Congress of 1910 that decisions were made on appropriate starting points for cryptogams. Myxomycetes and Lichens have the same starting point as do vascular plants: Linnaeus's Species Plantarum, ed. 1 (1753). Fungi were to start with Fries's Systema Mycologicum 1821-1832, except for Ustilaginales, Uredinales and Gasteromycetes which date from Persoon's Synopsis Methodica Fungorum 1801.[1]

The question of lists of nomina conservanda among cryptogams, also on the agenda for consideration at Brussels, was put off for

[1] The most remarkable decision, perhaps, reached by the special committees at Brussels, was to adopt Hirn's 1900 Monographie und Iconographie der Oedogoniaceen as a starting-point book, fewer than ten years after its appearance.

for the 1915 Congress, since it was evidently impossible to compile such lists before the dates of priority were fixed. World War I intervened, and the next International Botanical Congress, in Ithaca, 1925, did not take up nomenclature.

The Cambridge Congress of 1930 and the Amsterdam Congress of 1935 did not change the starting points proposed for fungi in 1910. It was not until 1950 that the next International Botanical Congress was held, following World War II, in Stockholm. At it, a distinction was made between starting-point **dates** and starting-point **books** that proved of major significance in citation of names of fungi.

Each of the Codes from 1910 to 1935 had listed a year (or a series of years), and then the name of an author and the title of a book, book-series, or monographic article. The major fungal entry, that of Fries's Systema Mycologicum, had the dates 1821-1832, often referred to in the literature as a "**sliding date.**" Just how that 12-year span was to be treated was not spelled out in the Codes, nor was there any agreement among practicing mycologists. The dates on which the various parts of the Systema had appeared was established with fair precision: volume **1** in 1821, **2**(1) in 1822, **2**(2) in 1823, **3**(1) in 1829, and **3**(2) and the Index in 1832. Fries's Elenchus Fungorum, both volumes appearing in 1828, was a supplement to the Systema, but whether or not it was a part of the "starting-point book" was neither spelled out in the Codes nor was there general agreement on its status among mycologists.

Some mycologists treated the later starting point of Fries's Systema to mean that each taxonomic group started with its first treatment in that series. Thus most Basidiomycetes were held to begin their nomenclature in 1821, since they were, for the most part, treated in volume **1**. Among Discomycetes, for example, the Geoglossaceae, treated in volume **1**, also had an 1821 starting date; many others date from 1822, with still others starting (along with most Pyrenomycetes) in 1823, etc. Some mycologists held to an 1821 start for all of these fungi, while others held that the 1832 index should be the deciding date. Confusion reigned, of course, since different interpretations gave rise to different name choices or author citations.

It is only fair to point out that the basic reason for choosing the works of Persoon and of Fries was that their work represented the first major comprehensive treatments of fungi. Both men were considered to be the real "fathers of mycology" as we know it. The confusion that existed in the earlier literature had been sorted out to a great extent in these two works, and the mycologists who voted for these works as starting-point volumes in Brussels in 1910 probably chose as wisely as it would be possible to choose today.

EXAMPLE 1: THE 1950 STOCKHOLM CONGRESS (DATES, NOT BOOKS, AND THE NON-ACCEPTANCE OF THE FILTER SYSTEM)

The most significant change in later starting-point procedures grew out of a decision implemented at the Stockholm Congress to assign precise dates to starting-point books. The exact date of publication of many books was not known, and **arbitrary** dates were chosen for those starting-point books where the actual date was un-

certain. Linnaeus's Species Plantarum ed. 1 was arbitrarily dated 1 May 1753. Persoon's Synopsis was arbitrarily dated 31 December 1801, and the first volume of Fries's Systema was arbitrarily dated 1 January 1821.

For mycologists these new dates had profound effects. The dating of Persoon's work clearly made all other works published in or before 1801 **pre-starting-point**. Similarly, the choice of 1.1.1801 for volume 1 of Fries's Systema made any publication appearing in 1821 **post-starting-point** (thus validating the publication of S. F. Gray's A Natural Arrangement of British Plants, over which much controversy had existed as to whether it was pre-Friesian or post-Friesian).

Starting points were thus to be dates, not books. For nearly all groups of plants a particular book was deemed to have been published on the starting-point date. This was not true, however, of certain algal groups[2] and of Fungi caeteri. The mycologists at Stockholm, aware that most of the Fungi caeteri were not included in volume 1 of the Systema, and that the starting-point date did not correlate with any starting-point book for such fungi, adopted a complicated, confusingly worded concept aimed at giving privileged status to Fries's names; they included for the first time the Elenchus under the umbrella of priviledged names:

"Art. 23, f. FUNGI CAETERI, 1 Jan. 1821 (Fries, Systema Mycologicum Vol. 1). Vol. 1 of the Systema is treated as having appeared on 1 Jan. 1821, and the Elenchus Fungorum (1828) is treated as part of the Systema. Names of FUNGI CAETERI published in other works between the dates of the first (Vol. 1) and last (Vol. 3 part 2 and index) parts of the Systema which are synonyms or homonyms of any of the FUNGI CAETERI included in the Systema do not affect the nomenclatural status of names used by Fries in this work."

This remarkable wording was the result of a compromise among members of the Special Committee for Fungi and Lichens, who had not seen fit to adopte the "filter" system proposed by M. A. Donk and others. That system had as its focus a simple process for determining name usage: one would first turn to the indices of the Systema, or of Persoon's Synopsis for the groups concerned there, to determine if the starting-point author had adopoted a name (or had placed it in synonymy). If the name was accepted in the starting-point book, one's literature search was over, and the name dated from its appearance there. If the name was lacking or unaccepted, it's date status would be from the first acceptance after the starting-point date. The filter system thus gave protected status to the names in Fries's and Persoon's major works, would have cut bibliographic work for most of the names accepted in these works, and would have given us two books that would have covered the great majority of older, pre-starting-point names.

The net result of the 1950 decision (and the rejection of the "filter" system) was to multiply the problems of citing names and au-

[2] For these algae arbitrary dates were finally assigned at the Leningrad Congress in 1975. The "sliding-dates" problems for Nostocaceae were solved by assigning one arbitrary early date to all parts of multi-year treatments. Had mycologists opted for all parts of the Systema arbitrarily dated 1.1.1821, theirs would have been a similar solution.

thorities correctly, not particularly for Basidiomycetes, but significantly for Ascomycetes, Fungi Imperfecti and "Phycomycetes." It is no longer sufficient to know that Fries may have adopted a certain name for a Pyrenomycete or Discomycete in 1823; if one finds such a name, one is aware it has a priviledged status ("do not affect the nomenclatural status of names used by Fries in this work"), but the starting point for the name is not it's use in the Systema in 1823, but is 1.1.1821. **This fact is the basis for a huge and unintended burden being placed on mycologists who attempt to follow the Code.** Failure to comprehend what is involved in bibliographic "busy-work" in searching from 1.1.1821-to-date-of-treatment-in-the-Systema is the main reason that those who have objected to changing the present wording have continued their stance.

EXAMPLE 2: THE PROTOLOGUE, WHY LATER STARTING POINTS FAIL TO "WIPE THE SLATE CLEAN," AND LECTOTYPIFICATION OF PRE-STARTING-POINT NAMES

Those naïve in nomenclatural procedures have assumed that the establishment of a starting-point date automatically "wipes the slate clean" in that materials published prior to the starting point need no longer to be consulted; the old, rare books, available in only a few libraries, can be ignored, since the names they contain are ruled "not validly published." This is not true, because though nomenclature for a group begins with a specific date, taxonomy begins with the earliest recorded writing. An exceptionally important nomenclatural concept is that of the **protologue**, defined in ICBN as:

"* Protologue (from πρωτος, first; λογος, discourse): everything associated with a name at its first publication, i.e. diagnosis, description, illustrations, references, synonymy, geographical data, citation of specimens, discussion, and comments."

When pre-starting-point names are validly published by a post-starting-point author, he/she may or may not provide a description or diagnosis, but usually does give some reference to the pre-starting-point name (even if only indication of the name of the pre-starting-point author). **Typification** of the validly published name is a crucial nomenclatural act with immense implications concerning what name must be applied following taxonomic decisions. Articles 7.12 and 7.13 of the ICBN bear specifically on the question of the protologue in later starting-point situations:

"7.12 The type of a name of a taxon assigned to a group with a nomenclatural starting-point later than 1753 (see Art. 13) is to be determined in accordance with the indication or description and any other matter accompanying its first valid publication (see Arts. 32-45).

"7.13 When valid publication is by reference to a pre-starting-point description, the latter must be used for purposes of typification as though newly published."

The effect of these portions of Art. 7 is to **require** consultation of the pre-starting-point literature cited by the post-starting-point author. Instead of the slate having been wiped clean, such materials are "newly published" as of the date of the validating, post-starting-point author having mentioned them at all. The need to consult the older literature is thus often undiminished by provision of later starting points, since mere reference to it in the validating post-starting-point publication brings it "back to life."

It thus becomes impossible to consider any of the names in post-starting-point publications, including the Synopsis and the Systema, as standing on their own if they contain references (nearly all do) to earlier literature. Note that the protologue includes "everything" that appears in the first publication (and since pre-starting-point names are not validly published, the definition's "first publication" can only mean "first valid [i.e., post-starting-point] publication"). Art. 7.13 specifically takes up the situation where the validating author gives no description or diagnosis: the pre-starting-point description becomes crucial then in deciding on the type. Similarly, Art. 7.12 admonishes us to determine the type of a name not only from indications or descriptions accompanying the first valid publication, but from "any other matter accompanying" that publication, i.e., the total protologue (including the references and thereby everything that was written therein of the older literature).

Persoon and Fries did not work solely as creators: their works stand on the accumulated research of their forebearers. The Code does not destroy that historical basis by providing later starting points. The older books must still be consulted to understand what synthesis Persoon and Fries may have done to bring order to the literature of their past.

The importance of the protologue is particularly crucial when one remembers that the arbitrary starting-point date of 1.1.1821 gives special status to many papers published in 1821 and soon thereafter, papers that might well be forgotten, since they are often only local floristic lists. Frequently such compilers of names had no specimens, may never have seen the fungus at all but merely have compiled the literature citation. If we were forced to select a type specimen from non-existant material, or from a compiler's misidentifications, we would be in difficult straits indeed. But because the pre-starting-point name was cited as part of the protologue, we are free to select a type from the original material (if it exists), even though the material and its basis in publication is pre-starting-point: it becomes post-starting-point by virtue of the protologue provisions of the Code.

EXAMPLE 3: ON LEGAL FICTIONS CREATED BY LATER STARTING POINTS: THE LOSS OF INFORMATION BY SUPPRESSING CITATION OF THE ORIGINAL AUTHOR, THE "TRANSFER" OF PRE-STARTING-POINT NAMES, AND OTHER PERNICIOUS PHENOMENA

In little of the literature dealing with later starting points has any attention been drawn to what we consider to be one of the most horrendous results of this system.

Nomenclaturally aware mycologists understand that the Code permits two methods of citing authorities for names that were originally pre-starting-point. In the words of the ICBN, Recommendation 46E,

"46E.1 When an author who first validly publishes a name ascribes it to an author who published the name before the starting point of the group concerned (see Art. 13), the author citation may include, when such indication is considered useful or desirable, the name of the pre-starting-point author followed by ex as in Rec. 46C.

Examples: Lupinus L. or Lupinus Tourn. ex L. - Boletus piperatus Fr. or

B. piperatus Bulliard ex Fr. - Euastrum binale Ralfs or E. binale Ehrenb. ex Ralfs."

An examination of TABLE 1 will reveal that we have retained the pre-starting-point authors' names in ranks 4, 6, 8, 10, 11, and 12, since without doing so it would be impossible to tell from the author citation where the probable type of the name resides (perhaps the only valid reason for citing an author's name at all). If we suppress the "ex" as Rec. 46E.1 allows, we will note that in Rank 4 Mérat, a mere compiler of Parisian fungi, is the originator of the name Peziza tuberosa Mérat 1821, and that his name can appear alone within the parentheses of the transfers in Ranks 8, 10, 11, and 12. Such a species name is a **legal fiction**: Mérat had no intention to introduce a novelty to science. Has anyone ever seen a Mérat specimen? He was a follower of Persoon, not an innovator. We have been unable to find any book or article that credits Mérat, and not Bulliard, with this epithet, in any combination. Were it not for the later starting-point provisions, there would be no such species name as P. tuberosa Mérat; what a pity Rec. 46E.1 commends such a citation.

In Rank 6 we find another entry, which can be "simplified" under Rec. 46E.1 to read "Peziza tuberosa Ficinus & Schubert 1823." They, too, of course had no intention of giving mycology a "new species," but were merely the first after 1.1.1821 to list a species, described in 1789 by Hedwig as Octospora tuberosa, within the genus Peziza. The transfer to Peziza was not even theirs: they were reporting Dickson's transfer of 1790 (Rank 2). Because of later starting-point provisions, P. tuberosa Ficinus & Schubert is a later homonym of Mérat's name, both being legal fictions.[3]

It is not even clear whether under the Code we can speak of "transfers" of pre-starting-point names. Could Dickson (Rank 2) really transfer Hedwig's name (Rank 1) if neither is validly published? Can one cite the authorities for the Ficinus & Schubert name (Rank 6) other than we have done and still retain some indication of the nomenclatural typification of the name? Can one really say that Bulliard's name (Rank 3) is a "later homonym" of Dickson's (Rank 2)? We felt obliged to put quotation marks around "later homonym" under Rank 3, since both are not validly published names, and thus **not names at all** under the Code (ICBN, Art. 6.6).

There are still two other legal fictions in the synonymy that come about by an interaction of later starting-point provisions and Art. 67.1 Note 2 and Art. 72.1 Note 1. These two notes point out that one cannot transfer an illegitimate epithet, but if there is no obstacle to the employment of the epithet in a new position or sense, it may be adopted but takes on a different authority. One of the examples under Art. 72.1 Note 1 is both mycological and instructive:

"Uredo aegopodii Strauss (Ann. Wetter. Ges. 2(1): 101. 1810) is a later homonym of U. aegopodii Schumacher (Enum. Pl. Saell. 2: 233. 1803). Röhling transferred the former to the genus Puccinia; the resulting combination (Deutschl. Fl. ed. 2. 3(3): 131. 1813) is treated as new and should be written P. aegopodii Röhl., not as P. aegopodii

[3] Note, too, that P. tuberosa (Hedw.) Dicks. (Rank 2) would be the correct name, dating from 1790, and P. tuberosa Bull. (Rank 3) the later homonym, dating from 1791, were it not for the provisions of later starting points.

(Strauss) Röhl."

Thus we find the citation of Sclerotinia tuberosa Fuckel for the entry in Rank 7. Fuckel intended to transfer Hedwig's Octospora tuberosa to his new genus, Sclerotinia. Hedwig's name has no nomenclatural status, being pre-starting-point. Ficinus & Schubert's use of the epithet in 1823 (Rank 6) did not constitute a reprieve for Hedwig's epithet, since their P. tuberosa (Hedw.) Dicks. ex Ficinus & Schubert is illegitimate because it is a (legally fictitious) later homonym of P. tuberosa Bull. ex Mérat of 1821. Fuckel appears to have been the first to attempt to transfer the Hedwig epithet following Ficinus and Schubert. The combination is thus not to be written as S. tuberosa (Hedw.) Fuckel, or as S. tuberosa (Hedw.) ex Fuckel, but as S. tuberosa Fuckel. This particular legal fiction has never, so far as we know, been adopted by anyone other than the junior author in her attempt to follow the Code (Kohn, 1979).

Our synonymy provides a final legal fiction, the citation for Phialea tuberosa Gillet (Rank 9). Gillet, like Fuckel in the preceding example, wanted to transfer Hedwig's species, this time to Phialea. For the same reasons, such a transfer is prohibited under the Code. But again Art. 72.1 Note 1 comes into play, for there is no obstacle to the employment of the epithet "tuberosa" in Phialea. So, again, the Code would have us suppress the original author, and to substitute Gillet. We gain still another insight into the operations of this part of the Code: note that even though Hedwig's name took on new life in 1870, now credited to Fuckel (Rank 7), another author, Gillet, gets credit for the same species in Phialea (Rank 9). All three are of course based on Hedwig's type specimen. [Had Gillet mentioned Fuckel's name, it would have been a new combination, Ph. tuberosa (Fuckel) Gillet.]

Are we overstating our case in terming these legal fictions, never emplyed by anyone except those determined to follow the Code, to be examples of a "pernicious phenomen"? We think not. If nobody is citing the names correctly, **something must be wrong.**

EXAMPLE 4: TRIVIAL FLORAS, A BIBLIOGRAPHER'S NIGHTMARE, A BOOKSELLER'S DREAM

The Stockholm decision of 1950 to set the date of 1.1.1821 as starting point for Fungi caeteri probably did more for the rare book trade than any other Botanical Congress action in memory. Immense nomenclatural significance suddenly descended upon a host of seldom-consulted works that appeared in the period 1821-1832. No longer was it possible to consider Fries's Systema as the place of validation of names that appeared therein. True, the names in the Systema still had favored status, but author citations would have to change. Where the senior author had written Arachnopeziza aurelia (Pers. ex Fr.) Fuckel in his thesis (Korf, 1952), he would now be obliged to write A. aurelia (Pers.) Fuckel; where he had written Eriopezia caesia (Pers. ex Fr.) Rehm he would need to change to E. caesia (Pers. ex Gray) Rehm [or even to E. caesia (Gray) Rehm under Rec. 46E.1]. He was now obliged to check every book and paper on fungi appearing between 1.1.1821 and late 1822 to find who first accepted the epithet concerned, if indeed anyone had done so prior to Fries's late 1822 "sanctioning" of P. aurelia and P. caesia.

The senior author had the very good fortune to become a friend of one of mycology's foremost experts on nomenclature, and a bibliographer of great repute, Dr. D. P. Rogers, at the New York Botanical Garden. Rogers quickly appreciated the senior author's interest in nomenclature, and early in the 1950's supplied him with a list of early mycological books and papers spanning the years 1821-1833; in 1955 he supplied a supplementary list. These two lists embodied much of Roger's bibliographic work on sequentially dating the various works that appeared in the 1821-1833 period, for Rogers was aware of how significant these works are in reaching a correct author citation under the Code. They have been a bible of sorts for the senior author during the ensuing quarter century. Of course the lists are incomplete, of course there is now more precise dating known for some of the items on the lists. But they did serve to give some insight into what the earliest valid name might be. The debt to Rogers is freely acknowledged here.

Another of the senior author's friends has an equally compelling claim to nomenclatural fame in matters of later starting points: Ronald H. Petersen. His work led him to a different conclusion than had ours, namely that a good index to the 1821 epithets and their pre-starting-point history would show that retention of the 1.1.1821 starting point was the only logical way to proceed, and would not be any great burden. To this end he published the results of a massive bibliographic study of those works published within the year 1821. (Why he restricted himself to this one year is not fully explained.) His papers (Petersen, **1975a, 1975b, 1976a, 1976b, 1977**) are a masterful compilation not only of the papers of that year, but also of the pre-starting-point works he consulted and from which the 1821 citations often took their roots. Despite his scholarship and diligence, he, too, like Rogers, was unable to sequentially date every article and book that appeared in 1821 (Petersen, **1975a, 1976a**). At least one has since been shown quite conclusively to have been published in 1820, thus making it pre-starting-point. Whenever one of these unsequenced 1821 sources has a name of interest and a second 1821 author has also used the name, there is of course no way to determine which to cite. And despite Petersen's valiant efforts, we have discovered with our work with Discomycetes that all too often no 1821 author has picked up the epithet, so we must turn to the 1822 (and, for epithets in Fries's Systema 2(2), to 1823) literature which Petersen did not consider. Then Rogers's lists have come in useful, though we suspect the lists are incomplete. For 1822 he provided only six references [of which four are partially sequenced (a fifth can be accurately dated from the recent Taxonomic Literature ed. 2 by Stafleu and Cowan, (1976)]. For 1823 Rogers's lists include only four entries, two of which are sequenced (again Stafleu and Cowan allow dating for one of the two unsequenced entries, but the important date, that of Fries's Systema 2(2) is uncertain).

In addition to the 25 or 26 1821 papers noted by Petersen (**1975a**), a mycologist ought to have at hand all of the 1822 to early 1832 literature if citing authorities for fungi is to be certain, even if the names appear in Fries's Systema. That no library in the world possesses such a complete treatment almost goes without saying. No serious attempt that we know of, save Rogers's lists, has ever been directed at the 1822-1832 literature. No listing by epithet for that 11-year period has been undertaken as Petersen did

so well for the single year, 1821. Whenever you attempt to follow the Code, and are using post-1821-pre-1833 names, your only hope is to cross your fingers and hope for the best that you have somehow caught the earliest use of any epithets mentioned. With such a sense of inadequacy hanging over every mycologist, **something must be wrong.**

EXAMPLE 5: ON JUGGLING AUTHORITIES

The synonymy in TABLE 1 has five instances where we have "juggled" the author citations significantly from the way they were published. In addition to the "legal fictions" discussed in Example 3 above (Ranks 4, 6, 7, and 9), the case of juggling in Rank 11, authors cited for Whetzelinia tuberosa, requires further comment.

When Korf and Dumont (**1972**) proposed the name, they cited it as "Whetzelinia tuberosa (Hedw. ex Mérat) Korf & Dumont." This was a clear error, since Mérat had cited only Bulliard as the authority for the epithet. Why, then, did Korf and Dumont cite Hedwig as authority? They consulted Fries's treatment in the Systema **2**(1), where no authorities are listed, and where both Hedwig's and Bulliard's pre-starting-point names are synonymized. They reasoned (incorrectly) that since Hedwig's was the older name, Fries chose that one (the senior author takes the blame for this error); what Korf and Dumont failed to do was to consult the index in **2**(2), where the entry reads "Peziza tuberosa Bull.", as it is also in **3** (index). What we have done in Rank 11 is to juggle the authorities they cited, but whether we are justified in doing so is not fully clear, since now we imply that it was a name based on a Bulliard type, not a Hedwig type, that was transferred. But their error in citing Hedwig and Mérat (and thus Bulliard) leaves open the question of what they did transfer; obviously they wanted to transfer the correct epithet (that sanctioned by Fries). Whether our juggle of authorities is acceptable we leave to others to argue. (If our final conclusions in this paper are accepted, the point becomes moot.)

A somewhat similar juggle of authorities can be seen in Dennis's (**1956**) citation of the combination we have in Rank 10. He cites this as "Hymenoscypha tuberosa ([Hedw.] Fr.) Phill." When one consults Phillips's book, one finds the entry as "H. tuberosa (Bull.)" both on page 113 and in the index. Dennis similarly cited "Rutstroemia tuberosa ([Hedw.] Fr.) Karsten" for the correct citation given in Rank 8.

One additional entry in our synonymy requires serious consideration, that of Rank 5. We have indicated this as a taxonomic synonym, and our entry, "Macroscyphus tuberosus [Hedw.? Bull.?] Gray" tells the story as we now see it: we cannot determine from Gray's treatment which epithet he transferred to Macroscyphus. Gray's (**1821**) entry reads:

"5. Macroscyphus tuberosus. Tubercus long-funnel. Root tuberous, irregular; stem very long; cup rather small, funnel-shape, chestnut or bay.

Peziza tuberosa, Dickson Crypt. 2, 25; Sowerby Fungi, 63; Persoon Syn. 644.

In woods; April."

None of the three references are to Hedwig or to Bulliard. Each can be traced, however. The Dickson reference predates Bulliard, and must be to Hedwig; Sowerby's reference again leads to Dickson (i.e., Hedwig), but also to Withering (1792), which in turn synonymizes (for the first time) Hedwig's and Bulliard's names; Persoon's reference again leads to both Hedwig and Bulliard, as the synonymy is accepted there, too. Which epithet did Gray transfer?

EXAMPLE 6: 1753 AS THE STARTING POINT, WITH PROTECTED STATUS FOR THE NAMES IN THE BASIC BOOKS OF PERSOON AND FRIES

The senior author, as a member of the International Association's Special Committee for Fungi and Lichens, and also a member of the Subcommittee on Later Starting Points of the International Mycological Association's Nomenclature Committee, has actively supported a change in the starting point for Fungi caeteri, and has openly pushed for adoption of 1 May 1753 (Linnaeus, Species Plantarum éd. 1) as the logical date. In the several years since he began his advocacy (see Hennebert and Korf, 1975), he has come to the conclusion that merely beginning with 1753 will not answer all our problems, nor will it necessarily simplify them. But a proposal originally put forth by the Czechoslovakian mycologist, Z. Pouzar, to treat Persoon's Synopsis and Fries's Systema (inclusive of the Elenchus) as "basic books" makes so much sense that he now fully supports the concept of Pouzar, which has been slightly modified by our Belgian colleague, V. Demoulin, among others on the Subcommittee. It is instructive to use the same synonymy we have been discussing to see what would happen to the names and author citations if 1753 were adopted without the provision of a "basic books" filter-system (TABLE 2) and with such a system (TABLE 3).

A simple return to 1753 causes, for this species, a major upheaval (TABLE 2). Hedwig's name, being the oldest, should have been used by Kohn in Dumontinia. But it cannot now be transferred there because Kohn (1979) transferred Bulliard's epithet to the genus (TABLE 2, Rank 10); and Art. 63 rules that a name is illegitimate if the taxon to which it was applied, as circumscribed by its author, included the type of a name or epithet which ought to have been adopted. The combination D. tuberosa would be illegitimate and would need to be rejected, and we would be forced to coin a new epithet for the species when treated in Dumontinia.

Note that we are still plagued by legal fictions and name juggles: Bulliard's illegitimate epithet took on new life and a new author citation when Karsten picked it up in 1871 without mentioning Hedwig. When Phillips and Kohn transferred Bulliard's epithet, they both cited Karsten's name, and thus can be held to have transferred the now valid epithet, but their combinations are illegitimate on another ground: they included Hedwig's name in their synonymy, and thus did not adopt the earliest available epithet.

On the other hand, if special status is still given to the names accepted in the "basic books" of Persoon (for Uredinales, Ustilaginales, and Gasteromycetes) and Fries (for Fungi caeteri), it appears our problems are greatly simplified (TABLE 3). Reintroduction of M. A. Donk's ": Pers." and ": Fr." notation for 'sanctioned' names is very desirable. Bulliard's epithet, accepted by Fries, becomes the correct one to use. The only unavailable name in the synonymy is

TABLE 2

1753 STARTING DATE ONLY

Rank by date		
11		Dumontinia [new epithet required] Korf & Kohn 1980
1	≡	Octospora tuberosa Hedw. 1789.
2	≡	Peziza tuberosa (Hedw.) Dicks. 1790.
5	≡	Sclerotinia tuberosa (Hedw.) Fuckel 1870.
7	≡	Phialea tuberosa (Hedw.) Gill. 1881 (1882?).
9	≡	Whetzelinia tuberosa (Hedw.) Korf & Dumont 1972.
3	=	Peziza tuberosa Bull. 1791 (validly published later homonym, **illegitimate**), not P. tuberosa (Hedw.) Dicks. 1790.
6	≡	Rutstroemia tuberosa Karst. 1871 (a **new name**).
8	≡	Hymenoscyphus tuberosus (Karst.) Phill. 1887 (**illegitimate**, Art. 63, ICBN)
10	≡	Dumontinia tuberosa (Karst.) Kohn 1979 (**illegitimate**, Art. 63, ICBN)
4	=	Macroscyphus tuberosus Gray 1821.

TABLE 3

1753 WITH PERSOON AND FRIES AS "BASIC BOOKS"

Rank by date		
10		Dumontinia tuberosa (Bull. : Fr.) Kohn 1979.
3	≡	Peziza tuberosa Bull. 1791 : Fries 1822, 1823, non P. tuberosa (Hedw.) Dicks. 1790.
6	≡	Rutstroemia tuberosa (Bull. : Fr.) Karst. 1871.
8	≡	Hymenoscyphus tuberosus (Bull. : Fr.) Phill. 1887.
1	=	Octospora tuberosa Hedw. 1789.
2	≡	Peziza tuberosa (Hedw.) Dicks. 1790 (**unavailable**: Art. 13.1 (f), ICBN, not P. tuberosa Bull. : Fr.)
5	≡	Sclerotinia tuberosa (Hedw.) Fuckel 1870.
7	≡	Phialea tuberosa (Hedw.) Gill. 1881 (1882?).
9	≡	Whetzelinia tuberosa (Hedw.) Korf & Dumont 1972.
4	=	Macroscyphus tuberosus Gray 1821.

Peziza tuberosa (Hedw.) Dicks., which is disqualified because Fries sanctioned the use of another author's later homonym. Significantly, too, the legal fictions which we complained so bitterly about in Example 3 above have miraculously disappeared. Fuckel and Gillet were free to transfer Hedwig's epithet (TABLE 3, Ranks 7, 9); so, too, were Korf and Dumont (Rank 9) and nobody has to resort to author-juggling to correct their "mistake" in citing the validating author. And we can forget all about those other legal fictions, the "new" names unintentionally coined by post-starting-point authors. The floras of Mérat and of Ficinus and Schubert can be replaced on the shelves, for we have no need to consult them (nor any of the score or more of 1821-1822 books we had to consult just to be certain we had really picked up the **first** post-1821 validating author).

CONCLUSION

The study of the synonymy of Dumontinia tuberosa leaves little doubt in our mind that continuance of the present provisions of a later starting point for Fungi caeteri is intolerable. Wasted hours in the bookstacks do not even yield consistent results. Many unanswered questions plague us about whether pre-starting-point names are even names, and about just who first validated a name after the starting point, questions that may be impossible to answer. What facts can we deduce? We note:

1. Later starting points do not relieve us of the necessity to consult old, pre-starting-point books.

2. Later starting points force us to examine scores of unimportant papers spanning 1821-1832 (and even after) merely to determine who first after an arbitrary date used a name already well-established in the literature.

3. Later starting points generate additional names in our synonymies which are merely legal fictions.

4. Later starting points demonstrably produce author citations never before used: in our example, we know of no author who has ever cited any of the post-starting point names in the synonymy correctly (except for the junior author's nomenclatorialistically exact thesis study).

5. Adoption of a 1753 starting-point date for all fungi, coupled with adoption of a special status for the names used in the "basic books" of Persoon and Fries will yield an immense simplification of bibliographic work, will not cause the creation of fictitious new names, and will yield author citations that are far more consistent with existing literature.

We call upon the members of the IAPT's Special Committee for Fungi and Lichens to support the proposed changes in the Code suggested by the IMA's Nomenclature Committe, Subcommittee D: Starting Point Dates (van Warmelo, 1979), and specifically Principle II therein, Proposal (32).

LITERATURE CITED

DENNIS, R.W.G. 1956. A revision of the British Helotiaceae in the herbarium of the Royal Botanic Gardens, Kew, with notes on related European species. Mycol. Pap. 62: 1-216, 1 pl. - GRAY, S.F. 1821. A natural arrangement of British plants. London. - GROVE, W.B. 1937. British stem- and leaf-fungi. Vol. 2. Cambridge. - HENNEBERT, G.L. & R.P. KORF. 1975. The peat mould, Chromelosporium ollare, conidial state of Peziza ostracoderma, and its misapplied names, Botrytis crystallina, Botrytis spectabilis, Ostracoderma epigaeum and Peziza atrovinosa. Mycologia 67: 214-240. - KOHN, L.M. 1979. A monographic revision of the genus Sclerotinia. Mycotaxon 9: 365-444. - KORF, R.P. 1952. A monograph of the Arachnopezizeae. Lloydia 14: 129-180. - KORF, R.P. & K.P. DUMONT. 1972. Whetzelinia, a new generic name for Sclerotinia sclerotiorum and S. tuberosa. Mycologia 64: 248-251. - LINNAEUS, C. 1753. Species plantarum. 2 vols. Holm. - PETERSEN, R.H. 1975a. Specific and infraspecific names for fungi used in 1821. Part I. Introduction, A & B. Mycotaxon 1: 149-188. - 1975b. Ibid. Part II. C, and supplement to Part I. Mycotaxon 2: 151-165. - 1976a. Ibid. Part III. D-G. Mycotaxon 3: 239-260. - 1976b. Ibid. IV. H-M. Mycotaxon 4: 185-210. - 1977. Ibid. V. N-Z. Mycotaxon 6: 78-126. - STAFLEU, F.A. [ed.] 1978. International code of botanical nomenclature adopted by the twelfth International Botanical Congress, Leningrad, July 1975. Utrecht. - STAFLEU, F.A. & R.S. COWAN. 1976. Taxonomic literature, ed. 2. Vol. 1. Utrecht. - VAN WARMELO, K.T. van. 1979. Proposals for modifications of the Code of Botanical Nomenclature: IMC proposals. Taxon 28: 424-431. - WITHERING, W. 1792. A botanical arrangement of British plants, ed. 2. Vol. 3. Birmingham.

MYCOTAXON

Vol. XI, No. 1, pp. 396-408 April-June 1980

REVUE DES LIVRES

par

G.L. HENNEBERT

Book Review Editor, Croix du Sud 3, Louvain-la-Neuve B-1348 Belgium

COLLECTED MYCOLOGICAL PAPERS (RECUEIL DES ESSAIS MYCOLOGIQUES) par Narcisse-Théophile PATOUILLARD (1854-1926), édité par L. Vogelenzang, xxi + 2400 p., 110 pls., 3 vols. 8°, relié toilé, Septembre 1978. A. Asher & Co., Keizersgracht 526, Amsterdam 1002, Nederland. Prix Dfl. 975.-.

A. Asher & Co. a publié en 1963 l'*Essai taxonomique sur les familles et les genres des Hyménomycètes* de N. Patouillard (Lons-le-Saunier, Imp. Duclume, 1900, 184 p., ill.). Aujourdhui, il nous offre dans une fort belle édition la presque totalité du reste de l'oeuvre mycologique de Narcisse Patouillard, soit 263 publications parues de 1876 à 1928, y compris les travaux posthumes édités par R. Heim, et additionnées de la motice nécrologique de L. Mangin (1927). Ce recueil met ainsi à la disposition de tous l'oeuvre d'un grand mycologue français qui consacra sa vie à l'étude des Basidiomycètes. On se rapellera que ce fut Patouillard qui distingua au sein des Basidiomycètes les deux sous-classes *Hétérobasidiomycètes* et *Homobasidiomycètes*. Ses travaux multiples, réalisés au Laboratoire de Cryptogamie de Paris, sur les flores exotiques les plus diverses étendirent au monde la réputation qu'il avait acquise en son pays. Pour être complète, la réédition de l'oeuvre de Patouillard devrait encore comprendre ses deux séries illustrées et commentées d'exsiccata, *Les champignons figurés et désséchés*, par E. Doassans et N. Patouillard, vôl. 1 (1880-1881) Exsiccata n° 1-44, vol.2 *Atlas* (1882-1883) 50 planches colorées, Paris, et les *Tabulae analyticae fungorum. Descriptions et analyses microscopiques des champignons nouveaux, rares ou critiques*, Fasc.1 à 7, Exsiccata n° 1-700, totalisant 338 p., 224 pls. Imp. Gindre, Poligny, (1883-1889), dont on aimerait voir réimprimées les étiquettes des exsiccata autant que les planches et le texte.

INTERESTING AND NEW SPECIES OF BASIDIOMYCETES FROM ECUADOR, par Rolf SINGER, Part I, réimpression du Supplément 51 de Nova Hedwigia 239-246, 1975, & II, réimpression de Nova Hedwigia, 29:1-98, 1977; 8°, broché, J. Cramer éd., 3301 Lehre, Deutschland. Prix DM 40.-.

Ces deux articles ont trait aux Basidiomycètes récoltés en Equateur par l'auteur (Partie 1) et par P.K. DUMONT et al. de New York (Partie 2). 123 espèces d'agaricales dont 3 nouvelles et 7 espèces d'aphyllophorales sont décrites et illustrées. On s'étonnera de voir la brochure s'ouvrir sur la 2e partie pour se terminer, après l'index, par la le partie.

BRITISH ASCOMYCETES, par R.W.G. DENNIS, 2e édition, xxiv+586 p.,31 pls. au trait, 44 pls. col., relié toilé, 1978. J. Cramer éd., poste 48, D-3301 Lehre, Deutschland. Prix DM 200.-.

Cette deuxième édition des *British Ascomycetes*, complètement revue et étendue, est en fait la troisième version de l'ouvrage d'abord intitulé *British Cup Fungi* (1960). Cette nouvelle édition comprend 876 espèces de 511 genres d'Ascomycètes, c'est-à-dire 84 espèces et 36 genres de plus que dans l'édition de 1968. Les commentaires taxonomiques et les références aux espèces voisines non encore observées dans les Iles Britanniques ont été largement amplifiées. L'illustration aussi a été modifiée. La planche en couleurs 12 est nouvelle; les planches en couleurs 1, 2, 7 et 8 remplacent les planches non colorées 3, 4 et 31 et la planche colorée 5 de l'édition de 1968. Les planches non colorées 6, 7, 12 et 31 sont nouvelles. Si l'auteur mérite toute la considération des mycologues pour cette mise à jour tant attendue d'un ouvrage déjà tant apprécié, il faut cependant regretter de graves imperfections de nature éditoriale. D'abord le texte revisé et amplifié sur les Acrospermataceae p.427 n'a pas donné lieu à la suppression de l'ancien texte sur *Acrospermum* p. 250. Une inversion de parties d'épreuves à la mise en page a fait apparaître les entrées de l'index *trichodea* à *undulata* aux pages 584-585 au lieu de la p. 583 entre *Trichobolus* et *unguicularia*. Et encore, le clichage offset, montre pour je ne sais quelle raison technique, un affaiblissement marqué, jusqu'à l'effacement, du texte à la partie gauche de très nombreuses pages, à tel point que de nombreux clichés durent être retracés à la main avant l'impression (quelques exemples: p.3ss, 130ss, 175ss, 201ss, 350ss, 416ss) pour les rendre lisibles. Enfin l'usage d'un papier épais et rude rend ce livre excessivement volumineux et d'une manipulation difficile et peu agréable, alors qu'il est destiné à se trouver dans les mains de tous les mycologues.

A SOURCE BOOK OF THE GENUS *PHYTOPHTHORA*, par Olaf K. RIBEIRO, xx + 417 p., ill., relié toilé, 1978, J. Cramer éd. FL 9490 Vaduz, Liechtenstein. Prix DM 80.-.

Cette compilation de toutes les informations disponibles sur les multiples aspects de l'étude des *Phytophthora* sera certainement bienvenue dans tous les laboratoires de phytopathologie autant que de mycologie. L'information, arrangée par rubrique, traite de la morphologie, des symptômes , de l'isolement et de la culture, de la sporulation sous toutes ses formes et de chaque espèce, de la survivance, de la pathogénécité, de la résistance de l'hôte, de la génétique, de l'écologie, de la cytologie, de la biochimie, du contrôle et enfin de la description et de l'identification des espèces. Les références bibliographiques sont dispersées dans le texte; les dessins des espèces sont de mauvaise qualité. Mais encore ce livre atteindra-t-il ceux à qui il est destiné, si son prix reste ce qu'il est. Si le texte avait été plus compact et la bibliographie réunie en une liste continue, près de 150 pages de papier blanc pouvaient être épargnées.

INDEX TO GENERA AND AUTHORS IN GREVILLEA, par Richard T. HANLIN. 167 p., 12°, broché, 1978, J. Cramer éd. FL 9490 Vaduz, Liechtenstein. Prix 40.-.

Il arrive fréquemmentqu'un mycologue désireux de gagner du temps décide d'établir l'index alphabétique d'un livre ancien sans index qu'il consulte souvent. Plus rare est l'idée de le publier. Aussi faut-il féliciter l'auteur de ce travail, d'autant plus que *Grevillea* paru de 1872 à 1894 fut un journal très riche en nouveautés mycologiques. L'index des noms d'auteurs fait d'ailleurs apparaître de grands noms, tels que

celui du fondateur M.C. Cooke, et ceux de Berkeley, Boudier, Crombie, de Bary, J.B. Ellis, E. Fries, Massee, Peck, Phillips, Flowright, Saccardo, Smith, Roumeguère et les Tulasne. R.T. Hanlin a aussi pris soin de rechercher la date précise de publication de chacun des 104 fascicules parus. Mais à nouveau, ce livre eut pu coûter la moitié de son prix, si la dactylographie du texte reproduit en offset avait été plus dense.

THE CLAVARIAS OF THE SIKKIM HYMALAYAS, par S.S. RATTA & I.P.S. KHURANA, 68 p., 89 figs., 12°, broché, 1978. J. Cramer éd., FL-9490 Vaduz, Liechtenstein. Prix DM 25.-.

The authors are of those Indian mycologists, under the direction of Dr K.S. Thind, devoted to the mycological flora of the Hymalayas. In this short paper , the authors report 30 species of Clavariaceae, including 1 new species and 2 new varieties. Descriptions and drawings are in the Corner's style. Probably aquarelles would have been in the same, if they had not been printed as worthless black and white photographs. It is certainly the freedom but also the responsability of both the authors and the editor to decide whether or not a paper as short as the present one has to be published in the shape of a book and at such a price. Should we suggest to J. Cramer taking advices from an editorial board?

LES FONDEMENTS DE LA TAXINOMIE DES RHODOPHYLLES ET LEUR CLASSIFICATION, par Henri ROMAGNESI, extrait de H. Romagnesi et G. Gilles *Les Rhodophylles des forêts côtières du Gabon et de la Côte d'Ivoire* (supplément 59 de Nova Hedwigia, p. 25-78 et 627-644, 1979) prépublié en 1978, paginé 1-80, 12° broché. J. Cramer éd. FL 9490 Vaduz, Liechtenstein. Prix DM 19,80 !

Ce tirage-à-part, prébublié sous un titre différent, est extrait d'un livre paru en 1979. H. Romagnesi le destine "aux mycologues qui ne seraient pas spécialement intéressés par la mycoflore de ces régions, mais qui désirent connaître d'une façon générale, les conséquences de cette étude sur la taxinomie et la classification de ce genre difficile". C'est en fait une forme de plaidoyer insistant en faveur de l'usage de caractères microscopiques tels que la forme des spores, la présence de granules lipidiques et la localisation des pigments et aussi en faveur d'une typification prudente des vieux genres friesiens. Malheureusement le style en est trop celui du réquisitoire contre "l'ostracisme" des mycologues moins convaincus et la "vésanie" d'autres, "certes très éminents" qui, appliquant "les dispositions de notre malheureux Code de nomenclature avec rigidité", conduisent la taxonomie "des pauvres Rhodophylles" à "ce calice amer" qu'est "trois fois hélas! la systématique dite moderne des Polypores et des Corticiés" (p. 7, 25,31).

BASIDIOMYCETES THAT DECAY ASPEN IN NORTH AMERICA, par J. Page LINDSEY et Robert L. GILBERTSON, 406 p., 260 figs., 12 pls. phot. b.n., 8°, relié toilé, 1978, J. Cramer éd., FL-9490 Vaduz, Liechtenstein. Prix DM 120.-.

Avec un autre livre de Gilbertson *The fungi that decay ponderosa pine*, cet ouvrage sur les champignons nuisibles au peuplier constitue un ensemble couvrant la plupart des champignons lignivores d'Amérique du Nord, et de cette manière apporte une base solide à une pathologie des arbres et du bois. 395 pages d'un texte dense mais bien lisible, où les auteurs décrivent et illustrent excellemment 260 espèces et

fournissent pour chaque genre des clés d'identification et pour chaque espèce les caractères microscopiques nécessaires. Une série de photographies, en particulier d'excellentes vues de détail au SEM, donne une touche vivante à la technicité du contenu. Un glossaire terminologique donne la signification de termes parfois inhabituels. L'index, comme malheureusement beaucoup d'index publiés, subordonne les épithètes spécifiques aux noms de genres de telle sorte qu'il est impossible de retrouver une espèce selon l'ordre alphabétique. Par le grand nombre d'espèces dont 224 sont des Aphyllophorales et dont la distribution est souvent cosmopolite, ce livre doit avoir une très large audience et la mérite.

MYCOLOGIE ET PATHOLOGIE FORESTIERES. I.MYCOLOGIE FORESTIERE, par L. LANIER, P. JOLY, P. BONDOUX et A. BELLEMERE, xiv +487 p., nbr. figs., 8°, relié toilé, 1978, Masson éd., 120 Bd. St-Germain, F-75280 Paris . Prix non donné.

Il est peu de pays où les ingénieurs et phytopathologues forestiers disposent d'un traité moderne de pathologie forestière. Cet ouvrage tant attendu est le fait de quatre spécialistes de langue française, un forestier, un phytopathologue et deux mycologues. Fruit d'une harmonieuse concertation des auteurs, cet ouvrage est scientifique, précis, moderne, didactique, parfaitement équilibré et témoigne de la compétence de ses auteurs. Le second volume déjà paru (Mycotaxon 7:523, 1978) traite de la *Pathologie forestière*, le présent volume de *Mycologie forestière*. Une introduction de 70 p. par A. Bellemère et P. Joly montre les multiples aspects de la vie des champignons et de leur structure. Le reste du volume est consacré aux clés d'identification des espèces significatives de chaque classe, famille et genre. Quelques 3500 espèces fongiques, par ailleurs reprises à l'index, sont citées, décrites, illustrées, ou commentées dans leurs caractères microscopiques ou leur rôle forestier. Les clés par P. Joly (Basidiomycètes) et par A. Bellemère (Ascomycètes) sont remarquables et dénotent de vues d'avant-garde sur certains groupes (Discomycètes). Les illustrations très nombreuses sont de grande précision. Ce livre est destiné à quiconque s'occupe de pathologie et mycologie des arbres et du bois. Son usage dans l'enseignement universitaire favorisera le développement de la pathologie forestière, discipline trop peu affirmée à ce jour. A ce niveau, une édition en langue anglaise lui assurerait une très large diffusion.

BOTRYOTINIA AND *BOTRYTIS* SPECIES: TAXONOMY, PHYSIOLOGY AND PATHOGENECITY. A GUIDE TO THE LITERATURE. par W.R. JARVIS, 195 p., 8°, broché, 1977. Canada Department of Agriculture, Information Div., Ottawa K1A OC7, Canada. Prix non indiqué.

Un guide dans la littérature abondante sur *Botryotinia* et *Botrytis* sous tous les aspects de la taxonomie à la lutte, en passant par l'écologie, la biologie et la pathogénie, l'auteur l'a fort bien réussi, par une sélection judicieuse de 960 références bibliographiques et l'intégration de l'information dans un texte analytique et détaillé. Ce livre est dorénavant l'outil de travail de tous ceux qui étudient ces champignons et leur biologie.

ATLAS DE MICOLOGIA BASICA, par M. ULLOA et R. HANLIN, xxix + 158 p., 37 pls. b.n. (dessins et 233 phot.), 1978, Editorial Concepto, Av. Cuauhtémoc 1434, México 13, D.F. Prix non donné.

Cet *Atlas* est en fait un manuel fort bien illustré de mycologie générale. Le texte expose d'abord la classification des champignons, ensuite leur croissance en milieu naturel et in vitro et enfin un commentaire morphologique, biologique et écologique sur chaque genre et leurs principales espèces. L'illustration abondante est composée d'une part de 233 excellentes microphotographies et d'autre part de dessins en demi-ton à la "Tulasne". Elle est l'oeuvre de M. Ulloa. Illustrant plus de 100 espèces, elle les montre dans leurs traits les plus significatifs pour un exposé didactique de la mycologie. Sans doute le texte gagnerait à s'enrichir d'informations à mon avis importantes. Si l'action hallucinogène de plusieurs espèces de *Psilocybe* mérite d'être mentionnée, la pathogénie d'*Armillaria mellea* ne peut être passée sous silence. Si ce livre doit servir à l'enseignement, maîtres et étudiants se plaindront du mauvais encollage du dos qui se brise à la première ouverture, par suite de l'utilisation d'une résine friable au lieu d'une colle flexible à base de latex acrylique.

FUNGUS-HOST INDEX FOR GREECE par Maria E. PANTIDOU, 382 p., broché, 1973, Benaki Phytopathological Institute, Kiphissia, Athens. Prix $ 10.50 poste incluse.

Cet index des champignons de Grèce et de leurs hôtes couvre plus de 2000 espèces de champignons et 1200 plantes-hôtes. Cette liste à laquelle l'auteur a mis tout le soin nécessaire se base sur le dépouillement de 129 publications mycologiques et phytopathologiques ainsi que sur les relevés des espèces préservées dans les collections de l'Institut phytopathologique Benaki. Cet index sera fort utile à tout mycologue et phytopathologue intéressé à ces régions.

A COMPENDIUM OF ALFALFA DISEASES, par J.H. GRAHAM, D.L. STUTEVILLE F.I. FROSHEISER et D.C. ERWIN, 80 p., 70 figs.b.n. & col., 4°, broché, juin 1978, The American Phytopathological Society, 3340 Pilot Knob Rd., St Paul, Minnesota 55121. Prix $ 7.-.

La première partie concerne les maladies abiotiques de l'Alfafa, *Medicago sativa*, la seconde partie les maladies biotiques, bactériennes, fongiques et autres. 24 maladies d'origine fongique sont décrites et illustrées. L'agent causal, les symptômes, les moyens de lutte sont précisés et soutenus par des références bibliographiques. L'illustration est de très bonne qualité, et pour la moitié en couleurs. Une clé d'identification des maladies sur la base des symptômes est aussi donnée. Toute la précision nécessaire est mise dans la description des champignons pathogènes; la nomenclature, elle, est a peu près correcte, '*Phymatotrichum*' restant encore d'usage là où devrait l'être *Phymatotrichopsis*.

ANNUAL REVIEW OF PHYTOPATHOLOGY, vol. 16, par R.G. GROGAN, G.A. ZETMYER, E.B. COWLING, éd., 528 p., 8°, relié toilé, 1978. Annual Reviews Inc. 4139 El Carmino Way, Palo Alto, Ca 94306. Price $ 17.

Bien qu'aucun article ne relève de mycologie systématique, on retiendra les progrès de la recherche mycologique et phytopathologique au Brésil (A.A. Bitancourt), une rétrospective sur l'oeuvre de J.C. Arthur (G.B. Cummins) et Julius Kuehn, la culture axénique de nématode pour l'amateur de 'nématode-traping fungi' (J. Vanfleteren), une revue biologique de '*Phymatotrichum omnivorum*' (aujourdhui *Phymatotrichopsis omnivora*) (S.D. Lyda), les facteurs de sporulation des champignons parasites in vivo (J. Rotem), enfin la génétique de la symbiose et des relations inter-organismes (W. Loegering).

ASCOMYCETES OF PAKISTAN, PART I, par Sultan AHMAD, Biological Society of Pakistan, Monograph n° 7, viii + 236 p., ill., 8°, agrafé, 1978, Biological Society of Pakistan, The Biological Laboratories, Government College, Lahore, Pakistan, imprimé par l'auteur.

"This publication, it is hoped, will provide an impetus to the student to work hard and bridge the existing gaps in our knowledge of this group of fungi" (p.v). Ainsi s'exprime l'auteur après 30 années d'étude de la mycoflore du Pakistan. 472 espèces d'Ascomycètes, dont 3 nouvelles, sont réunies dans ce volume de synthèse, décrites et illustrées selon une taxonomie et une nomenclature modernes. La bibliographie fait référence à des travaux de l'auteur des années 1946, 1955, 1968, 1970, 1971. Infatigable, l'auteur nous présente ce volume comme une première partie de la flore des Ascomycètes du Pakistan et implicitement nous promet une suite. Nous ne pouvons que l'encourager à poursuivre avec de nombreux disciples une oeuvre si bien commencée.

THE DIAPORTHALES IN NORTH AMERICA WITH EMPHASIS ON *GNOMONIA* AND ITS SEGREGATES, par Margaret E. BARR, Mycologia Memoir n° 7, 232 p. 132 figs., 8°, relié toilé, 1978, J. Cramer éd., p.o.b.48, D-3306 Lehre, Deutschland. Prix DM 80.- ($ 20.- for A.M.S. members).

Ce cinquième mémoire du *New York Botanical Garden* et de la *Mycological Society of America* est une importante addition au florilège mycologique de l'Amérique du Nord. L'auteur qui depuis longtemps fait autorité dans ce groupe de champignons Ascomycètes, présente ici, sur la base de son expérience sur le genre *Gnomonia*, un essai taxonomique des genres de Diaporthales connus en Amérique du Nord. Après un court aperçu historique, l'auteur introduit son concept de l'ordre et les caractères diagnostiques majeurs au niveau du genre, les tissus stromatiques de la fructification, la position de celle-ci sur l'hôte et les forme et dimensions des ascospores. Elle reconnaît 2 sous-ordres, les *Gnomoniineae* et les *Melanconidineae*. 53 genres sont recencés, 51 redéfinis et 2 décrits comme nouveaux, *Apioplagiostoma* et *Chapeckia*. Quelques 200 espèces sont décrites illustrées et commentées, 35 de celles-là dans le genre *Gnomonia*; quelques espèces extra-américaines sont incluses et revisées;6 espèces et 9 variétés sont nouvelles. Un index des noms et épithètes, un index des hôtes et une liste commentée des taxa rejetés terminent l'ouvrage. Qui n'a déjà ce Mémoire se doit de le connaître.

MOOSBEWOHNENDE ASCOMYCETEN I. DIE PYRENOCARPEN, DEN GAMETOPHYTEN BESIEDELNDEN ARTEN, by P. DOBBELER, Mitteilungen der Botanischen Staatssammlung, München, Bd. 14, 360 p., 64 figs., 12°, paperback, 1 june 1978, Botanische Staatssammlung München, Menzinger strasse 67, D-8000 München 19, Deutschland. Prix non indiqué.

This study, printed from a very well shaped manuscript ready copy, deals with the Pyrenoascomycetes which occur on the gametophytes of mosses. Out of the 123 know taxa pertaining to 33 genera, the author has been able to record 89 species in 21 genera from Europe and other countries through the world.In addition, 9 genera, 62 species and 3 varieties are described as new.Also, necessary redispositions and synonymies have been made. It is significant that most of the studied taxa belong to the Dothideales, a few only to the Hypocreaceae and the Lasiosphaericeae.Amongst the latter the genera *Lasiosphaeria*, *Leptoneliola*, *Pleosphaeria*, *Pleospora*, *Teichospora* have been intentionally omited. The literature on all taxa was thoroughly surveyed. These fungi appeared very common and restricted

to their host (over 250 species) and might have evoluted independently. This important piece of work is the doctoral thesis of its author.

LOWER FUNGI IN THE LABORATORY, par Melvin S. FULLER, ix + 123 p. 92 pls phot. b.n., 2 portraits, 4°, broché, 1978, Department of Botany, University of Georgia, Athens, Georgia 30602, USA. Palfrey Contributions in Botany n° 1. Prix $ 11.-.

Ce très bel album est un hommage à Ralph EMERSON offert par 60 mycologues qui ont bénéficié de son enseignement et de ses connaissances des Champignons Inférieurs et par la *Mycological Society of America*. Tout l'esprit, la méthode et l'enthousiasme du Maître (Mr Water Mold pour les intimes) transparaissent dans ces 120 démonstrations mycologiques sur les *Water Molds*. La bonne centaine d'espèce traitées appartiennent aux Chytridiomycètes, Hyphochytridiomycètes, Oomycètes, Zygomycètes Trichomycètes, Plasmodiophoromycètes et Labyrinthulomycètes. Ces exercices sont tous illustrés d'une iconographie photographique en pleine page assortis d'un texte variablement documenté. Un complément de notes méthodologiques sur la culture, la coloration, la préservation, l'observation au microscope électronique, etc, complète ce guide. Assemplé par la reproduction de'manuscript ready copies', l'ouvrage montre une certaine hétérogénéité dans la présentation des démonstrations, bien qu'elles suivent pour la plupart un modèle préparé par R. Emerson. Ce modèle est construit pour fournir un calendrier des observations à effectuer, mais n'est pas compréhensible sans se référer à un article d'Emerson dans Mycologia 50:589, 1958. Ces données indispensables devaient être reprises. Les illustrations, par contre, témoignent bien d'une générale fidélité au style de haute qualité toujours pratiqué par R. Emerson. De toute évidence, ce livre s'impose dans toute bibliothèque mycologique, dans tout laboratoire de mycologie, fût-ce comme exemple, et par dessus tout dans l'enseignement des *Lower Fungi*.

MANUEL DE MICROSCOPIE, par Marcel LOCQUIN et Maurice LANGERON, xxii + 352 p., 152 figs., 8° relié toilé, 1978, Masson & Co éd., 120 Bd St-Germain, F-75280 Paris 6, France. Prix non indiqué.

Depuis longtemps annoncé par son premier auteur, cet ouvrage est enfin paru, et, nous le croyons, à la satisfaction de tous. M. Locquin considérant son ouvrage comme une continuation du *Précis de Microscopie* de Maurice Langeron (Masson, 1942), s'est associé le nom de son ancien maître. L'ouvrage se divise en 6 chapitres. Le premier chapitre des principes directeurs de l'instrumentation et des techniques instrumentales de microscopie (microscopie photonique, interférentielle, la microphotographie, la stéréométrie, jusqu'à la microanalyse électronique). Le second chapitre détaille les méthodes préparatives de fixation, de coupe, de montage et d'examen. Les chapitres suivants donnent une liste de près de 2000 colorants, avec formule, synonymie et usage. Les derniers chapitres étudient les méthodes de coloration et d'imprégnation, les techniques propres à l'histologie animale et végétale, à la protistologie et à la mycologie. Une abondante information sur les constantes physicochimiques utiles en microscopie, un glossaire trilingue, en annexe, une bibliographie récente et un index général terminent l'ouvrage. Quel mycologue n'est pas à la recherche d'une technique plus appropriée à un probème particulier? A côté du *Mycological Guidebook* (New York, 1971), ce livre lui apportera des informations utiles.

BIOLOGICAL TRANSFORMATION OF WOOD BY MICROORGANISMS, Proceedings of the Sessions on Wood Products Pathology at the 2nd International Congress of Plant Pathology, September 10-12, 1973, Minneapolis, par Walter LIESE, éd., 203 p., ill., 8° broché, 1975. Springer Verlag, Berlin. Prix non indiqué.

Les communications présentées ont surtout porté sur la colonisation du bois par les champignons et les bactéries et les interactions entre les organismes, ensuite sur la micromorphologie du bois attaqué en relation avec la résistance naturelle ou acquise du bois et enfin sur les mécanismes enzymatiques de la dégradation de la cellulose, de la lignine et de la chitine par diverses espèces de champignons.

THE CORTICIACEAE OF NORTH EUROPE, VOL. 5 *MYCOACIELLA-PHANEROCHAETE*, par John ERIKSSON, Kurt HJORTSTAM et Leif RYVARDEN, pp. 885-1048, figs. 447-534, 8°, broché, 1978, Ed. Fungiflora, p.o.b. 95, Blindern, Oslo 3, Suède. Prix N.Kr. 80.-.

Ce volume 5 des "Corticiacées du Nord de l'Europe" est le bienvenu, après la publication tant appréciée des volumes 2, 3 et 4. (voir Mycotaxon 4:324, 1976; 5:364, 1975). Ce volume traite des genres suivants: *Amylostereum, Ceraceomyces, Hydrabasidium* (en addition), *Mycoaciella, Odonticium, Oliveonia, Paullicorticium, Peniophora, Phanerochaete*. Une nouvelle espèce et 10 nouvelles combinaisons sont proposées. Les auteurs maintiennent la qualité des descriptions et des illustrations. Les dessins de J. Eriksson sont caractéristiques. Cependant, contrairement aux volumes précédents et par suite de l'impression sur un papier non glacé, l'impression des photographies en blanc-noir a perdu beaucoup de la qualité présumée des originaux. Nous espérons que l'éditeur y paliera dans les prochains volumes. Le présent volume et les précédents susciteront certainement un renouveau d'intérêt pour ce groupe bien difficile de Basidiomycètes.

RUST FUNGI ON LEGUMES AND COMPOSITES IN NORTH AMERICA, par George B. CUMMINS, xii + 424 p., 355 figs., 8° broché, 1978, University of Arizona Press, Box 3398, Tucson, Arizona 85722, USA. Prix $ 9.-

L'auteur, expert bien connu des rouilles d'Amérique du Nord, apporte par ce livre une pièce de plus à l'édifice de la flore des Urédinales du continent américain. 355 espèces appartenant à 32 genres y sont méthodiquement décrites et figurées, relevées à elles seules sur les légumineuses et les composées. Les *Puccinia* sont représentés par 150 espèces, les *Uromyces* par 55. Bon nombre des espèces sont recensées également en Amérique centrale et en Amérique Latine. Un certain nombre sont aussi européennes. Edité à très bas prix, ce livre connaîtra une large diffusion.

1.ON CERTAIN SPECIES OF *MUCOR* WITH A KEY TO ALL ACCEPTED SPECIES. 2. ON THE GENERA *RHIZOMUCOR* AND *PARASITELLA*. par M.A.A. SCHIPPER, Studies in Mycology n° 17, 71 p., 34 figs., 8°, broché, 29.12.1978, Centraalbureau voor Schimmelcultures, Baarn, Nederland. Prix Hfl.20.

La revision des 23 dernières espèces de *Mucor* et les résultats de leur confrontation sexuelle termine la revision des espèces de *Mucor* disponibles en culture (voir Studies in Mycology 4(1973), 10(1975) et 12 (1976)). Une clé dichotomique d'identification est proposée pour l'ensemde ces 39 espèces, 2 variétés et 8 formes. Une clé synoptique n'eut-elle pas été préférable? L'auteur réhabilite aussi le genre *Rhizomucor* pour

trois espèces thermophiles, *Rhizomucor pusillus*, *R. miehe* et *R. tauricus*. Les genres voisins *Backusella* et *Parasitella* sont maintenus distincts.

A COMPILATION OF THE *ASPERGILLI* DESCRIBED SINCE 1965, par Robert K. SAMSON, Studies in Mycology n° 18, 38 p., 7 figs., 8°, broché, 30.1.1979, Centraalbureau voor Schimmelcultures, Baarn, Nederland. Prix Hfl. 10.-.

Il est souvent difficile, après la publication d'une monographie, de suivre la publication des espèces nouvelles qu'elle a pu susciter. Ainsi depuis la publication de *The genus Aspergillus* de Raper et Fennell en 1965, 89 taxa nouveaux ont été publiés. Samson les a revus. Il en accepte 34 et rejette les autres pour des raisons qu'il explicite. De plus il reconsidère le statut des 9 genres téléomorphiques dont les anamorphes sont des *Aspergillus* et les redécrit brièvement, *Chaetosartorya, Dichlaena, Emericella, Eurotium, Fennellia, Hemicarpenteles, Neosartorya, Petromyces et Warcupiella.*

FUNGORUM RARIORUM ICONES COLORATAE VII, par Meinhard MOSER, 48 p., 8 pls. col. 95 figs., 8°, 1978, J.Cramer, FL-9490 Vaduz. Prix DM 35.

Ce fascicule contient les descriptions et aquarelles de 25 espèces des genres *Hygrophorus, Tricholoma, Porpoloma, Mycena, Pholiota, Stropharia, Conocybe, Pachylepirium, Bolbitius, Melanotus, Agrocybe, Simocybe, Naucoria, Xerampelina, Lactorius* et *Inocybe*.

FUNGORUM RARIORUM ICONES COLORATAE IX, par Aurel DERMEK, 32 p., 8 pls. col., 18 figs., 8°, 1979. J. Cramer, FL-9490 Vaduz. DM 35.-.

Ce fascicule contient les descriptions et aquarelles de 18 taxa de Boletaceae dans les genres *Boletus, Boletinus, Xerocomus, Buchwaldoboletus* et *Leccinum*.

FUNGORUM RARIORUM ICONES COLORATAE X, par Solomon P. WASSER, 32 p., 8 pls. col., 6 figs., 8°, 1979, J. Cramer, FL-9490 Vaduz. DM 35.-

Ce fascicule contient les descriptions et aquarelles de 14 taxa dans les genres *Agaricus, Cystoderma, Leucocoprinus, Leucoagaricus* et *Galeopsis*.

FUNGORUM RARIORUM ICONES COLORATAE XI, par Marcel BON, 40 p., 8 pls. col., 6 figs., 8°, 1979, J. Cramer, FL-9490 Vaduz. DM 35.-.

Ce fascicule contient les descriptions et aquarelles de 17 taxa des genres *Hygrocybe, Lactarius, Russula, Calocybe, Hebeloma, Inocybe, Leucoagaricus, Lepiota* et *Amanitopsis*.

LES RHODOPHYLLES DES FORETS COTIERES DU GABON ET DE LA COTE D'IVOIRE par Henri ROMAGNESI et Gérard GILLES, Beihefte zur Nova Hedwigia 59, 649 p., 290 figs., 8°, relié toilé, 1979, J. Cramer, FL-9490 Vaduz, DM 200.-/250.-

Dix années de récoltes et d'annotations sur le vivant par Gerard Gilles au Gabon et en Côte d'Ivoire et dix années d'études microscopiques par H. Romagnesi ont été nécessaires pour mettre au point cette série de 184 espèces et variétés nouvelles de Rhodophylles d'Afrique.

Dans l'introduction, d'ailleurs déjà prébubliée par H. Romagnesi chez J. Cramer en 1978 et recensée dans ces pages, H. Romagnesi précise les caractères diagnostiques principaux: la forme géométrique des spores, la fréquence des boucles, les granules lipidiques de la trame, les accumulations de pigments et la texture de la cuticule. Dans la même introduction, H. Romagnesi n'apprécie pas l'application stricte des règles de la Nomenclature botanique bien qu'elle seule garantisse l'univocité du langage botanique. En effet la question est la suivante: *Entoloma* Fr.1836 ou *Rhodophyllus* Quélet 1886? H. Romagnesi a choisi *Rhodophyllus* Quelet. La contribution que lui-même et Gérard Gilles apportent à ce genre l'amplifie à 1318 espèces et variétés qu'ils acceptent et dont ils donnent une liste en fin de l'ouvrage. Aussi espérons-nous que soit un jour élaborée une clé synoptique de cet ensemble mycologique aussi attrayant que touffu.

KARSCHIA, REVISION EINER SAMMELGATTUNG AN DER GRENZE VON LICHENISIERTEN UND NICHTLICHENISIERTEN ASCOMYCETEN, par J. HAFELLNER, Beihefte zur Nova Hedwigia 62, 248 p., 46 figs., 8°, relié, 1979, J. Cramer, FL-9490 Vaduz, Liechtenstein. Prix 96.-/120.-.

Les unes libres, les autres lichénisées, 68 espèces de champignons jusqu'à ce jour classées dans le genre *Karschia*, sont ici revues et reclassées par l'auteur dans pas moins de 19 genres différents, les uns des Lecanorales, les autres des Dothidéales: chez les Lecanorales, *Buellia* (12 sp.), *Epilichen* (2), *Rhizocarpon* (3), *Rinodina* (1), *Dactylospora* (27), dont 9 espèces et variétés nouvelles, et chez les Dothidéales, *Buelliella* gen. nov. (3), *Cycloschizon* (1), *Colensoniella* gen. nov. (1), *Dothidea* (1), *Eutryblidiella* (2), *Gibbera* (1), *Heteresphaeriopsis* gen. nov. (1), *Karschia* (2), *Poetschia* (4), *Pseudodiscus* (1), *Rhizodiscina* gen. nov. (1), *Rhizogene* gen. nov. (1) et *Schrakia* gen. nov. (2), dont 3 espèce et variétés nouvelles. La taxonomie de l'auteur se fonde principalement sur la structure apicale de l'asque et la structure ontogénique de l'ascocarpe, en plus de les caractéristiques sporales et de la réaction à l'iode. Cette monographie d'un groupe inexploré, soignée dans son élaboration et dans son édition, est un exemple propre à susciter d'autres recherches.

ASCOMYCETEN AUF ERICACEEN IN DEN OSTALPEN, par Paula REMLER, in Bibliotheca mycologica n° 68, 322 p., 18 figs., 1 carte, 8°, relié 1979, J. Cramer, FL-9490 Vaduz. Prix DM 64.-/80.-

L'analyse mycologique d'un site écologique défini, qu'il soit géographique, microclimatique ou botanique, tel une plante-hôte, est une méthode conseillée d'une recherche à la fois limitée et féconde. Paula Remler qui a limité sa recherche aux Ericacées de la végétation alpine, y a relevé 94 espèces d'Ascomycètes dont 45 Discoascomycètes sur 13 espèces-hôtes. Les espèces de *Rhododendron*, en particulier *R. ferrugineum*, et de *Vaccinium*, en particulier *V. myrtillus*, sont les plus richement colonisées. 9 espèces nouvelles sont décrites. Si les résultats de ces 4 ans de recherche sont intéressants, leur présentation laisse à désirer. La dactylographie de la matrice eut beaucoup gagné à être plus compacte et dès lors moins longue et plus économique. Une clé dichotomique de 31 pages pour l'identification d'espèces très diversifiées d'une microflore tout de même encore incomplète et locale n'a que peu d'intérêt. Elle eut pu laisser la place à un dessin de chaque espèce décrite. L'ouvrage eut été alors d'un plus grand intérêt.

AUSTROBOLETUS AND *TYLOPILUS* SUBGENUS *PORPHYRELLUS* WITH EMPHASIS ON NORTH AMERICAN TAXA, by Carl B. WOLFE, Bibliotheca Mycologica 69, 148 p., 65 figs., 5 pls. phot. b.w., 8°, bound, 1979, J. Cramer, FL-9490 Vaduz. Price DM 32.-/40.-.

Porphyrellus Gilbert (type: *Boletus porphyrosporus Fr.*) is considered by Singer a genus related to *Strobilomyces* and segregated from *Tylopilus*. In *Porphyrellus*, Singer recognizes two sections, sect. *Porphyrellus* and sect. *Graciles*. Wolfe considers *Porphyrellus* sect. *Porphyrellus* more closely related to *Tylopilus* and agrees on the subgenus *Tylopilus* subg. *Porphyrellus* (Gilbert)Smith & Thiers. Regarding *Porphyrellus* sect. *Graciles* sufficiently distinct from *Tylopilus*, he elevates its synonymous subgeneric name to generic rank as *Austroboletus* (Corner) Wolfe. The author justifies his taxonomical treatment, but confusedly. Macroscopic and microscopic characters are given to both circumscriptions. *Tylopilus* sect. *Porphyrellus* is divided in 2 sections and accomodates 9 species. *Austroboletus* also has 2 sections but for 3 species. A key to world taxa is provided but with abreviated generic names and without explanations. In a separate chapter, the type materials are fully described and illustrated, even those of the species accepted and redescribed in the author's treatment. The illustrations are confusedly numbered. Line drawings are in the text and numbered 1 to 15 and 38 to 65. Figs. 16-37 are SEM photographs nicely assembled in three plates 'hors texte' but not referred as plates, and together with five photographs of pilei disposed in three full pages (really plates) but each of them being referred to as plate instead of figure and numbered 1-5.

The GASTEROMYCETES OF AUSTRALIA AND NEW ZEALAND, par G.H. CUNNINGHAM, Bibliotheca Mycologica 67, 236 p., 37 pls. 1942, John Mc Indoe, Dunedin, N.Z., réimpression 1979, relié, J. Cramer, FL-9490 Vaduz. Prix 64.-/80.-.

Ce livre de 1942 s'est avéré une pièce maitresse de la flore mycologique d'Australie et de Nouvelle Zélande. Résultat d'un labeur de 20 années et de l'examen de plus de 10000 specimens, ce livre garde sa valeur taxonomique bien la nomenclature et l'information soient dépassées. Cette réimpression, d'ailleurs bien faite, est bienvenue.

DIE PHYTOPATHOGENEN GROSSPILZE DEUTSCHLANDS, BASIDOMYCETES MIT AUSSCHLUSS DER ROST- UND BRANDPILZE, by Hanns KREISEL, 284 p., 45 figs., 65 pls. phot. b.w.(figs. 46-111), 8°, Gustav Fischer, Reprint 1979, bound, J. Cramer, FL-9490 Vaduz.

The scope of this book might have surprised, but it originated in the lack of updated identification keys to tree pathogenic fungi since the handbooks of Sorauer (1886-1908) and of Neger (1924). Restricted to the tree attacking and wood destroying Basidiomycetes, the book o-fers good identification keys and specific details about the biological behaviour of the selected species. It also includes 65 goods black and white photographs of fungi. The reprint is of good quality.

TABULAR KEY TO THE SPECIES OF *PHYTOPHTHORA* DE BARY, by F.J. NEWHOOK, G.M. WATERHOUSE and D.J. STAMPS, *Mycological Papers 143*, 20 p., 3 tabl., 4 pls. (55 figs.), 31.12.1978, Commonwealth Mycological Institute, Kew, England.

Synoptic keys for the identification of fungi are of easier use than dichotomic keys. Synoptic keys can have the shape of a table, like that one proposed by the authors for the species of *Phytophthora*. Such table has two entries, one to the taxa, the other to the characters. Another shape of the synoptic key is the one used by Korf (Mycologia, 64:937, 1972), which consists in the listing of the species reference numbers with each of the characters observed. The table might be large and their printing difficult; the numerical listing can hold in usual justification, but is of slower use. It should be noticed that the synoptic key table proposed for *Phytophthora* is assorted with a number of excellent photographs.

STUDIES ON *CERCOSPORA* AND ALLIED GENERA. VII NEW SPECIES AND REDISPOSITIONS, par F.C. DEIGHTON, *Mycological Papers 144*, 55 p. 28 figs., 8°, 1.8.1979, Commonwealth Mycological Institute, Kew.

Dr Deighton is wel known for his *Studies on Cercospora and allied genera*. With this VIIth part,he proposes 8 new species and 22 new combinations in *Pseudocercospora*, *Paracercospora* a new genus, *Mycovellosiella*, *Phaeoramularia*, *Stenella* and *Cladosporium*. The author claims that these genera can be recognized on the natural substratum and find himself in divergence with Ellis about some of their characters. Von Arx considers the four latter genera synonymous. A synoptic keys to all the genera of the group might be suggested.

GRAMINICOLOUS *ASCOCHYTA* SPECIES, by E. PUNITHALINGAM, *Mycological Papers 142*, 214 p., 108 figs., 17 pls. phot., 8°, 1.6.1979, Commonwealth Mycological Institute, Kew.

To enlight the taxonomy of an as large genus as *Ascochyta* is one of the most difficult task in the Sphaeropsidales. Restricting his task to the graminicolous species, the author segregated from allied genera 150 species of *Ascochyta* , of which he accepted 49 taxa only and added 28 new ones. Two new telemorphic species *Didymella phleina* and *Didymosphaeria loliina* are described with an *Ascochyta* anamorph. The diagnosis of the species is based on morphological features only and not host specificity, what is a real progress in the study of the genus. The conidiogenesis is also emphasised. At first purely holoblastic, the conidia are produced enteroblastically at an older stage only. Most of the species described are illustrated with line drawings and photographs.

PATTERNS OF DEVELOPMENT IN CONIDIAL FUNGI, par Garry T. COLE et Robert A. SAMSON, 190 p., 99 figs., 4°, relié, 5 juin 1979, Pitman Publishing Ltd, 39 Parker street, London WC2B 5PB, 6 Davis Drive, Belmont, California 94002.Prix £29.75.

Après les travaux de Vuillemin et de Mason et le très fameux article de Stanley J. Hughes *Conidiophores, conidia and classification* (Can. J. Bot. 1958), une révolution s'est opérée dans l'étude et la taxonomie des Hyphomycètes, qui s'étendit bientôt à l'ensemble des Deuteromycètes. Les caractères trop superficiels et changeants utilisés encore par Saccardo ont fait une plus large place aux caractères ontogéniques plus stables. A l'ancienne taxonomie s'est substituée une nouvelle Taxonomie. Les auteurs se sont succédés: Tubaki, Barron, Subramanian, Madelin, et d'autres. Ils ont tenté d'affiner. Un symposium s'est réuni: Kananaskis I, et ses actes *Taxonomy of Fungi Imperfecti*, édités par Kendrick (1971) ont

marqué une nouvelle étape : la microphotocinématographie discontinue au microscope optique. Aujourdhui, un autre sommet est atteint dans l'escalade: c'est le *Patterns of Development in Conidial Fungi* de Garry Cole et de Robert Samson. Le voile est levé, cette fois. Et on peut s'exclamer avec Harold Brodie *"Fungi: Delight of Curiosity!"* devant ces réels bourgeonnements du *Candida albicans* que l'on découvre à la première page du livre. Fiction? non, réalités micrométriques que le microscope électronique met à la portée du champ de notre vision. Le livre est un album d'images, il se veut agréable, même beau: c'est la nature qui est belle. La conidie nait, se tient en équilibre, vacille et tombe, une déchirure s'est produite. L'hélicoïde s'enroule, l'épi progresse, la grappe se déploie, la phialide éjecte sa derniere née et le filament s'allonge pour se briser en articles. Ainsi naissent et se succèdent les conidies des champignons conidiens. Ce que le mycologue depuis plus de vingt ans contemple à l'oculaire de son microscope, Cole et Samson nous le font voir. Mais au delà de cette imagerie, de la conidiogénèse, les auteurs en reprennentles principes, analysent les cas, soulèvent les inconnues. Deux types fondamentaux de conidiation, le type blastique et le type arthrique, chacun pouvant être holopariétal ou entéropariétal, donnent, suivant le nombre de conidies formées, leur ordre et leur position relatives, une surprennante diversité de types (*Patterns*) conidiogénétiques. Ainsi après Kendrick, Cole et Samson ont prouvé au yeux de tous l'existence de ce qu'avaient *vu* Vuillemin, Mason et Hughes. L'ouvrage est édité avec grand soin et esthétique. Non seulement il sera le compagnon de beaucoup de mycologues, et de biologistes, mais aussi un émerveillement pour le profane.

CO-EDITORS OF MYCOTAXON

G. L. HENNEBERT
FRENCH LANGUAGE EDITOR
& BOOK REVIEW EDITOR
UCL, Place Croix du Sud 3
B-1348 Louvain-la-Neuve, Belgium

RICHARD P. KORF
ENGLISH LANGUAGE EDITOR
& MANAGING EDITOR
P.O. Box 264
Ithaca, NY 14850, USA

MYCOTAXON is a quarterly journal devoted to all phases of mycological and lichenological taxonomy and nomenclature. It seeks to publish all papers within 4 months of acceptance, using photo-offset lithography. All articles are reviewed by specialists prior to acceptance. Publication is open to all persons. Papers may be in French or English, summaries in any language.

SUBSCRIPTION INFORMATION

Each issue of MYCOTAXON may vary in number of pages. Each volume, beginning with volume 3, consists of at least 512 pages, and consists of an irregular number of quarterly issues depending only upon the amount of copy received from authors. Subscriptions are on a **per volume** basis, not on an annual basis. If only one bill during each year is a requirement, please pay for 2 volumes, which will normally cover one year's issues. Personal subscriptions are available at a substantially reduced subscription rate for **individuals** who agree not to deposit their copies in another library than their own within three years of receipt. Prices for each volume, beginning with volume 3, are:

	Paid by June 30, 1980	Paid after June 30, 1980
REGULAR (multiuser)	$32.00	$40.00
PERSONAL (individual)	$14.00	$17.50

(Vols. 1 and 2 are available at **half** the above rates per volume)

(Complete runs, vols. 1 through the latest complete volume, are subject to a 10% discount)

MYCOTAXON is also available in **microform** (microfiche, microfilm) from University Microfilms, 300 North Zeeb Road, Ann Arbor, MI 48106, from whom prices may be obtained.

MYCOTAXON may also be obtained on a journal exchange basis. This may be arranged with journals, institutions, or individuals who have difficulty in obtaining foreign currencies. For details and journal exchange forms, write to a Co-Editor.

EDITORIAL SERVICES AND INFORMATION FOR PROSPECTIVE AUTHORS

Authors prepare their own **camera-ready** copy after having received comments from pre-submission reviewers. Detailed **Instructions to Authors** appeared in MYCOTAXON **1**: 3-12. 1974, and **6**: 370. 1977. A copy of each will be sent upon request to one of the Co-Editors.

We are able to provide prospective authors with two aids to publication. Both are sold at our cost, and are shipped postpaid from MYCOTAXON, LTD., P.O. Box 264, Ithaca, NY 14850 USA.

SPECIAL MANUSCRIPT PAPER is available in packages of 50 sheets, and is ruled in blue, non-photoreproducing ink for each of the two sizes of typeface called for in the instructions to authors (elite, pica). It is a convenience to typists, but certainly not an essential, since the appropriate size rectangles can be prepared on any paper using a non-photoreproducing blue pencil. Each package of 50 sheets is sent **postpaid** for $1.75.

BIOPLATE is a special sheet of transfer letters for the use of authors in the preparation of plates and graphs for publication. It is manufactured specifically for us by Prestype, and is available in either black or white. Each sheet is approximately 30 x 39 cm., with a wide assortment of numbers, letters (including important Greek characters), symbols, etc. These are sent **postpaid** for $4.95 (black will be shipped unless white is specified.)