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# DR. M. A. DONK, HIS LIFE AND WORK

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(With Plate 16)

With the death of Dr. M. A. Donk on 2 September 1972 the mycological world has lost one of its great personalities.

Born on 14 August 1908 at Situbondo, Java, of Dutch parents, Donk went to a secondary school at The Hague and entered the University of Utrecht in 1927. He received his doctor's degree on 7 July 1933.

Donk, who had become interested in fungi as a schoolboy, joined the Dutch Mycological Society in 1925, was in close contact with the French mycologist H. Bourdot, and published his first scientific paper before his twentieth birthday.

After having been a teacher from 1934 to 1940 in the then Dutch East Indies, Donk was appointed Mycologist at the Herbarium of the Botanic Gardens at Buitenzorg, Java (now Herbarium Bogoriense) in 1941. Japanese internment camps followed from 1942 to 1945, a period which was capped by further catastrophe: on emerging from the camp he found that his three manuscript copies of an unpublished mycological text-book had vanished. To recover from the shock he seriously considered dropping mycology and becoming a pteridologist.

From 1947 to 1955 he held the post of Head of the Herbarium Bogoriense, and was appointed Professor (Extraordinarius) of Botany in 1952 at the University of Indonesia at Bandung.

On his return to Holland in 1956 Donk became Head of the Mycological Department of the Rijksherbarium. He started by lecturing to graduate students, but on more than one occasion he refused to accept a professorship in order to devote all his time to mycology proper. His scientific output amounts to more than 2300 pages.

In 1954 Donk was elected Corresponding Member and in 1962 Full Member of the Royal Dutch Academy of Sciences, while from 1964 to 1969 he was Secretary of the Biological Section of this Society.

From 1969 to 1970 Donk spent a year in the U.S.A. (Beltsville, Chapel Hill, Knoxville, New York, Pelston, Syracuse, Tucson) as a National Science Foundation Visiting Professor.

Donk bequeathed his personal mycological herbarium and famous card-index to the Rijksherbarium, which also acquired part of his library.

Although he became more and more interested in broad relationships rather than species, Donk had an extraordinary knowledge of many groups of fungi. In this he was undoubtedly helped by the versatility of his mind and his phenomenal memory. His juridical leanings and acute intellect inevitably prompted him to

express his opinion on nomenclatural matters. Small wonder therefore that demands were made on his services from many sides: he was Secretary of the Committee for Fungi and Lichens as well as a Member of the General Committee of the Nomenclatural Section, acting in this capacity during several International Botanical Congresses; during the Xth International Botanical Congress, Edinburgh (29 July—12 August 1963) he was Chairman of the Symposium on 'Criteria for classification in the Higher Basidiomycetes'; he was President of the Third European Mycological Congress, Glasgow (1–7 September 1963); from 1963 to 1966 he was a Member of the Advisory Board for Biological Sciences of the 'Netherlands Organization for the Advancement of Pure Research (Z.W.O.)'; in 1964 he became Chairman of the International Commission for the European Mycological Congresses, IUBS; in the same year he was elected Honorary Member of the British Mycological Society; from 1966 until his death he was a Member of the Board of Trustees of the 'Centraalbureau voor Schimmelcultures', Baarn; he was an Invited Participant in the 'L. R. Hesler Symposium' held in 1968 at Knoxville, Tennessee; in 1971 he was Chairman of a Symposium on Heterobasidiomycetes at the First International Mycological Congress, Exeter.

Apart from the numbered publications listed below, there are several others, to which Dr. F. A. Stafleu kindly drew my attention. These were published in Taxon **3**: 25, 68, 75. 1954; **9**: 56–57, 267–268. 1960; **12**: 37–38. 1963; **13**: 178–180. 1964. Finally the generic name *Flagelloscypha* Donk was published apud Singer in Lilloa **22**: 312. 1951 ["1949"].

Donk maintained a detailed registry of his publications. It is inconceivable that he should have forgotten about those in Taxon or about the book reviews published from time to time in Persoonia. He simply did not put them on the same level with those enumerated below.

The following list of publications bears witness to the magnitude of his mycological work. This list is followed by a number of papers, mainly from authors abroad, collected in this Memorial Number as a lasting tribute.[1]

## The publications of M. A. Donk

*Mycological (and related) publications.*

**1928**

1. De geslachten *Cantharellus*, *Craterellus* en *Dictyolus* in Nederland. *In* Meded. Ned. mycol. Ver. **16–17**: 163–183.

**1930**

2. Nederlandse Basidiomyceten I. *In* Ned. kruidk. Arch. **1930**: 65–84.

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[1] Although a certain uniformity in the arrangement of the diverse papers is essential, the authors have been given considerable freedom. They have also been left free in their choice between the use of $\mu$ or $\mu$m.

**1931**

3. Revisie van de Nederlandse Heterobasidiomycetae (uitgez. Uredinales en Ustilaginales) en Homobasidiomycetae-Aphyllophoraceae. Deel I. *In* Meded. Ned. mycol. Ver. **18–20**: 65–200. (Reprinted, together with No. 4, in Bibliotheca mycologica **21**, 1969.)

**1933**

4. Revision der niederländischen Homobasidiomycetae-Aphyllophoraceae II. *In* Meded. Ned. mycol. Ver. **22**. (Reprinted, together with No. 3, in Bibliotheca mycologica **21**, 1969.)

**1941**

5. Nomina generica conservanda and confusa for Basidiomycetes (Fungi). *In* Bull. bot. Gdns, Buitenz. III **17**: 155–197.

**1948**

6. Notes on Malesian fungi. I. *In* Bull. bot. Gdns, Buitenz. III **17**: 473–482.
7. Non-mycological.

**1949**

8. New and revised nomina generica conservanda proposed for Basidiomycetes (Fungi). *In* Bull. bot. Gdns, Buitenz. III **18**: 83–168.
9. *Gyromitra* F. versus *Gyrocephalus* Pers. (Fungi: Helvellaceae). *In* Bull. bot. Gdns, Buitenz. III **18**: 169–170.

10–11. Non-mycological.

12. Nomenclatural notes on generic names of agarics (Fungi: Agaricales). *In* Bull. bot. Gdns, Buitenz. III **18**: 271–402.

**1950**

13. Summary of proposals. An annotated compilation of proposed nomina generica and nomina confusa relating to Hymenomycetes (Fungi), compiled from previous publications (Mimeographed).

**1951**

14. The generic names proposed for Hymenomycetes—I. "Cyphellaceae." *In* Reinwardtia **1**: 199–220.

**1952**

15. On generic type species indicated by misapplied names. *In* Reinwardtia **1**: 483–486.
16. Notes on Malesian fungi—II. On the genera *Auricularia*, *Hirneola*, and *Laschia*. *In* Reinwardtia **1**: 487–500.
17. The status of the generic name *Oxydontia* L. W. Miller ("Hydnaceae"). *In* Mycologia **44**: 262–263.

**1953**

18. Proposal for conservation of *Calocera* (Fr.) Fr. vs. *Corynoides* S. F. Gray (Mimeographed).
19. Proposal for conservation of *Lachnocladium* Lév. and *Ramaria* (Fr.) Bonord. (Mimeographed).

**1954**

20. Non-mycological.
21. Notes on resupinate Hymenomycetes—I. On *Pellicularia* Cooke. *In* Reinwardtia **2**: 425–434.
22. The generic names proposed for Hymenomycetes—II. Hymenolichenes. *In* Reinwardtia **2**: 435–440.
23. The generic names proposed for Hymenomycetes—III. "Clavariaceae." *In* Reinwardtia **2**: 441–493.
24. On Staude's new generic names for agarics. *In* Reinwardtia **2**: 495–498.
25. A note on sterigmata in general. *In* Bothalia **6**: 301–302.

**1955**

26. The generic names proposed for Hymenomycetes—IV. Boletaceae. *In* Reinwardtia **3**: 275–313.

**1956**

27. Notes on resupinate Hymenomycetes—II. The tulasnelloid fungi. *In* Reinwardtia **3**: 363–379.
28. The generic names proposed for Hymenomycetes—V. "Hydnaceae." *In* Taxon **5**: 69–80, 95–115.
29. The generic names proposed for Hymenomycetes—VI. Brachybasidiaceae, Cryptobasidiaceae, Exobasidiaceae. *In* Reinwardtia **4**: 113–118.
30. Notes on resupinate Hymenomycetes—III. *In* Fungus **26**: 3–24.

**1957**

31. The generic names proposed for Hymenomycetes—VII. "Thelephoraceae." *In* Taxon **6**: 17–28, 68–85, 106–123.
32. Typification and later starting-points. *In* Taxon **6**: 245–256.
33. Notes on resupinate Hymenomycetes—IV. *In* Fungus **27**: 1–29.

**1958**

34. Typification of the name *Hydnum* (Fungi). *In* Taxon **7**: 96–97.
35. The generic names proposed for Hymenomycetes—VIII. Auriculariaceae, Septobasidiaceae, Tremellaceae, Dacrymycetaceae. *In* Taxon **7**: 164–178, 193–207, 236–250.
36. Notes on the basidium. *In* Blumea, Suppl. **4**: 96–105.

37. The generic names proposed for Hymenomycetes—IX. "Meruliaceae" and *Cantharellus* s. str. *In* Fungus **28**: 7–15.
38. Notes on resupinate Hymenomycetes—V. *In* Fungus **28**: 16–36.

**1959**

39. Notes on 'Cyphellaceae'—I. *In* Persoonia **1**: 25–110.

**1960**

40. The generic names proposed for Polyporaceae [= The generic names proposed for Hymenomycetes—X]. *In* Persoonia **1**: 173–302. (Reprinted in Bibliotheca mycologica **11**, 1968.)
41. Nomenclature of conventional systems. *In* Taxon **9**: 103–104.
42. On nomina anamorphosium—I. *In* Taxon **9**: 171–174.
43. *Tylospora* nom. nov. *In* Taxon **9**: 220.

**1961**

44. The citation of authors of revalidated names. *In* Taxon **10**: 66–69.
45. Four new families of Hymenomycetes. *In* Persoonia **1**: 405–407.

**1962**

46. The generic names proposed for Polyporaceae. Additions and corrections [= The generic names proposed for Hymenomycetes—XIV]. *In* Persoonia **2**: 201–210.
47. Notes on the basidium—II. *In* Persoonia **2**: 211–216.
48. Notes on resupinate Hymenomycetes—VI. *In* Persoonia **2**: 217–238.
49. The generic names proposed for Hymenomycetes—XII. Deuteromycetes. *In* Taxon **11**: 75–104.
50. Confusion. *In* Taxon **11**: 120–122.
51. On Secretan's fungus names. *In* Taxon **11**: 170–173.
52. The generic names proposed for Agaricaceae [= The generic names proposed for Hymenomycetes—XI]. *In* Beih. Nova Hedwigia **5**.

**1962**

53. On nomina anamorphosium—II. *In* Taxon **11**: 243–245.
54 Notes on 'Cyphellaceae'—II. *In* Persoonia **2**: 331–348.

**1963**

55. The generic names proposed for Hymenomycetes—XIII. Additions and corrections to parts I–IX, XII. *In* Taxon **12**: 113–123, 153–168.
56. *Claviceps* L. Tul. (1853) not illegitimate. *In* Taxon **12**: 264–266.
57. Proposals for conservation of some names of fungi—I. *Monilia* 'Bon.' (Deuteromycetes). *In* Taxon **12**: 266–271.

58. Introductory note. From N. Patouillard, Essai taxonomique sur les familles et les genres des Hyménomycètes. Reprint-edition.
59. Bibliographical note. From L. Quélet, Les champignons du Jura et des Vosges. Reprint-edition [It should be noted that Dr. Donk indicated 1963 as the year of publication of this note. The publishers recently assured me that 1964 as mentioned in their reprint-edition was an error].
60. The riddle of the Sphinx. *In* Taxon **12**: 309–314.
61. A conspectus of the nomenclatural status of names. *In* Taxon **12**: 314–319.
62. On superfluous names. *In* Taxon **12**: 319–329.
63. On the status of later homonyms. *In* Taxon **12**: 329–332.

**1964**

64. On nomina anamorphosium—III. *In* Taxon **13**: 14–17.
65. On some old species of Dacrymycetaceae. *In* Proc. K. Ned. Akad. Wet. (C) **67**: 85–102.
66. Nomina conservanda proposita. I. Proposals in fungi (Deuteromycetes, Pyrenomycetes, Hymenomycetes). *In* Regnum veg. **34**: 7–43.
67. A conspectus of the families of Aphyllophorales. *In* Persoonia **3**: 199–324.
68. [Index to] The generic names proposed for Hymenomycetes I–IX, XII, XIII. Weinheim.

**1965**

69. The mycological publications of K. B. Boedijn. *In* Persoonia **3**: 325–330.
70. Veelvoudige overeenkomsten bij Hymenomyceten. *In* Versl. K. Ned. Akad. Wet. (Afd. Natuurk.) **74**: 24–32.

**1966**

71. A reassessment of the Cyphellaceae. *In* Acta bot. neerl. **15**: 95–101.
72. *Cicinnobolus* Bary (Fungi, Sphaeropsidales). *In* Taxon **15**: 149–151.
73. *Osteina*, a new genus of Polyporaceae. *In* Schweiz. Z. Pilzk. **44**: 83–87.
74. Check list of European hymenomycetous Heterobasidiae. *In* Persoonia **4**: 145–335.
75. Notes on European polypores—I. *In* Persoonia **4**: 337–343.

**1967**

76. Notes on European polypores—II. Notes on *Poria*. *In* Persoonia **5**: 47–130.

**1968**

77. On *Cristella*. *In* Taxon **17**: 277–278.
78. Report of the Committee for fungi and lichens 1964–1969. *In* Taxon **17**: 578–581.

**1969**

79. Notes on European polypores—III. Notes on species with stalked fruitbody. *In* Persoonia **5**: 237–263.
80. Notes on *Cantharellus* sect. *Leptocantharellus*. *In* Persoonia **5**: 265–284.
81. Introductory note. From M. J. Berkeley, Decades of fungi. Reprint-edition.
82. Notes on European polypores—IV. On some species of *Ganoderma*. *In* Proc. K. Ned. Akad. Wet (C) **72**: 273—282.
83. On the typification of *Hexagonia* Pollini per Fr. *In* Taxon **18**: 663–666 [= Notes on European polypores—V].

**1971**

84. *Paullicorticium curiosum*, presumably an imperfect state. *In* Gorteria **5**: 134–136.
85. Notes on European polypores—VI. *In* Proc. K. Ned. Akad. Wet. (C) **74**: 1–24.
86. Notes on European polypores—VII. *In* Proc. K. Ned. Akad. Wet. (C) **74**: 25–41.
87. Progress in the study of the classification of the Higher Basidiomycetes. *In* Evolution in the Higher Basidiomycetes. An international Symposium (Ed. R. H. Petersen) 3–25.
88. Multiple convergence in the polyporaceous fungi. *In* Evolution in the Higher Basidiomycetes. An international Symposium (Ed. R. H. Petersen) 393–420.
89. Notes on European polypores—VIII. *In* Persoonia **6**: 201–218.
90. Notes on European polypores—IX. On some species of Hymenochaetaceae. *In* Proc. K. Ned. Akad. Wet. (C) **74**: 405–421.

**1972**

91. Notes on European polypores—X. *In* Proc. K. Ned. Akad. Wet. (C) **75**: 165–178.
92. Notes on European polypores—XI. On some species of *Tyromyces*. *In* Proc. K. Ned. Akad. Wet. (C) **75**: 287–304.
93. The Heterobasidiomycetes: a reconnaissance—I. A restricted emendation. *In* Proc. K. Ned. Akad. Wet. (C) **75**: 365–375.
94. The Heterobasidiomycetes: a reconnaissance—II. Some problems connected with the restricted emendation. *In* Proc. K. Ned. Akad. Wet. (C) **75**: 376–390.

**1973**

95. The Heterobasidiomycetes—III. How to recognize a Basidiomycete. *In* Proc. K. Ned. Akad. Wet. (C).
96. The Heterobasidiomycetes—IV. *In* Proc. K. Ned. Akad. Wet. (C) **76**:109–125.
97. The Heterobasidiomycetes—V. *In* Proc. K. Ned. Akad. Wet. (C) **76**:126–140.
98. Maratti's generic names for fungi. *In* Taxon.
99. *Racodium* Pers. not a genus of Lichens. *In* Taxon.
100. Notes on European polypores—XII. *In* Proc. K. Ned. Akad. Wet. (C).
101. Check list of European polypores.

**1974**

102. Check list of European hymenomycetous Heterobasidiae. Supplement and corrections. *In* Persoonia **7** (4).

*Non-mycological publications.*

**1948**

7. Genera Filicum (The Genera of Ferns) by E. B. Copeland (Review). *In* Chronica Naturae **104**: 281–282.

**1949**

10. Dr. O. Posthumus as a pteridologist. *In* memoriam. In Bull. bot. Gdns, Buitenz. III **18**: 171–177.
11. List of Dr. O. Posthumus' palaeontological publications. *In* Bull. bot. Gdns, Buitenz. III **18**: 178–180.

**1954**

20. Notes on Malesian ferns—I. On the genus *Lemmaphyllum* Presl. *In* Reinwardtia **2**: 403–410.

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# FURTHER OBSERVATIONS ON SPOROTRICHUM AND SOME SIMILAR FUNGI

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(With four Text-figures)

*Sporotrichum azureum* Wright & v. Arx, isolated from wood in Argentina, is described and illustrated. The relationship of the genus *Sporotrichum* with *Ptychogaster* is discussed, both may represent conidial states of basidiomycetes (*Tyromyces*, *Oligoporus*).

The redescription of the genus *Sporotrichum* Link ex Fr. with *S. aureum* Link ex S. F. Gray as type was based on a comparison of the type specimen with a recently isolated strain (Nicot, 1970; von Arx, 1971). Some more strains belonging to the genus and to similar taxa became available in the meantime. Among them a second strain of the species described as *Sporotrichum dimorphosporum* v. Arx was sent by Dr. J. Boidin (Lyon). Other strains proved to be a fungus known as *Ptychogaster rubescens* Brefeld, while a further culture could not be identified with any known species. This will be described below.

The genus *Sporotrichum* is characterized by the formation of basidiomycete-like hyphae which mostly have clamp connexions on the septa and by one-celled conidia with a thick, strikingly pigmented wall. The conidia are separated from the conidiogenous cell by a crosswall without constriction and have a truncate, broad base. They are liberated by histolysis of the stalk cell, remnants of which often remain attached to the base of the conidia. The conidia form powdery masses.

## 1. **Sporotrichum azureum** Wright & v. Arx, *spec. nov.*—Fig. 1

Hyphae progredientes fere tenuitunicatae, hyalinae, 2–3 $\mu$ crassae, fibulis amplis ("medallion") praeditae, ramis e fibulis oriundis; rami laterales aerii hyalini, 1.2–2.8 $\mu$ crassi; hyphae conidiogenae saepe erectae, plerumque e fibulis oriundae, saepe ramosae; conidia terminalia, saepe acervata, raro intercalaria, obovoidea vel pyriformia, sursum late rotundata, a cellula conidiogena septo 2–3 $\mu$ lato separata, hyalina vel caeruleo-incrustata, glabra vel irregulariter verrucosa, 10–16 × 5.5–8 $\mu$.

Coloniae in agaro extracto cerasi addito 1.2–2 mm uno die 24 °C crescunt, velutinae, conidiis pulverulentis caeruleo-griseae.

Typus CBS 609.71, isolatus e ligno, Argentinia, Llavallol, 27 Apr. 1971, a J. E. Wright.

Advancing hyphae relatively thin-walled, hyaline, 2–3 $\mu$ wide, with rounded medallion clamp connexions (with a central space), branched at the clamps; lateral branches forming an aerial mycelium of hyaline, 1.2–2.8 $\mu$ wide hyphae; conidio-

genous hyphae often upright, mostly arising from clamp connexions, often branched; conidia borne terminally, often in brushes, rarely intercalary, obovoid or pyriform, broadly rounded above, separated from the conidiogenous cell by formation of a crosswall, 2–3 μ wide at the truncate base, hyaline or with a bluish encrustation of the wall, glabrous or irregularly verrucose, 10–16 × 5.5–8 μ in size.

The daily growth of the colonies on cherry-decoct-agar at 24 °C is 1.2–2 mm. The colonies become velvety and Deep Green-Blue Gray or Medici Blue (Ridgway, pl. XLVIII) owing to the powdery conidial masses.

Type: CBS 609.71, isolated from wood, Argentina, Llavallol, Santa Catalina, 27 Apr. 1971, by J. E. Wright.

The fungus grows well only on acidic fructose-rich cherry- or prune-decoct agar. At the CBS also dried cultures and a part of the original specimen are preserved.

2. PTYCHOGASTER RUBESCENS Boud. — Fig. 2.

*Ptychogaster rubescens* Boud. *in* J. Bot., Paris **1**: 10. 1887. — *Ceriomyces rubescens* (Boud.) Sacc., Syll. Fung. **6**: 387, 1888.

*Myceliophthora fusca* Doyer *in* Meded. phytopath. Lab. Willie Commelin Scholten **10**: 32. 1927.

Advancing hyphae 3–4 μ wide, hyaline, regularly provided with round medallion clamp connexions, branched at the clamps; lateral branches forming an aerial mycelium, at first lanose and hyaline, in age funiculose or fasciculate, soon becoming Purple Drab or Vinaceous Drab (Ridgway, Pl. XLV) owing to the powdery conidial masses; conidia borne terminally, laterally or intercalarily, mostly in branched chains, on branched hyphae with clamp connexions, obovoid or broadly clavate, with a truncate, 2–3 μ wide base or truncate at both ends, separated from each other by clamp connexions, rather thick-walled, at first hyaline, soon becoming reddish or rust brown, smooth or finely verrucose, 5.5–8.5 × 4–6 μ in size.

The daily growth rate on malt or cherry agar at 24 °C is 4–6 mm. The aerial mycelium may become dense and may form a thick, cushion-like, prosenchymatic mat.

STRAINS EXAMINED:

CBS 190.25, found in a culture of *Serpula lacrymans*, type of *Myceliophthora fusca*, 1925.

CBS 259.38, isolated from mine timber, Transvaal, S. Africa, 1938.

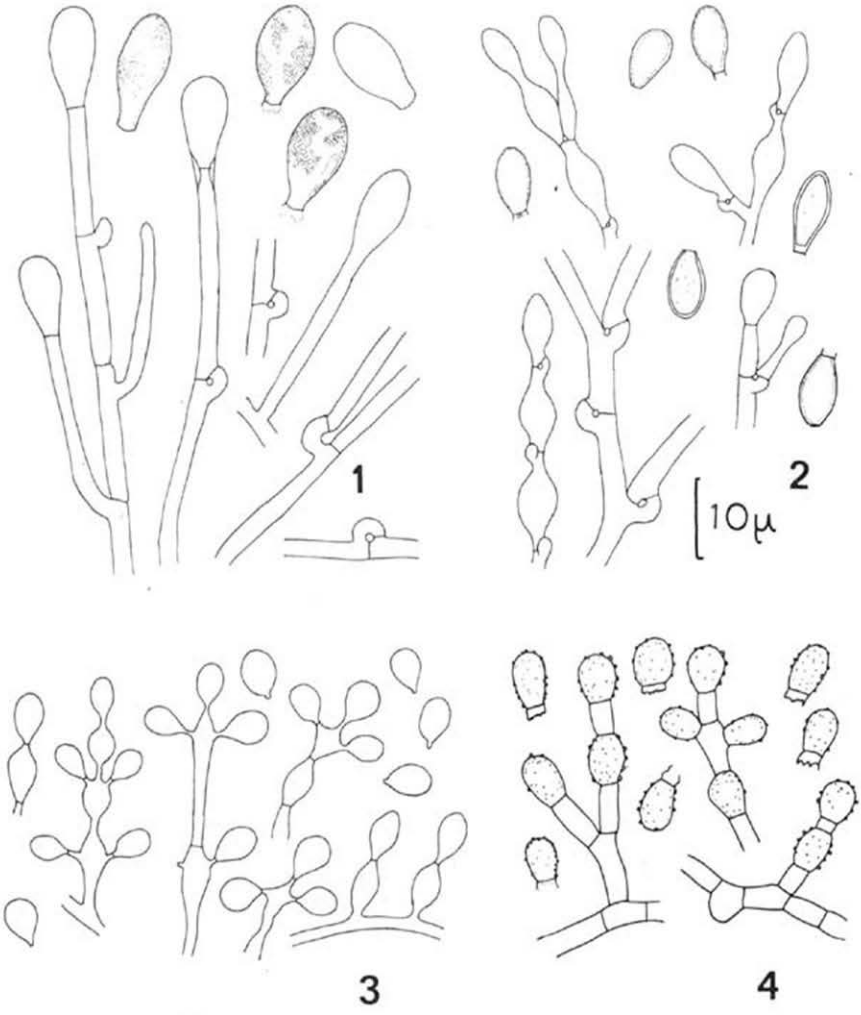
CBS 407.72, isolated from an unidentified fruitbody probably of a polypore on wood, Bareilly, U.P., India, by J. N. Kapoor, 1971.

This fungus has been discussed in detail by Brefeld (1888) and by Falck & Falck (1937) as a wood-attacking organism in buildings. Fidalgo (1958) considered this fungus to be the conidial state of *Polyporus guttulatus* Peck = *Tyromyces guttulatus* (Peck) Murrill. A comparison of 2 strains (CBS 371.29 and CBS 358.33) with *Ptychogaster rubescens*, however, revealed differences in growth rate, colour of the colony, and other characters, as indicated by Davidson & al. (1946).

The genus *Ptychogaster* was described by Corda (1838) for *Ptychogaster albus* Corda = *Ceriomyces albus* (Corda) Sacc. (1888) = *Ptychogaster fuliginoides* (Pers. ex Steudel) Donk (1972). It is the conidial state of *Oligoporus ustilaginoides* Bref. (1888) = *Tyro-*

*myces ptychogaster* (Ludwig) Donk (1933). Both states were described and illustrated by Brefeld (1888).

Morphologically similar is *Ptychogaster citrinus* Boudier (1887) = *Ceriomyces citrinus* (Boudier) Sacc., which was also studied by Brefeld (1888), and of which the basidiiferous state *Oligoporus rennyi* (Berk. & Br.) Donk (1971) was described as *Polyporus*




Figs. 1–4. Conidiogenous cells and conidia. — 1. *Sporotrichum azureum*. — 2. *Ptychogaster rubescens*. — 3. *Myceliophthora lutea*. — 4. *Chrysosporium merdarium*.

*rennyi* Berk. & Br. (1875) = *Oligoporus farinosus* Bref. = *Oligoporus citrinus* Falck & Falck (1937) = ? *Oligoporus friesii* Falck & Falck (1937).

The genus *Ptychogaster* Corda has been identified with *Ceriomyces* Corda by Saccardo (1888). According to Donk (1972), however, the type species *Ceriomyces fischeri* Corda has been based on a gall. The genus *Ptychogaster* without doubt is very closely related to *Sporotrichum*. It can be distinguished especially by the conidia, which in *Ptychogaster* are mostly formed in chains and are separated from each other by clamp connexions.

Another related fungus with larger, non-catenulate conidia, and forming also basidia in pure culture on wood has been described by Falck & Falck (1937) as *Multiporus chlamydoformans*. No material of it is preserved, but it may be identical with *Tyromyces destructor* (Schrad. ex Fr.) Bond. & Singer.

*Sporotrichum*-like fungi with hyphae lacking clamp connexions should be classified in *Chrysosporium* Corda. Such a fungus is *Sporotrichum thermophilum* Apinis. Typical species of the genus *Chrysosporium*, however, represent conidial states of Ascomycetes, especially of Gymnoascaceae. The small, hyaline conidia are separated from the conidiogenous cell by a crosswall; the conidia therefore are clavate (or cylindrical when catenulate) and have a broad, truncate base (Fig. 4).

Carmichael (1962) accepted *Chrysosporium* in a wider sense comprising also fungi forming conidia with a narrow, often apiculate base, hitherto classified in the genera *Myceliophthora* Costantin (Costantin & Matruchot, 1894) and *Emmonsia* Ciferri & Montemartini (1959). The two genera are closely related to each other and also to *Chrysosporium*, but can be easily distinguished from the latter by the formation of 'blastoconidia' with a narrow base and by the presence of thick-walled chlamydospore-like cells. *Myceliophthora lutea* Cost. (fig. 3) is a parasite of the cultivated mushroom; *Emmonsia parva* (Emmons & Ashburn) Cif. & Montem. and *Emmonsia crescens* Emmons & Jellison are parasites in the lungs of animals.

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# REMARKS ON SPECIES OF PHOMA REFERRED TO PEYRONELLAEA—IV

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The new combination *Cheiromycella chomatospora* (Corda) is proposed for the species described by Corda as *Coniothecium chomatosporum*, a name later often misapplied. The new combination *Phoma sorghina* (Sacc.) is introduced for the species discussed in a former paper under the misapplied name *Phoma glumarum* Ell. & Tracy.

Questions of synonymy and misapplications are the greatest obstacles to the revision of the taxonomy of *Phoma*-like fungi. In this fourth article on '*Peyronellaea*' (compare Boerema & al., 1965, 1968, 1971) certain misapplied names and additional synonyms are discussed.

## Phoma glomerata (Corda) Wollenw. & Hochapf.

Misidentifications: *Coniothecium chomatosporum* Corda not sensu Corda: Tryon *apud* Jarvis *in* Qd agric. J. **18**: 269–271. 1922. — *Peyronellaea chomatospora* (Corda not sensu Corda) Goid. *in* Atti Accad. naz. Lincei Rc. VIII **1**: 455. 1946 (as '*cromatospora*', not validly published). *Coniothecium scabrum* McAlp. not sensu McAlp.: Wiltshire *apud* Mason *in* Mycol. Pap. **2** (2): 1–14. 1933. — *Peyronellaea scabra* (McAlp. not sensu McAlp.) Goid. *in* Atti Accad. naz. Lincei Rc. VIII **1**: 455. 1946 (not validly published).

Diagnostic characteristics in vitro: described *in* Persoonia **4**: 53–54. 1965.

In our first paper on dictyochlamydospore-producing species of *Phoma* (Boerema & al., 1965) it was pointed out that Goidànich (1946) had incorrectly interpreted *Coniothecium chomatosporum* Corda and *Coniothecium scabrum* McAlp. as members of 'Peyronellaea'. Further study of the literature has confirmed this.

In various parts of the world *Coniothecium chomatosporum* was formerly regarded as a serious pathogen of apple (Argentina: Fernández Valiela & al., 1954; Australia: Osborn & Samuel, 1922; Ceylon: Park, 1941; Denmark: Gram & al., 1927; England: Massee, 1915, Pethybridge, 1926, Wormald, 1929, 1930, Moore, 1931; India: Kheswalla, 1936, Dey & Singh, 1939, Singh, 1942, 1943, Padwick, 1945; New Zealand: Cunningham, 1925; Rhodesia: Hopkins, 1937; South Africa: Anonymous, 1921, 1922) and, in milder form, also of pear (Argentina: Fernández Valiela & al, 1954; Australia: Osborn & Samuel, 1922;) and plum (India: Kheswalla, 1936; Padwick, 1945). The fungus was said to cause symptoms of scab, canker and blister on twigs and stems ('rough scab', 'apple bark canker', 'apple branch blister', 'apple blackstem'), often resulting in the death of the trees. Cracking, russeting, spotting

and rot of apple fruits were also ascribed to this fungus. All these disease symptoms are now considered to be non-parasitic in origin (Wormald 1934, 1935; Moore & al., 1939; Moore & Bennett, 1952; Mathur, 1968); they are caused by rootstock and soil conditions (e.g. by soils deficient in water and potash).

*Coniothecium chomatosporum* is now known to be a very common dematiaceous hyphomycete, widespread, and occurring on dead bark and wood of trees. The original description and figures of *C. chomatosporum* (Corda, 1837) on dead wood of pine demonstrate that it is conspecific with the type species of *Cheiromycella* Höhn., *Ch. speiroidea* (Höhn.) Höhn. (1910), described from dead wood of conifers and at present known as *Ch. microscopica* (P. Karst.) Hughes (1958). Since the specific epithet *chomatosporum* antedates all other names of this species (see Hughes, 1958) we propose the following recombination: **Cheiromycella chomatospora** (Corda) Boerema, Dorenb. & v. Kest., *comb. nov.* (basionym, *Coniothecium chomatosporum* Corda, Icon. Fung. **1**: 2, pl. 1 fig. 22. 1837). The characteristic features of the fungus in vivo have recently been illustrated by Ellis (1971: 325). For its characters in culture see Dey & Singh (1939).

In Australia a dictyochlamydospore-producing *Phoma* species was erroneously identified as *Coniothecium chomatosporum* (Tryon *apud* Jarvis, 1922). Based on this misidentification Goidànich appears to have proposed the recombination *Peyronellaea chomatospora*, but without validly publishing it. From the studies of Togliani (1952), Foschi (1956), Porreye (1961), and Mathur (1968) it is known that the ubiquitous *Phoma glomerata* very often occurs in association with the disease symptoms of apple mentioned above. It would therefore seem plausible to assume that Tryon's dictyochlamydospore-producing *Phoma* species is referable to *P. glomerata*.

In South Africa van der Bijl (1916) also obtained a dictyochlamydospore-producing *Phoma* species from apple twigs with disease symptoms ascribed to *Coniothecium chomatosporum*. The cultural and morphological characters of van der Bijl's fungus agree completely with those of *Phoma pomorum* (see below), incidentally a species also found by Mathur (1968 and personal communication) in association with the above mentioned disease.

*Coniothecium scabrum* has been described as the causal organism of a certain type of injury of the skin of *Citrus* fruits, called 'black scurf' (Australia: McAlpine, 1899; Samuel, 1925; S. Africa: Putterill, 1923). It is now known that the relevant faint scabbing or russeting of the skin is due to thrips or other injury while the fruit is developing and subsequently to the growth of secondary fungi which emphasize and discolor the injured areas (Fawcett, 1936: 561, 572).

The original description and figures of *Coniothecium scabrum* McAlp. (1899) do not differ essentially from the characteristics of the widespread *Cheiromycella chomatospora* (≡ *Coniothecium chomatosporum*); according to Fawcett l.c. this may also be found in association with the 'black scurf' of *Citrus*. In our opinion therefore it seems quite possible that *Coniothecium scabrum* is conspecific with *Cheiromycella chomatospora*.

In a paper by Mason (1933) Wiltshire misapplied the name *Coniothecium scabrum*

to a dictyochlamydospore-producing species of *Phoma* isolated from orange fruit. On this misidentification Goidànich based the combination *Peyronellaea scabra*, but this was not validly published. Close examination of the figures in Mason's paper convinced us that it is beyond doubt that Wiltshire's fungus pertains to *Phoma glomerata*. The study of Pupillo (1952) has proved that *P. glomerata* occurs on *Citrus* fruits (see Boerema & al., 1965: 59).

## PHOMA POMORUM Thüm.

MISIDENTIFICATIONS: *Ascochyta gossypii* H. Syd. not sensu H. Syd.; Chippendale *in* Trans. Br. mycol. Soc. **14**: 201–214. 1929.

*Coniothecium chomatosporum* Corda not sensu Corda; Bijl *in* Rep. S. Afr. Ass. Advmt Sci. **1915** (13th annual meeting): 649–657. 1916.

*Phoma mali* Schulzer & Sacc. not sensu Schulzer & Sacc.; Bijl *in* Rep. S. Afr. Ass. Advmt Sci. **1915** (13th annual meeting): 649–657. 1916.

DIAGNOSTIC CHARACTERS IN VITRO: described *in* Persoonia **4**: 60. 1965 under the synonym *Phoma prunicola* (Opiz) Wollenw. & Hochapf.

*Ascochyta gossypii* Woronich. (= *A. gossypii* H. Syd.) is the causal organism of the 'wet weather blight' of cotton (leaf spot and stem canker). In our first paper in this series (Boerema & al., 1965) it was pointed out that isolates of this species do not produce dictyochlamydospores like those described and illustrated by Chippendale (1929). Further studies showed that the 'wet weather blight'-fungus deviates completely from the fungus described by Chippendale, not only in cultural (see Thompson, 1950) but also in morphological characters. Chippendale had based his studies on a single tube culture ("having already been opened") made from a diseased cotton plant he had received from North Carolina, U.S.A. Inoculation of the fungus on cotton plants was stated to be "uniformly unsuccessful," whereas the true *A. gossypii* is known to be strongly pathogenic to cotton (compare Holliday & Punithalingam, 1970). The true *A. gossypii* is characterized by, among other things, relatively large pycnidiospores, 8–12 $\mu$ (mostly 10–12 $\mu$) long and 2.5–4 $\mu$ broad. Chippendale's fungus produced much smaller spores: 5.7 × 3 $\mu$. These spore dimensions as well as the description and figures of pycnidia, chlamydospores and dictyochlamydospores ("hypocysts") given by Chippendale fully agree with those of *Phoma pomorum*. Furthermore the growth characteristics on various media of Chippendale's fungus proved to be in accordance with those of *P. pomorum* on the same media. In our experience plurivorous weakly parasitic species of *Phoma* are often confused with the specialized parasites among the species of *Phoma*. *Phoma pomorum*, a ubiquitous weak parasite, is a case in point [compare Maas, 1965: 116; confusion between *P. pomorum* (syn. *Peyronellaea nicotiae* Leduc) and the footrot fungus of flax: *Phoma exigua* var. *linicola* (Naoum. & Vass.) Maas (syn. *Ascochyta linicola* Naoum. & Vass.)]. Another ubiquitous weak or wound parasite is *Phoma exigua* Desm. (Boerema & Höweler, 1967). In our opinion some of the supposed "*Ascochyta gossypii*"-isolates made in North Carolina by Crossan (1958) are likewise different from the true *A.*

*gossypii* and are very probably referable to this *Phoma exigua* Desm. (compare Boerema, 1972).

Another species which has also been confused with *Phoma pomorum* is *Cheiromycella chomatospora* (≡ *Coniothecium chomatosporum*), discussed above under *P. glomerata*. This is apparent from a study by van der Bijl (1916) in South Africa. Van der Bijl gave descriptions and illustrations of "*Coniothecium chomatosporium* Corda, isolated from diseased apple twigs, where the fungus produces a blister disease," that agree completely with those of *P. pomorum*. Apart from *Phoma*-pycnidia the cultures showed "intercalary chlamydospores," "*Alternaria*-like spores" and "packets of *Coniothecium*-spores," which areintermediate stages between chlamydospores and dictyochlamydospores. Van der Bijl (l.c.) stated that the pycnidia, "judging by the spore characters, evidently belong to *Phoma mali* Schulz. & Sacc." This name was obviously adopted from a paper by Massee (1915), who believed that *Coniothecium* is a stage in the life cycle of *Diaporthe ambigua* Nitschke (= *D. eres* Nitschke, fide Wehemyer, 1933). At that time this pycnidial state was known as *Phoma mali* Schulzer & Sacc. The latter is a typical *Phomopsis* and was accordingly named *Phomopsis mali* (Schulzer & Sacc.) Died., a later homonym and synonym of *Phomopsis mali* Roberts (see Boerema & Verhoeven, 1973). The pycnidia described and illustrated by van der Bijl (l.c.) are true *Phoma*-pycnidia with undifferentiated sporogenous cells, corresponding completely with those of *P. pomorum* Incidentally Mathur (1968 and personal communication) also isolated *P. pomorum* [= *P. prunicola* (Opiz) Wollenw. & Hochapf.] from apple branch blister in Iraq (appel black stem).

PHOMA JOLYANA Pirozynski & Morgan-Jones

ADDITIONAL SYNONYM: *Phoma jolyi* Morelet *in* Bull. Soc. Sci. nat. Archéol. Toulon Var **177**: 9. 1968.

DIAGNOSTIC CHARACTERS IN VITRO: described *in* Persoonia **4**: 63. 1965 under the synonym *Phoma musae* (Joly) Boerema & al.

Almost simultaneously with Pirozynski & Morgan-Jones' publication of *Phoma jolyana* Morelet proposed the new name *Phoma jolyi* to replace *Phoma musae* (Joly) Boerema & al. (non *Phoma musae* Sacc.). The binomial *Phoma jolyana* dates from 25 June 1968, whereas *Phoma jolyi* was published in July 1968 (personal communication Dr. Morelet).

**Phoma sorghina** (Sacc.) Boerema, Dorenb. & v. Kest., *comb. nov.*

*Phyllosticta sorghina* Sacc. *in* Michelia **1** (2): 140, 1878 (basionym).
*Phyllosticta sacchari* Speg. *in* Revta Fac. Agron. Univ. naz. La Plata **2**: 239. 1896.
*Phoma insidiosa* Tassi *in* Boll. R. Orto bot. Siena **1**: 8. 1898.
*Phyllosticta setariae* Ferr. *in* Malpighia **16**: 18. 1902.
*Phyllosticta glumarum-sorghi* P. Henn. *in* Annls Mus. r. Congo belge Sér. 4to, Bot. V **2**: 101. 1907.
*Phyllosticta glumarum-setariae* P. Henn. *in* Annls Mus. 2. Congo belge Sér. 4to, Bot. V **2**: 101. 1907.

*Phyllosticta phari* Speg. *in* An. Mus. nac. Hist. nat. B. Aires III **13** (= **20**): 337. 1910 (preprint; vol. dated 1911).

*Phyllosticta penicillariae* Speg. *in* An. Mus. nac. Hist. nat. B. Aires **26**: 129. 1914 (preprint; vol. dated 1915).

*Phyllosticta hawaiiensis* Caum *in* Hawaii Plrs' Rec. **20**; 278. 1919.

MISAPPLICATION: *Phoma glumarum* Ellis & Tracy not sensu Ellis & Tracy: Boerema, Dorenbosch & van Kesteren *in* Persoonia **6**: 174–176. 1971.

DIAGNOSTIC CHARACTERS IN VITRO: described *in* Persoonia **5**: 203. 1968 under the synonym *Phoma indianensis* (Deshpande & Mantri) Boerema & al.

This is a ubiquitous species in tropical and subtropical regions. It may occur on all kinds of plants and other substrata (Boerema & al., 1968 under the synonym *Phoma indianensis*), but more particularly the fungus appears to be a common weak parasite of Gramineae. It is not only well known from rice (*Oryza sativa*) (Boerema & al., 1971 under the misapplied name '*Phoma glumarum*') but it also attacks such important gramineous crops as sorghum (*Sorghum vulgare*), with its varieties (e.g. 'Brown durra', 'Sudan grass', 'Sweet sorghum'), sugar cane (*Saccharum officinarum*) and wheat (*Triticum aestivum*). In phytopathological literature on these crops the fungus is usually treated under the names *Phoma insidiosa* Tassi (e.g. Koch & Rumbold, 1921; Rumbold & Tisdale, 1921a,b; Saccas, 1954; Nema & al., 1971; Punithalingam & Holliday, 1972) and *Phyllosticta sorghina* Sacc. (e.g. Bourne, 1934; Sprague 1941, 1950 and Anonymous, 1960). Two isolates from sorghum (IMI 139349 and IMI 140622 under the name *Phoma insidiosa*), one isolate from sugar cane (CBS 288.35 = ATCC 12115 under the name *Phyllosticta sorghina*, isol. made by Bourne, 1934) and two isolates from wheat obtained from Prof. K. G. Nema, J. N. Agricultural University, Jabalpur, India (see Nema & al., 1971) and Dr. W. F. O. Marasas, Plant Protection Research Institute, Pretoria, S. Africa, showed the typical cultural characters we described earlier (Boerema & al., 1968, under the synonym *Phoma indianensis*). The cultural characters described by Koch & Rumbold (l.c.) for *Phoma insidiosa* and by Bourne (l.c.) for *Phyllosticta sorghina* also accord with our observations of the fungus in vitro.

Saccardo's *Phyllosticta sorghina* antedates *Phoma insidiosa* Tassi; further it turned out that so far it is the oldest known valid name for this typical dictyochlamydospore-producing *Phoma*-species. Consequently it has been transferred to the genus *Phoma*.

The other synonyms listed above are adopted from the comparative cultural and morphological studies by Bourne (l.c.) and Sprague (1941). They can be added to the synonyms discussed in our previous papers (Boerema & al., 1968, 1971), viz. *Phoma glumicola* Speg. ≡ *Phyllosticta glumicola* (Speg.) Hara, *Phyllosticta glumarum* Sacc. ≡ *Phyllosticta oryzina* Padw., *Phoma depressitheca* Bub., *Phoma chartae* Verona, *Peyronellaea indianensis* Deshpande & Mantri ≡ *Phoma indianensis* (Deshpande & Mantri) Boerema & al.

Apart from rice, sorghum, sugar cane and wheat various other gramineous hosts are mentioned in literature (generally under *Phyllosticta sorghina*), e.g.: common reed (*Phragmites communis*), 'Johnson grass' (*Sorghum halepense*), maize (*Zea mays*), millet (*Pennisetum typhoides*), and species of *Eragrostis*, *Chloris*, *Panicum*, *Pharus*, *Setaria*,

*Rhynchelytium* and *Tricholaena* (Anonymous, 1960; Boughey, 1946, Bourne, l.c.; Koch & Rumbold, l.c. and Sprague, 1941, 1950, 1958, 1960, 1962). The disease symptoms on these gramineous hosts are generally similar: infection of the seeds ('glume blotch', -blight') and spots on leaves and stems (compare Boerema & al., 1971, Nema & al., 1971 and Punithalingam & Holliday, 1972).

The binomial *Phoma glumarum* as used in our previous paper (Boerema & al., 1971) for this fungus is not correct. *Phoma glumarum* had been described by Ellis & Tracy (apud Ell. & Ev., 1888: 123) but as we were under the impression that the original material was no longer in existence we chose another collection as neotype (Boerema & al., 1971). This is the specimen "on glumes of *Oryza sativa*, Ocean Springs, Mississippi, Sept. 1889," identified by S. M. Tracy himself and preserved at BKL. There is no doubt that this material and the fungus we described represent the same species but the choice of a neotype was superfluous. Dr. C. T. Rogerson kindly informed us (letter of January 1972) that the Ellis herbarium (NY) contained "two packets bearing the holotype data exactly as published: *Phoma glumarum* Ell. & Tracy, on living glumes of *Oryza sativa*, Starkville, Miss., Oct. 1888, Tracy No. 122." Unfortunately this material does not conform with the collection in BKL; it represents a species of *Coniothyrium*. Hence the binomial used in our paper (l.c.) is a misapplication.

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# PODOSCYPHA INVOLUTA (KLOTZSCH) IMAZ. EST UNE ESPÈCE COMPOSITE (BASIDIOMYCETES, PODOSCYPHACEAE)

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(Avec 2 tableaux et 2 figures)

En Afrique intertropicale trois espèces au moins, interstériles entre elles, sont couramment confondues sous le nom de *P. involuta*: *P. involuta* (Klotzsch apud Fr.) Imazeki, *P. vespillonea* (Berk.) nov. comb. et *P. gillesii* nov. sp.

*Podoscypha involuta* est un représentant quelque peu atypique du grand genre tropical *Podoscypha* Pat. Sa place pourrait aussi bien être parmi les *Cymatoderma* cystidiés du sous-genre *Cladoderris* (cf. Boidin, 1966: 100; Berthet & Boidin, 1966: 41 en bas) mais il n'en possède pas l'ornementation hyméniale, veines ou (et) verrues.

Si comme il est d'usage pour les champignons tropicaux assez apparents et à conservation facile en herbier, de nombreuses récoltes ont été dénommées différemment de 1832 à 1925, l'étude plus attentive des exsiccata jointe à l'emploi des caractères microscopiques a réduit peu à peu le nombre de «bonnes espèces». C'est ainsi que se basant sur le port, la présence de cystides et la petitesse des spores nous donnions en 1960, 10 synonymes et que Reid dans sa belle monographie récente (1965: 183) en cite 13.

On serait tenté de dire que la microscopie a conduit à regrouper sur 1 ou 2 noms ce que des études physionomiques superficielles avaient dispersé sous de nombreuses dénominations spécifiques.

Remarquons toutefois que dans les mises au point citées ci-dessus, et où sont proposées les diverses synonymies, les auteurs signalent la diversité d'aspect des récoltes: «*Podoscypha involuta* is one of the most variable of all stipitate stereoid fungi» écrit Reid (1965: 189).

On est en droit de se demander si l'on n'est pas tombé d'un excès dans l'autre. Nous n'entrevoyons que deux moyens d'aborder le problème: effectuer dans son ère très large de répartition à l'intérieur du triangle Afrique—Philippines—Australie de nombreuses récoltes et les décrire aussi exactement que possible sur le frais aux divers stades du développement. Ceci n'a pu être esquissé qu'en Afrique par l'un des auteurs (séjours en République Centrafricaine en 1965 et 1967), mais de fort précieuses collaborations lui ont été apportées par Madame A. David (séjour au Gabon en 1970) et par M. G. Gilles (au Gabon de 1968 à 1972, en Côte d'Ivoire

depuis 1972). Isoler des cultures monospermes de diverses récoltes et les confronter dans des tests systématiques, ce fut le travail du second auteur (P.L.).

L'aspect des carpophores à leur arrivée, les notes des récolteurs et surtout les résultats des confrontations amènent à la conclusion que trois espèces au moins du «complexe *involuta*» coexistent en Afrique intertropicale. Cette certitude acquise, il est par contre beaucoup plus délicat de rapporter les divers synonymes, même après étude des types, à l'une des 3 espèces et de choisir pour chacune d'elles les noms prioritaires en accord avec les règles de nomenclature.

## PODOSCYPHA INVOLUTA (Klotzsch apud Fr.) Imazeki, *sensu stricto*

*Stereum involutum* Kl. *apud* Fr., Epicr. 546. 1838. — *Podoscypha involuta* (Kl. apud Fr.) Imazeki *in* Bull. Govt Forest Exp. Stn Meguro **57**: 98. 1952.
*Stereum pulchellum* Sacc. & Berl. *in* Revue mycol. **11**: 203. 1889 (TYPE, PAD!).
*Stereum hollandii* Lloyd, Mycol. Writ. **4** (Syn. Stip. Ster.): 30, fig. 549. 1913 (TYPE, BPI!).
*Stereum proximum* Lloyd, Mycol. Writ. **4** (Syn. Stip. Ster.): 40. 1913 (TYPE, BPI!).
*Stereum bresadoleanum* Lloyd, Mycol. Writ. **4** (Syn. Stip. Ster.): 41. 1913 (TYPE, BPI!).
? *Stereum nigrobasum* Lloyd, Mycol. Writ. **7**: 1339, pl. 325 fig. 3112. 1925 (TYPE, BPI!).

Très généralement pétaloïde, exceptionnellement subinfundibuliforme ou vraiment en entonnoir complet, atteignant 8 cm de hauteur. Sur un disque mycélien appliqué, stipe généralement court et aplati, peu différencié coté stérile, mieux délimité coté hyménien par un tomentum formant bourrelet transgressif sur l'hyménium.

Sur le frais la face supérieure tomenteuse un peu zonée, un peu strigueuse sous la loupe dans la moitié âgée, presque blanche à la marge, crème pâle (2,5 Y 9,25/4)[1] passe à chamois pâle (2,5 Y 9/8) ou isabelle (7.5 YR 7/4), alutacé clair (10 YR 8,5/4 à 8/6) et peut atteindre chamois (10 YR 7/8) ou même, vers le stipe, isabelle ocré (7,5 YR 7/8). Le stipe lui même est chamois (10 YR 7/6 et 7/8) et peut s'assombrir jusque chocolat (5 YR 3,5/5). L'hyménium blanc ou blanchâtre à la marge devient vite ocre pâle (10 YR 8/6), isabelle ocré (7,5 YR 7/8), fauve doré (7,5 YR 8/10 et 7/10) et sur les plus grands spécimens atteint, près du stipe, bai (2,5 YR 4/8).

Après quelques années d'herbier, l'hyménium des petits spécimens peut rester pâle vers le stipe: rose saumon terne (5 YR 8/4) ou atteindre «vinaceous fawn» R. (2,5 YR 7/6 à 6/4), mais ceux qui dépassent 2,5 cm de rayon ont des teintes beaucoup plus soutenues, isabelle ocré (7,5 YR 7/8) fauve doré (7,5 YR 7/10), fauve (5 YR 6/8) ou même bai clair (vers 2,5 YR 5/6) et atteignant chatain (10 R 4/4). La face stérile, va de même de couleurs pâles sur les petits spécimens, depuis alutacé clair (10 YR 8/4), isabelle ocré (7,5 YR 7/8) à ombre (5 YR 4/4) sur les plus grands.

La microscopie a été bien précisée (Boidin, 1960; Reid, 1965) et il est inutile d'y revenir. Elle n'est d'ailleurs pas différente chez *P. vespillonea* (cf. plus loin) confondu jusqu'ici avec *P. involuta*.

Rappelons simplement que sur une croûte peu différenciée et faiblement teintée sur les coupes très minces, naissent des poils longs jusqu'à 300–350 $\mu$ à paroi épaisse même à l'extrémité; le contexte, dimitique, est constitué d'hyphes squelettiques à

[1] Ces notations renvoient aux Codes de la Munsell Color Company, Baltimore, U.S.A., notamment Soil Color Charts de 1954; la lettre R. renvoie au Color Standards and Color nomenclature de Ridgway, Washington, 1912.

lumen étroit à subnul (dans KOH 3 %) et d'hyphes génératrices bouclées; que l'hyménium formé d'hyphes grêles et serrées terminées par des basides petites et étroites est parcouru par de nombreuses et longues gloeocystides au contenu homogène, et peut montrer à tous niveaux des cystides fusiformes à paroi épaisse, hyalines, un peu incrustées surtout lorsque leur sommet émerge. Spore 2,75–3 × 2–2,2 $\mu$ (sur sporées).

RÉCOLTES EXAMINÉES. —LY 6035, tronc abattu dans une plantation de café, Boubakiti (RCA) 27 Sept. 1967; LY 6074, La Maboké (RCA) 1er Oct. 1967; LY 6503, Makoku (Gabon) Juil. 1970, leg. A. David; LY 3952, Bangassou (RCA) Juil. 1961 et LY 4300, id. Mai 1962, leg. Cantournet; LY 6914, forêt du Banco, Abidjan (Côte d'Ivoire), 1er Juil. 1972, leg. G. Gilles. On peut ajouter Eala (Zaïre) Juin 1923, leg. Goossens-Fontana 224 (BR); De Witte 10990, forêt ombrophile, alt. 800m, Abyalou, Parc National Albert, 20 Août 1954 (BR); J. Louis 15311, xylophage dans la litière, 25 km NE Yambao (Zaïre), alt. 470m, 22 Juin 1939 (BR).

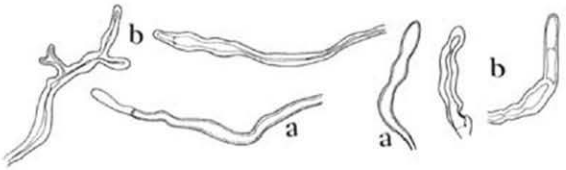


Fig. 1. *Podoscypha involuta*, LY 6074, culture. — a. Hyphes différenciées du mycélium jeune à 1 cm de la marge. — b. du mycélium superficiel âgé de 6 semaines.

Il faut encore citer les types de l'espèce et des synonymes figurant plus haut: *Stereum involutum* Ins. Mauritius no. 4, Telfair; *Stereum pulchellum* Sacc.& Berlese, I. de Principe (Afrique occid.); *Stereum hollandii* Lloyd, Cross River Exp. overland to Okuni, Old Calabar (Nigeria), 21 Mars 1900, leg. J. H. Holland 40; *Stereum proximum* Lloyd, (Samoa), leg. C. G. Lloyd 1904–1905.

ILLUSTRATIONS. —a) couleurs: Boidin 1961, Flore iconographique des champignons du Congo fasc. 10, pl. 34, fig. 6 a (il faut ajouter les lettres suivantes à la figure: a, pour aquarelle; b, pour le spécimen figuré recto et verso *en bas*; d. pour les spécimens recto et verso au-dessus; c, pour les spores).

Il est possible que les aquarelles de Corner s'y rapportent (*in* Reid, 1965: pl. 1 fig. 3, 4, spécimens de Malaisie).

b) microscopiques: Boidin (1960: fig. 45).

## **Podoscypha vespillonea** (Berk.) *nov. comb.*

*Stereum vespilloneum* Berk. *in* J. Linn. Soc. (Bot.) **16**: 44. 1877 (basionyme; TYPE, K!).
*Stereum maculatum* Beeli *in* Bull. Soc. r. Bot. Belg. **58**: 208. 1925 (TYPE, BR!).
? *Stereum prolificans* Berk. *in* J. Linn. Soc. (Bot.) **16**: 41. 1877 (TYPE, K!).

Sessile, à nettement stipité, flabelliforme parfois soudé par les bords à infundibuliforme. Chez les stipités, sur un disque mycélien s'élève un stipe plus ou moins individualisé, aplati et court ou plus différencié, d'abord à section circulaire, haut jusqu'à 7 mm mais s'aplatissant pour faire passage progressif à la face stérile mate, veloutée, un peu strigueuse sous la loupe, zonée par alternance de zones claires, ocre pâle (10 YR 8/6) et de zones sombres, brun havane (7,5 YR 7/4) à ombre olivacé (5 YR 4/3). Marge entière pâle; hyménium sublisse, pâle, puis chaume (5 Y 8/4), chamois clair (2,5 Y 8/6, jaune de Naples R.) miel argillacé (7/6), fonçant davantage encore vers le pied, ou *par tâches*, brun havane (7,5 YR 4/4) et même ombre (5 YR 3,5/4) comme le stipe. Sur de plus vieux spécimens, l'hyménium qui vers la marge est encore alutacé chamois (2,5 Y 8/5), argillacé miel (7/6), passe ensuite à ocre pâle (10 YR 8/8), à chamois (10 YR 7/8, 7/6 et même 6/6, 6,5/4) puis se tâche de brun rouge très foncé.

En herbier, la face stérile pâle à la marge (crème alutacé 2,5 Y 8/4 à alutacé clair 10 YR 8,5/6), encore zonée, *tend à brunir* (brun ombré de 5 YR 4,5/4, jusqu'à 3,5/2,5) *par zones ou tâches à développement radial*, la zonation s'estompant peu à peu à partir du pied. L'hyménium plus ou mois pruineux a, de la marge au pied, l'échelle des teintes suivantes: crème alutacé (2,5 Y 8/4), alutacé (10 YR 8/6), chamois (7/6), ou ocracé pâle (7,5 YR 8/6), ocre isabelle (7,5 YR 7/8) à canelle (6/6), passant enfin soit par plage soit vers le stipe à bai (2,5 YR 4/4) et à chatain (3/4).

L'aspect de la face stérile est le principal caractère distinctif; même sur d'assez petits exemplaires le brunissement par tâches ou plages est souvent déjà sensible et contraste avec le tomentum plus ou moins clair ou foncé selon l'âge mais toujours beaucoup plus unicolore de *P. involuta*. Sur spécimens âgés, très développés et colorés la distinction est moins aisée.

Même microscopie que *P. involuta*. Les variations qui peuvent être notées entre représentants d'une même espèce et qui portent surtout sur le port (stipité à subrésupiné) l'épaisseur, la richesse en cystides ou gloeocystides sont telles qu'aucun caractère microscopique même quantitatif ne peut être retenu pour les différencier. Remarquons cependant que les hyphes squelettiques de *P. vespillonea* semblent atteindre un diamètre un peu moins large et que les basidiospores apparaissent aussi un peu plus étroites, mais ces différences sont si faibles qu'elles ne sont pas sensibles dans les mesures faites en série.

On peut seulement souligner—mais ceci est directement lié aux différences d'aspect des deux espèces—que le contexte et la base de l'hyménium ne gardent pas avec l'âge la blancheur des sections de *P. involuta*: le contexte se teinte de paille, et peut montrer de chaque côté un liseret brun (base de l'hyménium, et croûte). Au microscope cela se traduit par un brunissement (coupe dans KOH phloxine) modéré du contexte et notamment des parois des hyphes squelettiques, de la croûte et des parois des poils qui peuvent être nettement brunis; de même les cystides les plus profondes sont souvent brunâtres.

RÉCOLTES EXAMINÉES.—La description sur le frais a été donnée d'après LY 5429, sur bois en partie enfoui, forêt de Lolomo (RCA) 15 Mai 1965; LY 5557, sur tronc pourri, La Maboké (RCA) 25 Mai 1965; et LY 6733, sur branche morte de *Baphia* sp., forêt de La Mondah, Libreville (Gabon) 31 Janv. 1972, leg. G. Gilles 82, tous

trois interfertiles. Pour l'allure des spécimens d'herbier nous avons tenu compte de LY 6501, Makoku (Gabon) Juil. 1970, leg. A. David, lui aussi interfertile.

Citons en outre comme récolte de notre herbier se rapportant à ce *Podoscypha*: LY 3108, route de Douala à Edéa, km 16 (Cameroun) 3 Août 1958, leg. P. Berthet 236; LY 3113, bois mort près de Japoma (Cameroun), 15 Mai 1958, leg. P. Berthet 211; LY 3115, route de Douala à Edéa, km 32 (Cameroun) 29 Sept. 1958, leg. P. Berthet 260; LY 3569, bois des Singes près Douala (Cameroun) 17 Août 1959, leg. P. Berthet 316; LY 4129, Bangassou (RCA) Juil. 1961 leg. Cantournet; LY 4301, id. Mai 1962; LY 5571, sur *Petarsia africana*, M'Balé (RCA), 28 Mai 1965; LY 6026, sur tronc couché, route de M'Balé (RCA) 25 Sept. 1967; LY 6511, Makoku (Gabon) Juil. 1970, leg. A. David; LY 6533, id. A. David; LY 6854, forêt du Banco, Abidjan (Côte d'Ivoire), 11 Juin 1972, leg. G. Gilles 40; LY 6919, id. 8 Juil. 1972, leg. G. Gilles 106; ainsi que LY 3095, Aningeje, Calabar Province (Nigeria), 27 Juin 1953, leg. R. Harries, det. D. Reid comme *St. involutum*. Pour la répartition géographique certaine, on peut ajouter les types de *St. vespilloneum* Berk., Challenger Exp. (Aru Islands, Océanie) 22 Sept. 1874, et de *St. maculatum* Beeli, en groupe sur arbre mort en forêt inondée, Eala (Zaïre) Juin 1923, leg. M. Goossens-Fontana 227 (BR).

ILLUSTRATIONS.—Couleur: Berthet & Boidin, 1966: pl. IV fig. 1 et 2.

## **Podoscypha gillesii**, *nov. sp.*—Fig. 2.

Species affinis *P. involutae* et *P. vespilloneae*; differt dissimilis propter colores non splendidos; superficies superior brunnea praeter marginem; hymenium primum album, fit alutaceum deinde brunneum. Insignia microscopica simillima, tamen hyphae skeletales servant lumen satis latum et pilis faciei sterilis est brunnescens paries. Lignicola, in Africa crescit.

Attaché par un point, flabelliforme à subinfundibuliforme à marge souvent lobée, sessile ou à très court stipe aplati. Face stérile blanchâtre à la marge, gris rosâtre (5 YR 8/1-2) sur 0,5 à 1 mm, puis velouté tomenteux, obscurément zoné car de teinte assez uniforme, brun tabac, ombre (5 YR 4/5, 5/4, ou fawn R.), plus sombre au pied, chocolat (5 YR 3/3). Hyménium sublisse blanchâtre sur le jeune, beige rosâtre (7,5 YR 7/2 à 6/2) puis bistre pâle (5/2), il peut ensuite brunir (5 YR 5/4, fawn R., à 3/4 près du stipe).

En herbier, l'hyménium va de blanc pruineux à écru (10 YR 8/3), puis alutacé (8/4), beige (7/3), brun fuligineux (7,5 YR 5/2), atteignant parfois brun grisâtre pruineux (5 YR 5/1 à benzo brown R.). La face stérile, très caractéristique, étroitement zonée dans les bruns, tabac, ombre (5 YR 5/3, 4/3), avec quelques lignes plus sombres, très contrastantes avec le liseret clair sur 0,5–2 mm à la marge (vers écru 10 YR 8/3, 8/3,5), s'estompant peu à peu avec le temps.

Sur une coupe *l'hyménium est hyalin* tandis que la *croûte est brune* et porte des poils sombres. Le contexte peut aussi se teinter légèrement.

On retrouve ici encore les caractères microscopiques de *P. involuta*. Notons toutefois que si les spores (2,5–3 × 2–2,2 $\mu$), basides, cystides et gloéocystides sont celles des 2 espèces précédentes, les hyphes squelettiques larges de 3–4,8 $\mu$, ont presque

toujours gardé un lumen assez large (par exemple 1 $\mu$ pour une hyphe de 3 $\mu$) même après 30 minutes d'observation dans la potasse (KOH 3 %).

Les poils de la face stérile ont toujours une paroi jaune à brunâtre sous le microscope, un lumen net; les parois bien qu'épaisses s'amincissent généralement vers le sommet.

RÉCOLTES EXAMINÉES.—LY6 698, forêt de la Mondah, km. 17, près Libreville (Gabon) 20 Nov. 1971, leg. G. Gilles, Type; LY 6827, sur petit bois mort en forêt humide, Forêt du Banco près Abidjan (Côte d'Ivoire), 21 Mai 1972, leg. G. Gilles 13; LY 6906, idem, 29 Juin 1972, leg. G. Gilles 85; LY 6920, idem, 8 Juil. 1972, leg. G. Gilles 110.

Il semble possible de rattacher à cette espèce une autre récolte non cultivée: LY 3096, on dead trunk of *Terminalia ivorensis* (Sierra Leone), 2 Avril 1954, leg. F. C. Deighton M 5665 (l'un des 2 spécimens est nettement infundibuliforme).

Quelques autres récoltes de *Podoscypha* africains de ce groupe n'ont pu être placées parmi ces 3 espèces.

Ce sont par exemple: LY 5285, sur tronc de *Croton aubrevillei*, la Maboké(RCA), 30 Avril 1965; LY 3114, Douala (Cameroun), 15 Oct. 1958, leg. P. Berthet 265;

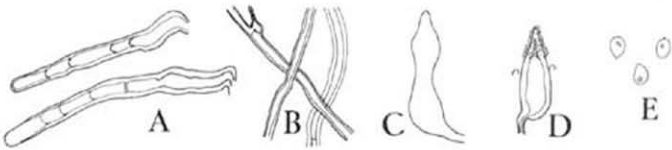


Fig. 2. *Podoscypha gillesii*, A à D, LY 6920 (× 500). — A. Poils bruns. — B. Hyphes squelettiques. — C. Gloeocystides. — D. Cystides. — E. Spores du type LY 6698 (× 1000).

citons encore LY 5373, sur bois, la Maboké (RCA) 10 mai 1965, dont nous possèdons cependant une culture polysperme qui confrontée en phénomène de Buller à *P. involuta* 6503 et 6035, à *P. vespillonea* 5429 et 6501, et à *P. gillesii* 6698, a toujours donné des résultats négatifs.

DISCUSSION.—Macroscopiquement ce champignon se différencie bien de *P. involuta* et *P. vespillonea* par l'absence de couleurs vives allant du jaune au bai. Par ses couleurs brunes de la face stérile et blanche de l'hyménium jeune et de la marge, il évoque parfois certains spécimens de *Laxitextum* du complexe *bicolor*, mais la mollesse des carpophores de ces derniers, leur hyménium qui reste blanc laiteux permettent sur le terrain une différenciation aisée.

*P. gillesii* se rapproche indiscutablement de *P. moselei* (Berk.) Reid, mais les deux remarques de Reid, qui le compare avec raison à *P. involuta* sont que *P. moselei* «have rather long, slender, erect stipes . . . especially when growing on the lower portions of stout sticks» et que «surface tomentum of *P. moselei* is much less evident

than in the vast majority of collections of *P. involuta* . . . *P. moselei* appears pulverulent to the naked eye».

Le type de *P. gillesii*, et les récoltes que nous croyons devoir lui rapporter, sont presque toutes sessiles et avec un tomentum plus grossier en tous cas plus visible que celui de *P. involuta*. Identifier les récoltes africaines à *P. moselei* risque de créer d'inutiles confusions. Il faudra attendre de nouvelles cueillettes fraîches de ce champignon, connu par une seule récolte des Philippines, et attendre de même le résultat de tests d'interfertilités.[2]

La répartition géographique de ces 3 espèces ne peut être à ce jour qu'esquissée, et encore pour une partie de l'Afrique seulement.

*P. involuta* est certain en Afrique: de l'Ile Maurice, de l'Ile de Principe et pour les récoltes en notre possession du Gabon, du Zaïre, de République Centrafricaine, de Nigeria et de la Côte d'Ivoire, c'est à dire de tous les états où des recherches ont été effectuées par nous ou en liaison avec nous depuis 1958, à l'exception du Cameroun.

*P. vespillonea* s'est montré plus abondant dans ces mêmes états, nous l'avions seul récolté lors de notre séjour en RCA de Mai-Juin 1965, comme P. Berthet au Cameroun en 1958–59.

Tous deux ont donc, à notre connaissance, une répartition similaire le second apparaissant plus fréquent.

*P. gillesii*, beaucoup plus rare, semble-t-il, n'est à citer aujourd'hui avec certitude que du Gabon et de Côte d'Ivoire; nous y rapportons une récolte plus ancienne du Sierra Leone. Ni nos récoltes de 1965 et 67 en RCA, ni la collection des spécimens congolais accumulés dans l'herbier de Bruxelles ne comportent de *Podoscypha gillesii*. L'aire de répartition de ces derniers semble donc à ce jour moins méridionale: absence au Zaïre mais celà reste bien sûr à prouver.

## Étude des Myceliums

Sous le nom de *P. involuta*, nous avons décrit en 1966 les caractères culturaux et de polarité du LY 5429, qui est en fait *P. vespillonea*. Comme pour les carpophores, les caractères microscopiques sont de faible utilité pour la distinction des 3 espèces, par contre les couleurs des mycéliums jeunes sont caractéristiques: cf. Tableau I.

### P. INVOLUTA (LY 6035, LY 6074, LY 6503)

*Croissance*: extrêmement lente (R. atteint au maximum 45 mm à 6 semaines).

*Aspect*: marge blanche peu régulière, appliquée ou submergée sur quelques mm, puis mycélium aérien uniformément feutré, coloré, dès la 1ère semained 'ocre pâle

[2] Le specimen type de *P. moselei* ne nous ayant pas été communiqué, nous avons eu recours à l'amabilité de D. A. REID qui nous écrit au sujet de LY 6827 (in litt. 7 Nov. 72) «I do not think it can be referred to *P. moselei*, which has rather different appearance, especially as when stipitate the stipes are relatively long and gracile».

TABLEAU I

**Principaux caractères distinctifs**

| | *P. involuta* | *P. vespillonea* | *P. gillesii* |
|---|---|---|---|
| Hyménium | couleurs vives, jaune devient orangé, fauve puis bai. | jaune chamois clair puis brunissant | blanc puis beige rosé puis brunissant jamais de teintes vives |
| Face stérile | alutacé clair à ombre vers le pied | tend à brunir par tâches | brun tabac avec marge pâle |
| Chair | pâle, croûte jaunâtre | pâle puis se teinte avec l'âge notamment les hyphes squelettiques, les cystides profondes | croûte brune portant des poils à paroi de suite teintée |
| Culture jeune | orangée | jaune soufre | blanche |
| Croissance | extrêmement lente | lente | très lente |
| Microscopie des cultures | éléments renflés à paroi très épaisse | non | non |
| | non | non | hypes formant puzzle |

(10 YR 8/7 à 8/8); à 6 semaines, le mycélium aérien toujours blanc à la marge, se teinte sur quelques mm d'alutacé (2,5 Y 8/4), puis d'ocre (10 YR 8/10), ensuite il forme une peau très coriace, orange (7,5 YR 7/14), avec plages plus rouges (2,5 YR 7/10, atteignant 2,5 YR 6/16).

*Microscopie*: ne diffère de celle de *P. vespillonea* (cf. Boidin, 1966b) que par la présence d'éléments irréguliers, renflés, parfois ramifiés, à paroi très épaisse de 1 à 3 $\mu$ (cf. fig. 1).

Nous résumerons les caractères culturaux selon le code de Nobles, 1965 modifié (cf. Boidin, 1966 a).

*Code*: 2 — 3c — 8 — 13 — 15 — 32 — 36 — 38 — 47 — 54 — 58 — 61.

P. VESPILLONEA (LY 5429, LY 6501, LY 6511, LY 6733)

*Croissance*: lente (la culture remplit la boite à la 5e semaine).

*Aspect*: marge appliquée; le mycélium aérien est parfois localement aranéeux, cachant mal le milieu, mais le plus souvent cotonneux dense, subfeutré, de surface irrégulière, grumeleuse dans lap artie âgée. Le jeune mycélium aérien, blanc, se teinte rapidement de jaune pâle (7,5 Y 9,25/2 à 9,25/4). Apparaissent ensuite de grandes

plages subfeutrées crème (5Y 8,5/4) avec quelques petites touches plus vives,chamois pâle (2,5 Y 9,25/4 à 9/8), dans la partie âgée. Vers la bouture, il atteint parfois ocre pâle (10 YR 8/8), ou isabelle saumon (7,5 YR 7,5/4).

*Code*: 2 — 3c — 8 — 15 — 32 — 36 — 38 — 45 — 54 — 60 — 61.

P. GILLESII (LY 6698 - 6906 - 6920)

*Croissance*: très lente (rayon entre 45 et 90 mm en 6 semaines).

*Aspect*: marge régulière, courtement appliquée, puis mycélium duveteux, peu élevé, *blanc pur* devenant rapidement feutré, dense, de surface irrégulièrement élevée, toujours blanc pur. A 6 semaines, une culture sur 3 présente quelques petites plages saumon très pâle (5 YR 7/3). Cette teinte apparaît dans toutes les cultures plus gées, laissées à la lumière du jour.

*Microscopie*: ne diffère de celle de *P. vespillonea* que par la présence d'une croûte blanche formée d'hyphes à paroi très épaisse, fortement imbriquées et soudées comme dans un puzzle.

*Polarité*: La tétrapolarité de *P. gillesii* a été déterminée à partir de LY 6698.

$A_1$ $B_1$: 1 — 2 — 5
$A_1$ $B_2$: 6 — 9
$A_2$ $B_2$: 7 — 10
$A_2$ $B_1$: 3 — 4 — 8

Des fausses boucles et des crochets en série sont observés dans quelques confrontations $A_1$ $B_1$ x $A_2$ $B_1$ et $A_1B_2$ x $A_2$ $B_2$

*Code*: 2 — 3c — 8 — 11 — 15 — 32 — 36 — 38 — 47 — 54 — 60 — 61.

## Interfertilités

Des cultures ont été obtenues à partir d'un certain nombre de récoltes. Les résultats des croisements sont consignés dans le tableau II.

Dans ce tableau les signes + ou — indiquent un résultat obtenu sur un nombre de confrontations allant de 6 à 12 pour chaque type de croisement. Les croisements ont été effectués entre haplontes sauf pour LY 6511 et LY 6074. Pour ces récoltes, ne disposant que d'une culture polysperme, nous avons fait appel au phénomène de Buller (cf. Tableau II). La parfaite cohérence des résultats prouve une fois encore le grand intérêt pratique de ces confrontations et souligne l'apport capital que les cultures mono- et polyspermes fournissent au systématicien moderne.

## Résumé

At least three intersterile species have usually been confused in intertropical Africa under the name of *P. involuta*: *P. involuta* (Klotzsch apud. Fr.) Imazeki, *P. vespillonea* (Berk.) nov. comb. and *P. gillesii* nov. sp.

TABLEAU II

**Interfertilités**

| | | *P. vespillonea* | | | | | | *P. involuta* | | | *P. gillesii* | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 5429 | 5557 | 6501 | 6511 | 6733 | 6854 | 6074 | 6035 | 6503 | 6698 | 6827 | 6906 | 6920 |
| *P. vespillonea* | 5429 | | + | + | | + | + | — | — | — | — | — | — | — |
| | 5557 | + | | + | | | + | | — | | — | | — | |
| | 6501 | + | + | | + | + | + | — | — | — | — | — | — | — |
| | 6511 | | | + | | | | | — | — | | | — | — |
| | 6733 | + | | + | | | + | | | — | | — | — | — |
| | 6854 | + | + | + | | + | | | — | — | | — | — | — |
| *P. involuta* | 6074 | — | | — | | | | | + | + | — | | | — |
| | 6035 | — | — | — | — | | — | + | | + | — | — | — | — |
| | 6503 | — | | — | — | — | — | + | + | | — | — | — | — |
| *P. gillesii* | 6698 | — | — | — | | | | — | — | — | | + | + | + |
| | 6827 | — | | — | | — | — | | — | — | + | | + | + |
| | 6906 | — | — | — | — | — | — | | — | — | + | + | | + |
| | 6920 | — | | — | — | — | — | — | — | — | + | + | + | |

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# DEFINITION AND TYPIFICATION OF THE GENUS LYCOPERDON TOURN. PER PERS. (GASTEROMYCETES)

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An account of the history of the variations in delimitation of the genus *Lycoperdon* is presented and the typification of the genus is discussed. It is pointed out that in application of art. 43 of the Code of nomenclature no Myxomycete has been validly published as *Lycoperdon* between 1753 and 1801.

The genus *Lycoperdon* was introduced by Tournefort (1700 : 563) and the name was used during the eighteenth century to refer to the more or less globose fungi with a pulverulent content.This concept allowed the inclusion of most Gasteromycetes and also of Myxomycetes, Pyrenomycetes, Tuberales, Elaphomycetales, Uredinales as one may for example find by Linnaeus (1753: 1183–1185). As long as the genus is considered to belong to the Gasteromycetes its valid publication is to be found in Persoon's Synopsis Fungorum (1801 : 140). Persoon's diagnosis is rather elliptic: "*Peridium* caulescens, apice demum ruptum, verrucis squamulosis, aut spinulosis obsitum. (*Pulvis semimalis viridis*)" However the enumeration of included species (*L. giganteum*, *L. bovista*, *L. pratense*, *L. utriforme*, *L. mammaeforme*, *L. excipuliforme*, *L. perlatum*, *L. candidum*, *L. echinatum*, *L. umbrinum*, *L. quercinum*, *L. pyriforme*, *L. gossypinum*) shows a concept of the genus somewhat wider than the one in current use but very natural, including only Gasteromycetes that are still retained in the same family Lycoperdaceae.

Some radically conservative authors still used the genus *Lycoperdon* in a very wide sense during the first quarter of the nineteenth century. Some of them like Poiret (1808) even recombined in *Lycoperdon* species described by Persoon in *Scleroderma* or *Geastrum*. For example Poiret (1808 : 588) combined *Scleroderma spadiceum* Schaeff. trans Pers. in the genus *Lycoperdon* with the unfortunate consequence that it turned *Lycoperdon spadiceum* Pers. (1809 : 20) into a later homonym. So this classical name must be replaced by the contemporary but little used *L. lividum* Pers. (1809:18).

With the Friesian era however Persoon's concept of the genus was definitively admitted and a tendency appeared even to restrict it further. Rostkovius (1839) was the first to emend *Lycoperdon* by excluding species whose opening is irregular and not through a pore. This conception was generally accepted after the paper of Morgan (1890), who brought in common use Fries's (1849 : 442) little noticed genus

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*Calvatia*. This genus is to be conserved against *Langermannia* of Rostkovius (Stafleu & al., 1972 : 254); though the type species are widely different, the genus *Langermannia* is frequently used by authors subdividing *Calvatia* (cf. Kreisel, 1962).

Quélet (1873) abandoned previous genera *Lycoperdon* and *Bovista* and created instead *Utraria* and *Globaria*, two fully superfluous names that would have had no consequences had not *Globaria* been adopted by Schroeter (1889) and Fisher (1900) in an emended sense to refer to species with a poorly developed subgleba but without the *Bovista* type capillitium. The exclusion of those species from *Lycoperdon* was taken up again by Kreisel (1964, 1967) who treated them as the subgenus *Globaria* of *Bovista*. The name *Globaria* cannot be used at the generic rank for either is it attributed to Quélet and illegitimate because it is superfluous (Art. 63) or it is attributed to Schroeter and then illegitimate because it is homonymous (Art. 64). However as a subgenus of *Bovista* it can certainly be used but its paternity must then be given to Kreisel (Art. 72, note).

Lloyd (1906) made an attempt to exclude from *Lycoperdon* all species with pedicellate spores, but he was never followed.

The latest emendation of *Lycoperdon* comes from the exclusion of species devoid of capillitium with the creation of the genera *Vascellum* by Šmarda (1958) and *Morganella* by Kreisel & Dring (1967).

The actual concept of the genus can be considered the one developed by Kreisel in his study of Lycoperdaceae culminating in his monograph of *Bovista* of 1967. According to that concept *Lycoperdon* should contain species with an endoperidium opening by a pore, having a subgleba with large cells, a pseudocolumella and a capillitium, the latter not of the *Bovista* type. So defined the genus is fairly homogeneous and, with the exception of a few species like *L. rimulatum* Peck, whose capillitium does not exactly fit the usual type, easy to separate from neighbouring taxa. However as Malençon (1969) already noted, by transferring the borderline between *Lycoperdon* and *Bovista* this conception makes the genus *Bovista* less homogeneous. Personally I also consider that the subgleba character used to separate *Bovista* from *Lycoperdon* is of little taxonomic weight. Similarly the character of breaking up of the endoperidium, diagnostic of *Calvatia*, does not appear to me a good one in a natural classification. I believe that an analysis of Lycoperdaceae based on various characters and taking into account the world flora would lead us to significant remodelling of our generic concept. It is probable then that we would have to follow Smith (1968) and use again larger genera. For the present, however, I consider that Kreisel's conceptions of genera offer the best possible framework for studying Lycoperdaceae and I think that only after all those genera are adequately monographed can their limits be discussed again.

## Typification of the genus

*Lycoperdon perlatum* Pers. per Pers. is currently considered the type of the genus *Lycoperdon*. This tradition seems to go back to Cunningham (1942) or in some way

to Clements & Shear (1931) who cite the devalidated synonym *L. gemmatum* Batsch.

This typification should be accepted following Art. 8 (first choice of a lectotype), Recommendation 7 B (preservation of current use) and Guide for the determination of types § 4 C (respect of segregations).

A possible reason to oppose the designation of *L. perlatum* as type is to admit that since the genus *Lycoperdon* included Myxomycetes for eighteenth century authors, it was validly published by Linnaeus in 1753 since this is the starting point for the nomenclature of Myxomycetes (Art. 13) and so that it must be typified according to Linnaeus' conceptions.

This hypothesis is self destructive. Linnaeus' diagnosis published in the Genera Plantarum, ed. 5 : 493. 1754 (cf. Art. 13, Note 1) runs as follows:

1082. Lycoperdon. **Tournef.* 331. *Mich.* 97. *Vaill.* B.P. XVI: 4–10. *Bovista* Dill. *Lycoperdoides* Mich. 98. *Lycoperdastrum* Mich. 99. *Geaster* Mich. 100. *Carpobolus* Mich 101.
Fungus subrotundus, Seminibus farinaceus impalpabilibus repletus, ab apice dehiscens.

This is of course vague but the reference to Tournefort is explicit and is only made to Plate 331 which only represents Gasteromycetes. Genera cited as synonyms are also Gasteromycetes. As a matter of fact it seems that to pre-linnean authors, *Lycoperdon* is the scientific name for puff-balls and that Myxomycetes, mainly *Lycogala epidendrum*, are only accessorily added. Linnaeus was probably the first to enlarge considerably the genus with his section "Parasitica in farinam fatiscentia." It does not appear he intented to treat this section as essential for the definition of the genus. Fries summarises well this situation (1829 : 28): "Genus Lycoperdon (h.e. *Crepitus Lupi* Patrum) constituit Tournefort, optime limitavit Micheli dein latissime fluctuans, praesente angusto, nimis fere angusto, constrixit Persoon."

If the genus *Lycoperdon* of Linnaeus is to be typified it seems that following already mentioned principles (Rec. 7 B, Guide for the determination of types) as well as according to the attention one should obviously give to the concepts of Tournefort and other authors to whom Linnaeus refers, the type must be *L. bovista* L. This species practically encompasses the whole family Lycoperdaceae. Consequently the genus *Lycoperdon* is a genus of Gasteromycetes and cannot have been validly published before Persoon.

An apparently unnoticed consequence of this is that Myxomycetes published in the genus *Lycoperdon* between 1753 and 1801 are not validly published (Art. 43). I leave it to specialists of Myxomycetes to work out the nomenclatural consequences of this which affect at least some twenty names listed in Martin & Alexopoulos (1969).

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# PORIA ELONGATA OVERH. IN POLAND

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(With six Text-figures)

A description is given of *Poria elongata* based on fruitbodies found in Poland. The new combination *Perenniporia elongata* is proposed for this species and its relationships are extensively discussed.

Until recently the saprobic polyporaceous fungus *Poria elongata* Overh. was known only from the United States (Michigan, New York, and Pennsylvania), where it occurs on wood of angiosperms, causing a white rot (Lowe, 1966: 121).

In Poland a number of fruitbodies were found on a fallen log of *Fagus silvatica*, covering a rather extensive surface of the wood, which showed symptoms of white rot.

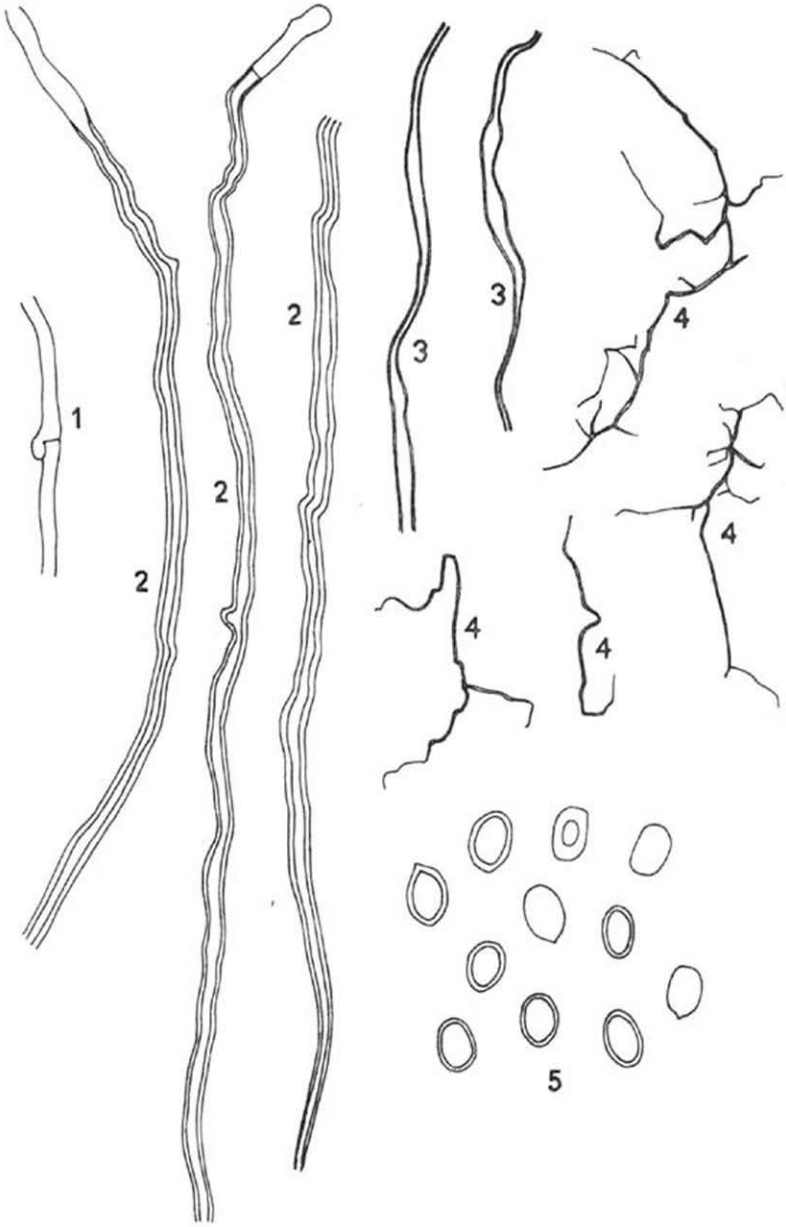
The present paper deals with the results of my studies on this fungus carried out mainly with the view to establish its possible relationships. For this purpose the following material was examined: —

Poland: Carpathian Mountains, distr. Ustrzyki Dolne, Zatwarnica, on *Fagus silvatica*, Aug. 1965, S. Domanski (HMIPC 4820).

USA: New York, White Lake near Jamesville, on *Acer* (?), 27 Sept. 1951, J. L. Lowe (SYRF 5208).

The description given below was drawn up from the Polish material; microscopic observations, measurements, and drawings were made from sections mounted in Melzer's reagent.

Fruitbody annual, effused, at first more or less circular, 2–3 cm in diameter, 0.2–0.3 cm thick, white with shallow tubes, subsequently confluent with adjoining fruitbodies to form large, flat-pulvinate, resupinate patches up to 30 cm in diameter and up to 0.5–1 cm thick, soft-fibrous, firmly attached to the substratum, white, with fimbriate-fibrous, 0.1–0.3 cm wide, sterile, white margin. When dry and old the colour of the fruitbody turns cream or wood-colour or somewhat yellowish-brown, the margin often a brownish-red, soft leathery, up to several cm wide, sterile. Context thin, up to 0.1–0.3 cm thick, white, soft-fibrous, becoming wood-colour and somewhat tough with age and when dry, taste mild. Tubes of the same colour and consistency as the context, 1-layered, 0.2–0.7 cm long, the dissepiments thin, with entire edges, finally becoming fimbriate. Pores small, rather regular, circular to angular, 3–4(–5) per mm. Hyphal system trimitic. Generative hyphae hyaline, thin- to somewhat thick-walled, nodose-septate, branched, 3–5 $\mu$ in diameter, sparse, comparatively most numerous in the marginal area. Skeletal hyphae slightly to rather thick-walled (with thin-walled apical portions in the edge of the dissepiments), of equal diameter or gradually tapering towards the base or, often




Figs. 1–5. *Poria elongata* Overh. — 1. Generative hypha. — 2. Skeletal hyphae from dissepiment. — 3. Skeletal hyphae fairly numerous in the context. — 4. Binding hyphae from context. — 5. Spores. (Figs 1–4, × 800; Fig. 5, × 1600.)

mainly in the context, irregularly and repeatedly contracted, 1.5–5 $\mu$ in diameter, rarely branched, often flexuous, non-septate or rarely septate, without clamps, acyanophilous, dextrinoid in the subhymenium, slightly amyloid both in the dissepiments and the context, quickly dissolved in KOH solution. Skeletal hyphae making up the bulk of both the context and the dissepiments, interwoven in the former, predominantly parallel in the latter. Binding hyphae scarce, relatively more numerous in the context, slightly thick-walled to thick-walled, non-septate, strongly twisted and intricately branched, 1–3 $\mu$ in diameter. Hymenium composed of cystidia and basidia. Cystidia not numerous, usually variable, slightly projecting or mostly immersed, thin-walled, subulate to clavate, sometimes with a bulbous base, 15–17.5 × 5–7 $\mu$. Basidia broadly clavate, 10–12(–15) × 6–8 $\mu$, with 4 sterigmata. Spores ellipsoid to broadly ellipsoid, sometimes as if indistinctly truncate at one end, 4–5.5 × 3–3.5 $\mu$, thin-walled, rarely with thickened cell-walls which are hyaline, smooth, cyanophilous, slightly dextrinoid, inamyloid.

In trying to determine whether the present species is related to one of the 'natural' groups of polyporaceous fungi thus far known, I paid attention to four elements generally considered to be an index of the rank of evolution or of the relationship of polypores, at least of those associated with rot in wood: (i) the type of rot since this may indicate the rate of physiological evolution in a wood-rotter (Nobles, 1958: 888; 1965: 1103); (ii) the shape of the fruitbody since this shows the rate of the external evolution in this important organ (Kreisel, 1967); (iii) the hyphal construction which to a high degree determines the characteristics of context and dissepiment trama; and finally (iv) the composition of the hymenium and the features of its elements.

Considering the data enumerated above, the possible relationships of *P. elongata* have to be looked for among the polypores, which (i) cause white rot in wood, showing them to be physiologically more advanced, (ii) produce resupinate fruitbodies, and (iii) have a trimitic hyphal system consisting of hyaline hyphae, with nodose-septate generative hyphae. Thus far only eight species of polypores are known to answer this set of characters, seven of which are 'resupinate' and one 'effused-reflexed' with tendency to form resupinate portions. These are: —

I. *Pachykytospora tuberculosa* (DC. ex. Fr.) Kotl. & Pouz., *Poria alabamae* (Berk. & Cooke) Cooke, and *Poria papyracea* (Schw.) Cooke. The first is the type species of the natural monotypic genus *Pachykytospora* Kotl. & Pouz.; the other two species, although probably related to this genus, are as yet retained in the artificial genus *Poria* Pers. ex S. F. Gray. All three species differ sharply from *P. elongata* in their peculiar spores which are characterized by oblong-cylindric shape, large dimensions (7–17 $\mu$ long) and, often, the possession of echinulae. Moreover, as pointed out by Kotlaba & Pouzar (1963: 27), the walls of the spores of *P. tuberculosa* are not only cyanophilous, but also double and of a specific structure.

II. *Leptotrimitus semipileatus* (Peck) Pouzar, the type species of the monotypic genus *Leptotrimitus* Pouzar, is the fourth species to be discussed. Its fruitbody is effuso-reflexed, more rarely resupinate, and its context is trimitic. Notwithstanding

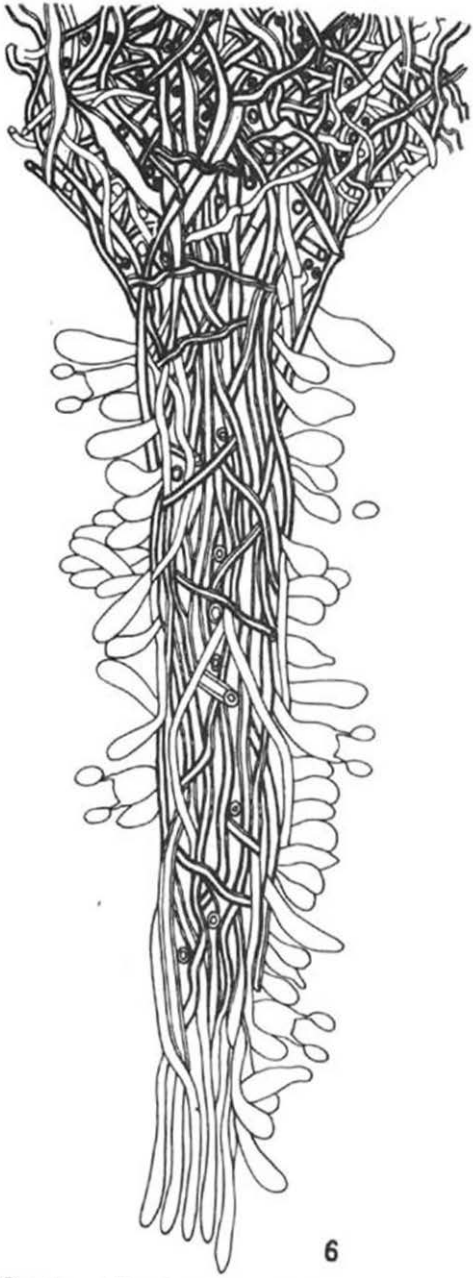



Fig. 6. *Poria elongata* Overh. — Dissepiment in vertical section, from Polish collection (× 800).

this, the species was recently transferred by Donk (1971: 39) to *Incrustoporia* Domanski, a genus of resupinate species with dimitic context. The arguments for this transfer were found in a set of characters that connect *L. semipileatus* with *Incrustoporia*, such as the composition of the hymenium, the very small, allantoid spores which are neither cyanophilous nor dextrinoid, the incrusted hyphal ends at the edge of the dissepiments (an important feature by which the species can be distinguished from *P. elongata*), and the cultural behaviour of the mycelium. These characters have so much weight that I am inclined to agree with Donk's point of view in regarding, in this case, the trimitic hyphal structure of *L. semipileatus* as a feature of infrageneric importance. It is necessary, however, to emphasize the structural difference between the hyphal systems within the genus *Incrustoporia* Domanski em. Donk (1971: 37) by introducing the following two subgenera:—

1. Subgenus *Incrustoporia*, comprising such 'resupinate' species with dimitic context like *I. stellae* (Pilát ex Pilát) Domanski, *I. tschulymica* (Pilát) Domanski, *I. subincarnata* (Peck) Domanski, and *I. alutacea* (Lowe) Reid.

2. Subgenus **Leptotrimitus** (Pouzar) Domanski, *comb. nov.* (basionym, *Leptotrimitus* Pouzar *in* Česká Mykol. **20**: 175. 1966) with the 'effused-reflexed' species *I. semipileata* (Peck) Donk whose context is trimitic.

III. Of the artificial genus *Poria* the two species *P. linearis* Murrill and *P. cinerascens* (Bres.) Sacc. & Syd. require a discussion.

*Poria linearis* I find difficult to regard as closely related to *P. elongata* because the former has oblong-cylindric spores and a hyphal system, in which the binding hyphae are abundant and the skeletals more sparsely represented.

On the other hand *Poria cinerascens* seems to be more closely related to *P. elongata* even in spite of its spores being narrow, allantoid, and neither cyanophilous nor dextrinoid. It is not only that the two species, *P. cinerascens* and *P. elongata*, do not differ in the structure and number of skeletal hyphae in context and dissepiment trama, but more in particular do they resemble each other in having in common skeletals that dissolve quickly in a KOH solution. In most specimens of *P. cinerascens*, moreover, e.g. those from the Bialowieza virgin forest in Poland, the walls of these skeletals are slightly amyloid like those in *P. elongata*. Their amyloidity, however, is hard to see in individual skeletals and best observed where these hyphae form compact masses, e.g. in longitudinal sections of dissepiments.

IV. *Perenniporia medulla-panis* (Jacq. ex Fr.) Donk is the type species of the natural genus *Perenniporia* Murrill. The generic name has recently been reintroduced by Donk (1967: 74) to replace *Poria* Pers. ex S. F. Gray. In order to avoid further taxonomic complications, Donk rightly suggested (1960: 269 and 1967: 51) that the name *Poria*, although a valid name for a natural group of polypores, be retained for the artificial (residual) genus, in which a large number (more than one hundred) of miscellaneous species of resupinate polypores must find a place as long as their natural classification is being elaborated.

In this genus *Perenniporia* Donk also included *P. subacida* (Peck) Donk, a species to

which *Poria elongata* shows great affinity. This is apparent above all from the composition of the hymenium and certain features of its elements: (i) the spores are broadly ellipsoid, sometimes slightly truncate, especially in the Polish material, fairly thick-walled, and cyanophilous as well as dextrinoid; (ii) the cystidia are small, thin-walled, subulate to clavate, and thus far only in the Polish material seen to project somewhat beyond the basidia; (iii) the basidia are broadly clavate to subovate. Moreover, the hyphal structure of the fruitbody in both species is very similar: the skeletal hyphae with somewhat thickened to fairly thick walls are by far the dominant type, whereas the generative and binding hyphae are very rare and similarly shaped (cf. Domanski, 1964: fig. 2). Lowe (1966: 120) described *Poria elongata* as dimitic, and it is certainly true that the binding hyphae in the American specimen examined were exceedingly difficult to find.

Taking together the data mentioned above, *Poria elongata* appears to be a species with features partly intermediate between those of *Poria cinerascens* and *Perenniporia subacida*, but with a distinctly more pronounced affinity with the latter. This affinity is expressed in the removal of the species from the artificial genus *Poria* and the proposal of the recombination **Perenniporia elongata** (Overh.) Domanski, *comb. nov.* (basionym, *Poria elongata* Overh. *in* Techn. Bull. Pa. agric. Exp. Stn **418**: 28. 1942).

*Perenniporia elongata* differs from both *P. medulla-panis* and *P. subacida* particularly in (i) having skeletals whose slightly amyloid walls dissolve quickly in a KOH solution, and (ii) producing annual fruitbodies.

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# PHIALIDES WITH SOLITARY CONIDIA?

## Remarks on condium ontogeny in some hyphomycetes

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(With six Text-figures)

Conidium formation in some species of *Aphanocladium* W. Gams, *Verticimonosporium* Matsushima, *Sibirina* Arnold, *Pseudofusarium* Matsushima and *Craspedodidymum* Hol.-Jech. is discussed and compared with other examples. Conidiogenous cells with solitary and with serial conidia may occur in apparently closely related species. It is questionable, whether the term phialides has to be restricted to the latter group.

The new species *Aphanocladium spectabile* and *Sibirina orthospora* are described.

Conidium ontogeny is becoming the dominating criterium in the taxonomy of hyphomycetes. One of the most common propagative structures is the phialide, which since Hughes (1951 and 1953) and more explicitly in Kendrick (1971) is defined as a 'cell producing from a fixed locus a basipetal succession of conidia whose walls arise de novo'. In the introduction to the monograph of *Cephalosporium*-like hyphomycetes (Gams, 1971a) several morphological types of phialides were distinguished according to the insertion in the subtending hyphae and designated with the nouns orthophialide, plagiophialide, schizophialide, etc. Although an adjectivic terminology is now preferable (Kendrick, 1971), the distinctions introduced have proved their usefulness.

The term phialide was introduced in a rather vague circumscription by Vuillemin (1910) to include also fungi with solitary conidia, such as *Beauveria* (cf. Mason, 1933). Whereas this type of conidium formation is now considered as holoblastic, some other fungi exist whose conidiogenous cells very strongly resemble phialides but produce only solitary conidia; they will be discussed in this contribution.

### A. Aphanocladium W. Gams

The genus *Aphanocladium* (Gams, 1971a) was defined as having phialoconidia borne on either fully differentiated swollen phialides or on reduced narrow thread-like outgrowths ('aphanophialides') in heads or in chains. Further examination of numerous strains has, however, shown that in the type species *A. album* (Preuss) W. Gams conidia are always solitary; head-like agglomerations can arise when the conidia from neighbouring denticles contact one another. In this respect the generic diagnosis has to be corrected.

A similar and much more pronounced example of solitary conidia borne on phialide-like conidiogenous cells is found in the strain CBS 340.70, obtained from Mme J. Nicot, Paris, as 'Charpin 2' and originating from the atmosphere in Marseille; it will be described as a new species of *Aphanocladium*. The species with catenate conidia hitherto included in this genus will have to be accommodated in a new genus.

**Aphanocladium spectabile** W. Gams, *spec. nov.*—Fig. 1

Coloniae fere celeriter crescunt, ad 35 mm diametro post 10 dies, albae vel pallide roseae, floccosae-lanosae et conidiis pulverulentae; hyphae vegetativae 1.5–1.8 $\mu$ crassae, hyalinae, leves, saepe fasciculatae. Cellulae conidiogenae e hyphis aeriis singulae vel 3–5 verticillatae fere rectangulariter oriuntur, 9–11 $\mu$ longae, e basi 2.0–2.8 $\mu$ crassa sursum ad 0.5–0.8 $\mu$ attenuatae; nonnumquam proliferunt; raro conidiophora lateralia composita adsunt. Conidia semper singula, ellipsoidea, basi modice apiculata, hyalina, fere crassitunicata, levia, 7.2–9.2 × 2.9–3.3 $\mu$. Chlamydosporae absunt.

TYPUS CBS 340.70, isolatus ex aere, Massiliae in Gallia.

Colonies on 2 % malt extract agar (and other media) spreading rather rapidly, attaining at room temperature a diameter of 30–35 mm within 10 days; white to very pale pink, deeply floccose-lanose and powdery from abundant conidia; margin lobulate, reverse pinkish. Hyphae of the aerial mycelium 1.5–1.8 $\mu$ wide, hyaline, smooth-walled. Hyphae bearing phialides nematogenous or plectonematogenous;

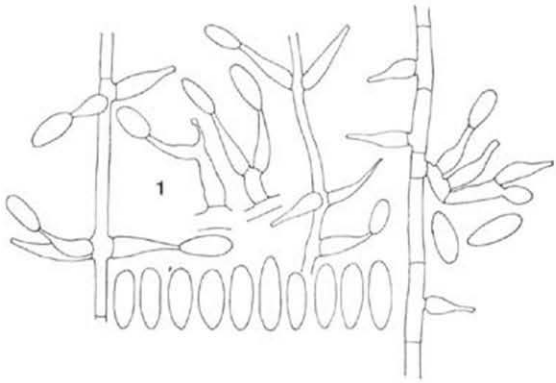


Fig. 1. *Aphanocladium spectabile*, from colony on malt-extract-agar (1000 : 1).

conidiogenous cells solitary or usually 3–5 in whorls, arising at almost right angles from the supporting hyphae, 9–11 $\mu$ long, tapering from a swollen, 2.0–2.8 $\mu$ wide base sigmoidally towards a narrow tip, 0.5–0.8 $\mu$ wide. Sometimes a proliferation occurs below the tip; rarely short lateral compound conidiophores are formed. Conidia always solitary, deciduous, ellipsoidal with slightly apiculate base, hyaline, rather thick-walled, smooth, 7.2–9.2 × 2.9–3.3 $\mu$, length/width ratio 2.4–3.0. Chlamydospores not observed.

Although the conidiogenous cells are never reduced to conidium-bearing necks, this species is placed in *Aphanocladium* rather than in *Verticimonosporium* because of its spreading growth habit.

### B. Verticimonosporium Matsushima

The genus *Verticimonosporium* is characterized by Matsushima (1971) as having verticillate conidiogenous cells (not phialides) with solitary conidia. The type strain of *V. diffractum* Matsushima (CBS 310.72) kindly supplied by T. Matsushima does not show much affinity with *Aphanocladium*. The growth is more restricted with a diameter less than 5 mm after 7 days; sporulation is rather scanty; conidiogenous cells are always fully differentiated and separated from the supporting hypha by a septum. The genus therefore is considered as sufficiently distinct; its affinities are not yet known.

### C. Sibirina Arnold

Arnold (1970) described the genus *Sibirina* with the type species *S. fungicola* Arnold (Fig. 2) explicitly as producing conidia in slimy heads. Examinition of the type strain (CBS 458.71) and another isolate (CBS 821.70) collected on *Polyporus varius* Pers. ex Fr. near Abisko, Swedish Lappland, showed that conidia are strictly solitary; for each new conidium a new phialide is successively formed, leading eventually to extraordinarily dense verticils. By contact of neighbouring phialides, conidia may appear as if formed in heads. The phialides are 1.0–1.3 $\mu$ wide at the tip and almost imperceptably plugged with wall material. The conidia are two-celled, slightly curved and typically show a wall-thickening at the base and sometimes also at the tip. The smell is reminiscent of some agarics.

Another somewhat different strain, CBS 145.71, isolated by J. A. Stalpers from decaying wood at Schovenhorst near Putten, shows great similarity to *S. fungicola*, but has phialides with more than one conidium. Nevertheless, since no other appropriate genus and species name is available, it is described as a new species of *Sibirina*.

**Sibirina orthospora** W. Gams, *spec. nov.*—Fig. 3

Coloniae celeriter crescunt, ad 45 mm diam. post 5 dies, albidae, laxe floccosae-lanosae; conidiophora erecta e hyphis aeriis oriuntur. Hyphae aeriae hyalinae, leves, 2–3.5 $\mu$ crassae; conidiophora ad 400 $\mu$ alta, deorsum 4–4.5 $\mu$ crassa, sursum repetite verticillata, praecipue in ultimo verticillo ad 10 phialides ferunt. Phialides 20–26 $\mu$ longae, e 2.0–2.5 $\mu$ gradatim ad 0.7–1.0 $\mu$ attenuatae, conidia singula, rarius bina vel terna ferunt. Conidia cylindrica, recta, bicellularia, apice rotundata, basi fere apiculata, truncata, levia, hyalina, 16–21 × 4.0–6.0 $\mu$. Chlamydosporae absunt.

TYPUS CBS 145.71, isolatus e ligno putrido, Putten.

Colonies spreading rapidly, on 2 % malt extract agar reaching a diameter of 45 mm within 5 days, whitish, loosely floccose-cottony. Odour absent. Moderately sporulating on erect conidiophores which arise from aerial hyphae. Aerial hyphae hyaline, 2–3.5 $\mu$ wide, smooth-walled. Conidiophores up to 400 $\mu$ high, 4–4.5 $\mu$


Fig. 2. *Sibirina fungicola*, CBS 821.70, conidiophores and conidia (Left 500 : 1, right 1000 : 1).
Fig. 3. *Sibirina orthospora*, conidiophores and conidia (1000 : 1).

wide at the base, in the upper part repeatedly verticillately branched, especially in the uppermost whorl bearing up to 10 phialides. Phialides 20–26 $\mu$ long, gradually tapering from 2.0–2.5 $\mu$ towards 0.7–1.0 $\mu$ at the tip, bearing usually one, rarely 2 or 3 conidia. Conidia cylindrical, straight, two-celled, with rounded tip and slightly apiculate and truncate base, smooth-walled, hyaline; a very slight wall-thickening may be present only at the basal end; they measure 16–21 × 4.0–6.0 $\mu$. Chlamydospores absent.

*S. orthospora* differs from *S. fungicola* not only by multiple conidium formation, but also by non-pigmented colonies and perfectly straight conidia without apical wall-thickening.

### D. Pseudofusarium Matsushima

Matsushima (1971) defined the genus *Pseudofusarium* as having sympodially elongating, geniculate, denticulate, often proliferating conidiogenous cells and solitary septate conidia. These details would approach the genus to *Dactylaria* as redescribed by Bhatt & Kendrick (1968). The spreading growth habit, however, besides the sometimes sickle-shaped conidia, is sufficient evidence of an affinity with *Fusarium*. In this genus, *F. chlamydosporum* Wollenw. & Reinking has a similar structure with one-celled solitary microconidia borne on proliferating denticulate conidiogenous cells, while macroconidia are procuced at a very late stage serially on true phialides (Seemüller, 1968; Booth, 1971). In related species, such as *F. sporotrichioides* Sherb., similarly proliferating conidiogenous cells produce serial conidia. On the other hand there are strains with septate solitary conidia in which serial conidia have not yet been observed. It is likely that the conidium-bearing denticles in these *Pseudofusarium* species and in *F. chlamydosporum* are homologous to the phialide openings in *F. sporotrichioides*.

### E. Craspedodidymum Hol.-Jech.

The genus *Craspedodidymum* was recently described by Holubová-Jechová (1972). The author regards the conidiogenous cells as phialides although they bear only solitary conidia. While releasing the conidium, the conidiogenous cell forms a cup-shaped collarette; after a subapical swelling the conidiogenous cell is somewhat constricted to 5–6 $\mu$ outer diameter with an internal wall-thickening and subsequently opens with flaring lips up to 12 $\mu$ in diam. The conidium develops endogenously. This may constitute a dematiaceous example of phialides with solitary conidia.

## Discussion

In several cases a relationship between species with phialides producing serial conidia and others with solitary conidia can be demonstrated. In phialidic hyphomycetes so far investigated according to modern criteria the first formed conidium has a wall continuous with that of the conidiogenous cell, while the subsequently

formed conidia obtain a wall de novo. It would be attractive to assume that for some reason subsequent conidium formation has stopped, so that species with solitary conidia may be thought to be descendants from others with serial conidia. A possible mechanism for this interruption may be that the conidiiferous opening is too narrow and becomes blocked immediately; moreover it is a common phenomenon in phialidic fungi that the phialide opening is gradually plugged because with each subsequent conidium some wall material is left behind. In *Sibirina* such a plugging may occur already during the development of the first-formed conidium. This mechanism will require further study of the fine structure.

The relationship of *Aphanocladium* is unknown and it is premature to argue for or against a phialide nature of the conidiogenous cells. A similar genus with true phialides is *Tolypocladium* (Gams, 1971b), whereas holoblastic conidia are formed on geniculate conidiogenous cells in *Beauveria* (de Hoog, 1972). A relationship between these genera cannot theoretically be excluded; entomo-(araneo-)genous species or strains occur in all of them, and the growth pattern is similar. In the myco-

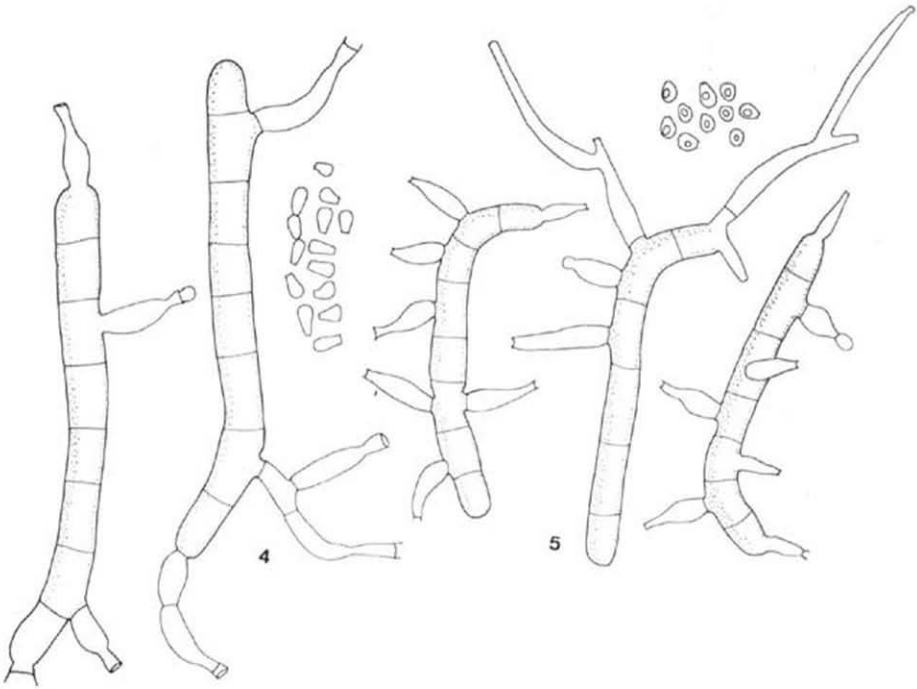


Fig. 4. *Lasiosphaeria hirsuta* and
Fig. 5. *Lasiosphaeria ovina*. Germinating ascospores in fresh collections from the Teutoburger Wald, W.-Germany, 1972 (1000 : 1).

and entomogenous genus *Cordyceps* conidial states of *Verticillium* (Gams, 1971a) and of other phialidic genera are known, while in *Ophiocordyceps clavulata* (Schw.) Petch a conidial state with sympodial conidiogenous cells and solitary (?) conidia has been observed. It was placed by Petch (1933) and Balazy (1971) in *Hirsutella* as *H. lecaniicola* (Jaap) Petch because of the conidiogenous cells with a strongly swollen basal part and slender apical elongations. Mains (1950) accommodated the species in *Hymenostilbe* Petch because of the absence of a slimy sheath on the conidia. The type species of this genus *H. muscaria* Petch, however, has conidiogenous cells of constant width with closely aggregated slightly prominent conidiiferous scars at the tip, and forms blastoconidia. Moreover, Balazy (l.c.) observed a thin slime sheath on the conidia in pure culture. Typical species of *Hirsutella* have non-proliferating phialides with usually more than one conidium. But more information from pure cultures is still lacking.

Another case of closely related species with phialides and with sympodial conidiogenous cells with holoblastic conidium formation has been found in the ascomycete genus *Lasiosphaeria*. In *L. hirsuta* (Fr.) Ces. & de Not. (Hughes, 1951; Fig. 4) and *L. ovina* (Fr.) Ces. & de Not. (Fig. 5) the germinating ascospores form *Phialophora*-like phialides, whereas in *L. spermoides* (Hoffm. ex Fr.) Ces. & de Not. (Fig. 6) the conidiogenous cells proliferate in a densely sympodial manner and each denticle apparently forms only a single conidium.

In this paper two species with solitary and serial phialoconidia have been merged into one genus. On the other hand it seems questionable, whether the species with solitary conidia borne on denticles placed by Deighton & Pirozynski (1972) in the genus *Sympodiophora* Arnold are really congeneric with the type species *S. stereicola* Arnold, the conidial state of *Hypomyces semitranslucens* Arnold; in this species the acrotonously proliferating conidiogenous cells bear star-like clusters of conidia on each opening (cf. Gams & Hoozemans, 1970, under *Cladobotryum* spec.). Some of

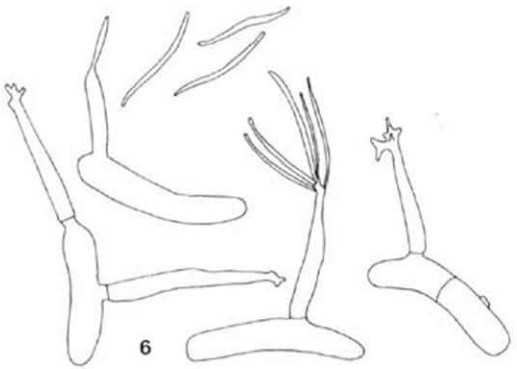


Fig. 6. *Lasiosphaeria spermoides*. Germinating ascospores in fresh collection from Rosenfelder See, Kr. Plön, W.-Germany (1000 : 1).

the species described by Deighton & Pirozynski might be better accommodated in *Pseudofusarium*.

The examples of the present study show a great deal of similarity between species with phialides forming serial conidia and others with solitary conidia. Further investigations are required to determine whether the term phialide should be refused to the latter group. Especially in the case of *Sibirina fungicola* the conidiogenous cells cannot be regarded as being of the holoblastic type.

Moreover, these examples show that conidium ontogeny is only one criterium amongst others which cannot be neglected in constructing a natural classification of Hyphomycetes. An illustrative example supporting this view is the genus *Cladobotryum* as redefined by Gams & Hoozemans (1970) in which conidial states of related *Hypomyces* species are combined. Study of conidium ontogeny, however, has shown (Cole & Kendrick, 1971), that in the type species *C. varium* Nees per Duby [= *Hypomyces aurantius* (Pers. per S. F. Gray) Tul., *stat. con.*] the conidia are abstricted in a retrogressive way, while in *C. mycophilum* (Oudem.) W. Gams & Hoozem. (= *Hypomyces odoratus* Arnold, *stat. con.*) the conidiogenous locus remains stable, and in the most closely related *C. dendroides* (Bull. per Mérat) W. Gams & Hoozem. [= *Hypomyces rosellus* (Alb. & Schw. per Fr.) Tul., *stat. con.*] it is progressive. Distribution of these species over different genera does not seem desirable not only for reasons of affinity in the perfect states, but also because of their great similarity in many other characters, such as pigmentation, mycelium structure and ramification of the conidiophores.

I would like to thank Mme. J. Nicot, Paris, and Mr. J. A. Stalpers, Baarn, for supplying strains of the new species described. Mr. R. A. Samson kindly contributed some informations on entomogenous fungi. Dr. J. A. von Arx and Dr. K. M. Old gave helpful suggestions regarding the manuscript, and Miss J. E. Sytema inked the drawings.

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# NOTES ON SOME CORTICIOID LIGNICOLOUS FUNGI ASSOCIATED WITH SNOWBANKS IN SOUTHERN ARIZONA[1]

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(With seven Text-figures)

Seven species of corticioid Hymenomycetes that fruit on wood in snow or near the edges of snowbanks in southern Arizona are discussed. Basidiocarps of *Coniophora corrugis* and *Corticium lepidum* apparently develop only in snow. *Athelia decipiens*, *A. epiphylla*, *Leptosporomyces galzinii*, *Confertobasidium olivaceo-album*, and *Byssomerulius hirtellus* produce actively sporulating basidiocarps in snow, but also fruit readily during the late summer and fall rainy season.

One of the most fascinating elements of the fungal biota of western North America consists of species with fruiting bodies developing in snow or in close proximity to it. A large and diverse group of fungi has been observed to occupy this ecological habitat. Cooke (1944, 1955) and Miller (1965, 1967) have published accounts of snowbank fungi in western North America. Few corticioid fungi have been reported to fruit under these conditions.

This paper concerns observations on seven lignicolous corticioid Basidiomycetes, all found fruiting in snow or near the edges of snowbanks in southern Arizona. Although two of the mountain ranges in the area exceed 10,000 feet (3048 meters) in elevation and several are over 9,000 feet (2743 meters), snowfall is generally much less than at more northern latitudes in North America and the snow persists for a shorter time. Consequently, snowbank fungi in southern Arizona must be collected from January to May. In the northern Rocky Mountains snowbank fungi may be found throughout the summer at higher elevations.

One of the striking features of the complex of snowbank fungi in southern Arizona is the relative scarcity of agarics. Species such as *Lyophyllum montanum* A. H. Smith and *Lentinellus montanus* O. K. Miller, so prominent near snowbanks in the northern Rocky Mts., have not been found here.

Morphological data were obtained from free hand sections or crushed tissue mounted in 2 % KOH and stained with phloxine. Sections were also mounted in Melzer's reagent to disclose amyloid or dextrinoid reactions. Drawings were made with the aid of a camera lucida. Capitalized color names are from Ridgway (1912).

[1] University of Arizona Agricultural Experiment Station Journal Article No. 2036.

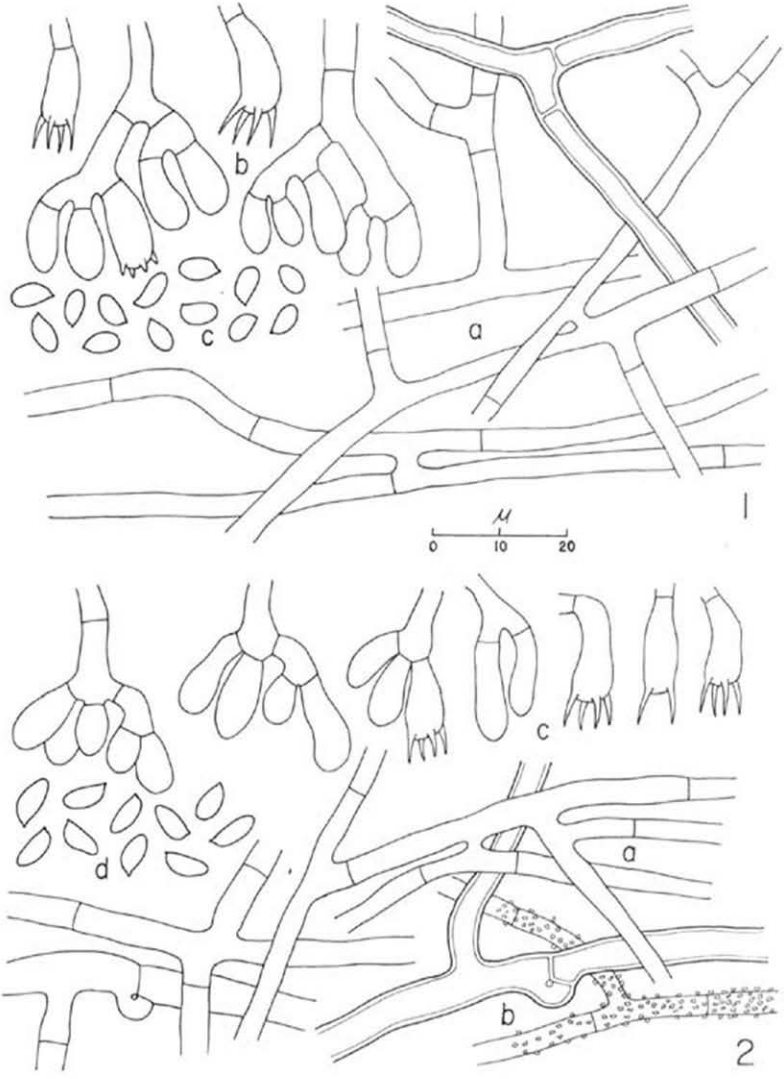


Fig. 1. Microscopic characters of *Athelia decipiens* (RLG 8512). — a. Subicular hyphae. — b. Basidia. — c. Basidiospores.

Fig. 2. Microscopic characters of *Athelia epiphylla* (RLG 8527). — a. Simple-septate subicular hyphae. — b. Subicular hyphae with clamp connections. — c. Basidia. — d. Basidiospores.

ATHELIA DECIPIENS (Höhn. & Litsch.) J. Erikss.—Fig. 1

*Corticium decipiens* Höhn. & Litsch. *in* Sber. Akad. Wiss. Wien (Math.-naturw. Kl.) **117** (1): 1116. 1908. — *Athelia decipiens* (Höhn. & Litsch.) J. Erikss. *in* Symb. bot. upsal. **16** (1): 86. 1958.

Basidiocarps resupinate, becoming widely effused, thin, fragile, easily separable from substratum; hymenial surface white to grayish-white, smooth, cracking on drying; hymenial layer a very thin, discontinuous pellicle on a delicate whitish, arachnoid subiculum; in some areas the subiculum so inconspicuous the hymenial layer appears to be directly on the substratum.

Hyphal system monomitic; subicular hyphae simple-septate with no clamp connections, thin- to moderately thick-walled, often incrusted, with frequent branching, 2–5 $\mu$ in diam., branches usually at a right angle or nearly so (Fig. 1a); cystidia lacking; basidia in candelabrums, compactly arranged in a euhymenium, clavate, 10–14 × 4–5 $\mu$, 4-sterigmate, with a basal septum (Fig. 1b); basidiospores oblong to ellipsoid, hyaline, smooth, negative in Melzer's reagent, (4-)5–6.5 × 2–3 $\mu$, with a small but prominent apiculus (Fig. 1c). Associated with a white rot.

*Athelia decipiens* is also found fruiting on conifers and hardwoods during the late summer fruiting season in Arizona. It is characterized by the very thin, grayish-white basidiocarp, simple-septate hyphae with no clamps and the oblong, apiculate basidiospores.

SPECIMENS EXAMINED: RLG 8512 on log of ponderosa pine (*Pinus ponderosa* Laws.) in snow, Rustler Park, Chiricahua Mts., Cochise County, Arizona, April 25, 1969; RLG 7571, on ponderosa pine log, Rustler Park, October 5, 1967; RLG 8201, on ponderosa pine log, Rustler Park, August 27, 1968; RLG 7930, on ponderosa pine log, Rustler Park, July 25, 1968.

ATHELIA EPIPHYLLA Pers.—Fig. 2

*Athelia epiphylla* Pers., Mycol. europ. **1**: 84. 1822.

Basidiocarps resupinate, becoming widely effused, thin, fragile, easily separated from substratum; hymenial surface white to grayish or bluish-white, smooth; hymenial layer very thin, pelliculose, discontinuous over a very thin, arachnoid subiculum or appearing to develop directly on the substratum.

Hyphal system monomitic; subicular hyphae hyaline, mostly simple-septate, with frequent branching, 2.5–4.5 $\mu$ in diam., some lightly incrusted with fine crystalline material (Fig. 2a); also some larger hyphae with clamp connections, these moderately thick-walled, 4–6 $\mu$ in diam., also with frequent branching (Fig. 2b); cystidia lacking; basidia in candelabrums, cylindric to clavate, mostly 4-sterigmate, but some 2-sterigmate, 12–15 × 5–8 $\mu$, with a basal septum (Fig. 2c); basidiospores cylindric or slightly fusiform, hyaline, smooth, negative in Melzer's reagent, 5–7 × 2.5–3 $\mu$ (Fig. 2d). Associated with a white rot.

*Athelia epiphylla* is similar to *A. decipiens*, but the latter species has no clamp connections on any hyphae and has slightly smaller basidiospores. The incidence of clamp connections seems to vary considerably among specimens of *A. epiphylla* from relatively rare to rather frequent and conspicuous.

SPECIMENS EXAMINED: RLG 7796, on dead, fallen, silver leaf oak (*Quercus hypoleucoides* Camus), in snow, General Hitchcock Picnic Area, Santa Catalina Mts., Pima County, Arizona, January 31, 1969; RLG 7864, on ponderosa pine (*Pinus ponderosa* Laws.) log, East Side Game Road, Kaibab Plateau, Coconino County, Arizona, June 5, 1968; RLG 8527, on Arizona alder (*Alnus oblongifolia* Torr.) log, Palisades, Santa Catalina Mts., Pima County, Arizona, May 8, 1969.

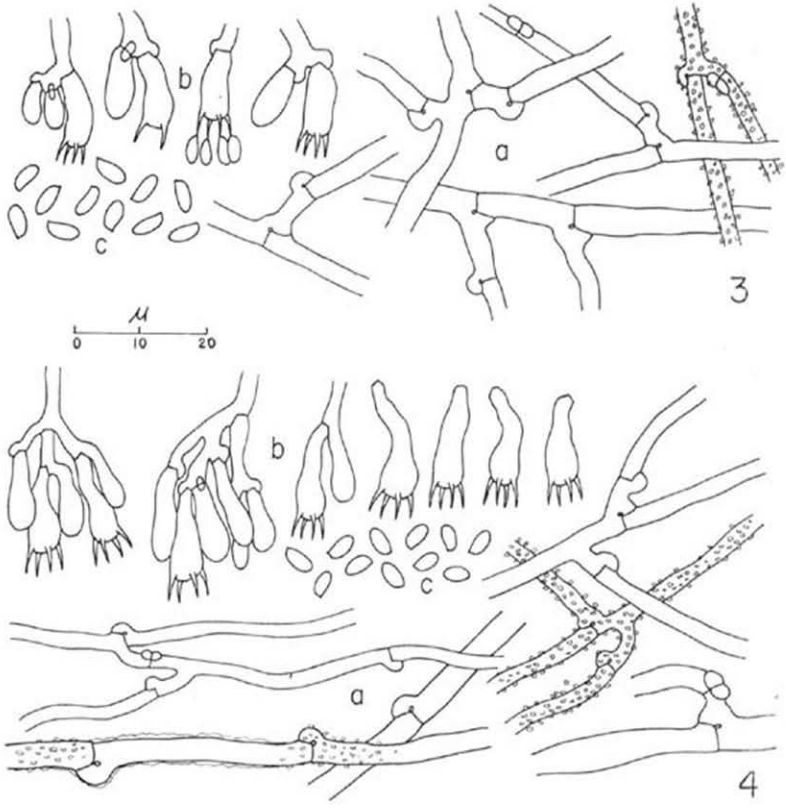


Fig. 3. Microscopic characters of *Leptosporomyces galzinii* (RLG 9370). — a. Subicular hyphae. — b. Basidia. — c. Basidiospores.

Fig. 4. Microscopic characters of *Confertobasidium olivaceo-album* (ABB 1498). — a. Subicular hyphae. — b. Basidia. — c. Basidiospores.

LEPTOSPOROMYCES GALZINII (Bourd.) Jülich—Fig. 3

*Corticium galzinii* Bourd. *in* Revue scient. Bourbon. Cent. Fr. **23**: 11. 1910. — *Athelia galzinii* (Bourd.) Donk *in* Fungus **27**,: 12. 1957. — *Leptosporomyces galzinii* (Bourd.) Jülich *in* Willdenowia Beih. **7**: 192. 1972.

Basidiocarps resupinate, becoming widely effused, very thin, fragile, easily separated from substratum; hymenial surface white to grayish or slightly bluish-white, hymenial layer loosely pelliculose or finely tomentose, interrupted, very thin; subiculum inconspicuous in some specimens or virtually lacking with the hymenial layer appearing to develop directly on the substratum.

Hyphal system monomitic; subicular and subhymenial hyphae with clamp connections at all septa, hyaline, thin-walled, with frequent branching, often branching from a clamp, 2–4 $\mu$ in diam. (Fig. 3a); cystidia lacking; basidia in candelabrums, cylindric to clavate, mostly 4-sterigmate but a few 2-sterigmate, with a basal clamp connection, compactly arranged in a euhymenium, 9–12 × 3.5–4 $\mu$ (Fig. 3b); basidiospores hyaline, smooth, cylindric to oblong, negative in Melzer's reagent, with a small apiculus, 4–4.5 × 2 $\mu$ (Fig. 3c). Associated with a white rot.

Three macroscopically similar athelioid fungi are common in Arizona forests. These are *Athelia decipiens*, *A. epiphylla*, and *L. galzinii*. The latter can be recognized by the clamp connections at all septa and at the base of the basidia, and the smaller basidiospores. *Leptosporomyces galzinii* is also found during the rainy season in late summer.

SPECIMENS EXAMINED: RLG 8370, on crustose vegetative tissue of *Fomes annosus* (Fr.) Karst. on white fir [*Abies concolor* (Gord. & Glend.) Lindl.] log in snow, Summerhaven, Santa Catalina Mts., Pima County, Arizona, May 13, 1970; RLG 7784, on silver leaf oak (*Quercus hypoleucoides* Camus), General Hitchcock Picnic Area, Santa Catalina Mts., June 31, 1968; RLG 8177, on white fir log, Marshall Gulch, Santa Catalina Mts., August 26, 1968.

CONFERTOBASIDIUM OLIVACEO-ALBUM (Bourd. & Galz.) Jülich—Fig. 4

*Corticium olivaceo-album* Bourd. & Galz. *in* Bull. trimest. Soc. mycol. Fr. **27**: 239.1911. — *Athelia olivaceo-alba* (Bourd. & Galz.) Donk *in* Fungus **27**: 12. 1957. — *Confertobasidium olivaceo-album* (Bourd. & Galz.) Jülich *in* Willdenowia Beih. **7**: 167. 1972.

*Corticium fuscostratum* Burt *in* Ann. Mo. bot. Gdn **13**: 299. 1926. — *Athelia fuscostrata* (Burt) Donk *in* Fungus **27**: 12. 1957.

Basidiocarps resupinate, becoming widely effused, soft, easily separated from substratum; hymenial layer a thin, compact, Light Buff to Ivory Yellow (Cinnamon Buff to Clay Color) colored pellicle, cracking on drying to expose the pale-brownish to pale buff, arachnoid subiculum; margin thinning out, usually with fine cream-colored rhizomorphs.

Hyphal system monomitic; subicular hyphae with abundant clamp connections, those in the subhymenial layer hyaline, thin-walled, loosely arranged, with frequent branching, hyaline to pale yellowish in KOH, 2–3 $\mu$ in diam.; those in the basal brown layer with thin to moderately thickened walls, light brown in KOH, 3–5 $\mu$ in diam., some lightly to heavily incrusted with a fine, pale brownish crystalline

material (Fig. 4a); cystidia lacking; basidia clavate, 4-sterigmate, 10–12 × 4–4.5 μ (Fig. 4b); basidiospores hyaline, smooth, negative in Melzer's reagent, ellipsoid to short-cylindric, flattened on one side, 3–4 × 2–2.5 μ (Fig. 4c). Associated with a white rot. Gum guaiac reaction positive on fresh hymenial surface.

*Confertobasidium olivaceo-album* is also found fruiting in late summer. It is distinguished by the cream to buff, pellicular hymenial layer, the pale brownish arachnoid subiculum, and nodose-septate subicular hyphae.

SPECIMENS EXAMINED: RLG 9363, on corkbark fir log [*Abies lasiocarpa* var. *arizonica* (Merriam) Lemm.] under snow, Mt. Lemmon, Santa Catalina Mts., Pima County, Arizona, May 8, 1970; ABB 1496, on Rocky Mountain maple (*Acer glabrum* Torr.), in snow, Mt. Bigelow, Santa Catalina Mts., January 29, 1970; ABB 1498, on quaking

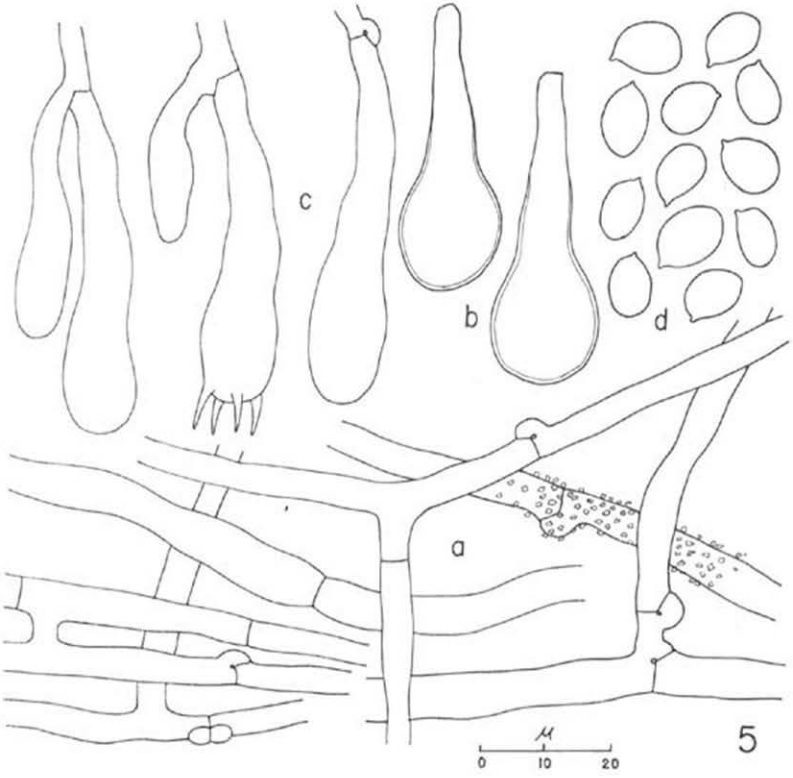


Fig. 5. Microscopic characters of *Coniophora corrugis* (RLG 5988). — a. Subicular hyphae. — b. Cystidia. — c. Basidia. — d. Basidiospores.

aspen (*Populus tremuloides* Michx.) log, Mt. Lemmon, Santa Catalina Mts., May 28, 1970; ABB 1002 and 1003, on ponderosa pine, Palisades, Santa Catalina Mts., May 11, 1969; ABB 1106 on ponderosa pine, Schultz Pass. Rd., San Francisco Peaks, Coconino County, Arizona, August 7, 1969; ABB 1135, on Douglas fir [*Pseudotsuga menziesii* (Mirb.) Franco], Snow Bowl Rd., San Francisco Peaks, August 7, 1968.

### CONIOPHORA CORRUGIS Burt—Fig. 5

*Coniophora corrugis* Burt *in* Ann. Mo. bot. Gdn **13**: 310. 1926.

Basidiocarps resupinate, becoming widely effused, easily separated; hymenial surface merulioid to smooth, pale tan to darker brown (Ochraceous-Tawny to Cinnamon-Brown), hymenial layer compact and pelliculose on a thin, soft, white, floccose to arachnoid subiculum which extends beyond the hymenial layer at the margin.

Hyphal system monomitic; subicular hyphae thin-walled, with occasional branching, with abundant clamp connections and also simple septa, 4–6 $\mu$ in diam., some lightly to heavily incrusted with coarse crystalline material (Fig. 5a); cystidia broadly clavate with a greatly expanded apex with distinctly thickened wall, hyaline, projecting slightly or imbedded; 40–45 $\mu$ long and up to 18 $\mu$ in diam. at apex (Fig. 5b); basidia compactly arranged in a typical euhymenium, clavate, 4-sterigmate, with a basal clamp connection, up to 60 $\mu$ long and 8–12 $\mu$ in diam. (Fig. 5c); basidiospores broadly ellipsoid, hyaline, or slightly yellowish in KOH when mature, negative in Melzer's reagent, 7–10 × 5–7 $\mu$ (Fig. 5d). Associated with a white rot.

*Coniophora corrugis* was placed in that genus by Burt because of a slight pigmentation of mature spores apparently observed in only one of several specimens. However, the basidial ands pore characters are not typical of *Coniophora* as exemplified by *Coniophora puteana* (Schum. ex Fr.) Karst. or *Coniophora arida* (Fr.) Karst., common species in Arizona. Rogers & Jackson (1943) state that *C. corrugis* "is probably a member of Bourdot and Galzin's section Membranacea." Burt (1926) also stated that *C. corrugis* "seemed related to *C. polyporoidea*", a reference to *Corticium polyporoideum* Berk. & Curt. However, Petersen (1971) has concluded that *C. polyporoideum* should be placed in the genus *Cristella* Pat., and *Coniophora corrugis* does not show close relationships to species of *Cristella*. *Coniophora corrugis* commonly develops profusely in snow over the surfaces of living plants and foliage of fallen conifers as well as on dead branches and other dead wood on the ground. It is a common fungus in and around snowbanks at high elevations throughout the coniferous forests of western North America.

SPECIMENS EXAMINED: RLG 7881, on spruce twigs (*Picea* sp.), in snow, East Side Game Rd., Kaibab Plateau, Coconino County, June 6, 1968; ABB 1016 and 1021, on quaking aspen (*Populus tremuloides* Michx.), Snow Bowl Rd., San Francisco Pks., Coconino County, June 17, 1968; RLG 7858, on Rocky Mountain maple (*Acer glabrum* Torr.), Mt. Lemmon, Santa Catalina Mts., Pima County, May 15, 1968; P. D. Keener, on corkbark fir [*Abies lasiocarpa* var. *arizonica* (Merriam) Lemm.], Pt. Sublime Rd., North Rim, Grand Canyon Nat. Park, June 25, 1957.

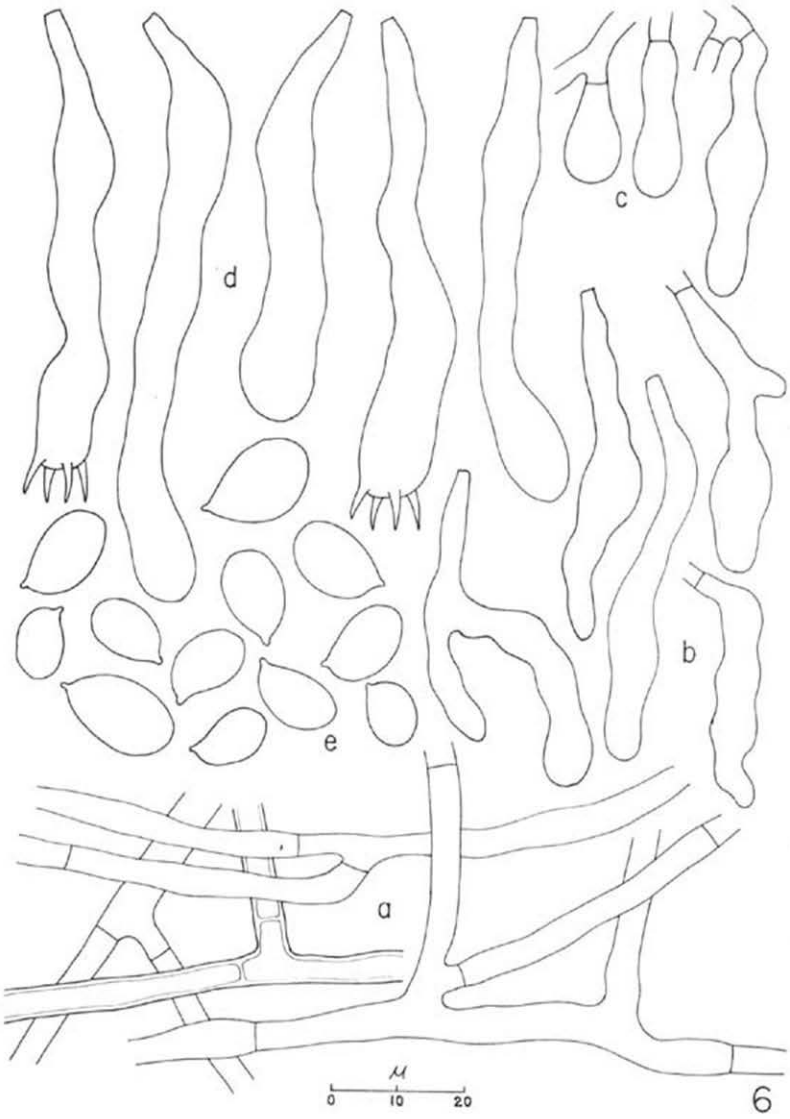


Fig. 6. Microscopic characters of *Corticium lepidum* (RLG 9356). — a. Subicular hyphae. — b. Imbedded sterile elements from hymenial region. — c. Basidioles. — d. Basidia. — e. Basidiospores.

CORTICIUM LEPIDUM (Rom.) Bourd. & Galz.—Fig. 6

*Merulius lepidus* Rom. *in* Ark. Bot. **11** (3): 29. 1911. — *Corticium lepidum* (Rom.) Bourd. & Galz., Hym. Fr. 187. 1928.

Basidiocarps resupinate, developing under snow, enveloping twigs, conifer needles, and other litter and growing over logs, stumps and on the base of standing living trees; in small patches or becoming widely effused; hymenial surface bright orange when fresh (Apricot-Orange to Light Salmon-Orange), fading slightly on drying, shallowly merulioid to smooth, hymenial layer pelliculose on a loose, white, cottony subiculum which extends beyond the hymenial layer to form a white, cottony, sterile, margin.

Subicular hyphae loosely arranged, with abundant septa but no clamp connections, with frequent branching, thin- to thick-walled, 3–5.5 $\mu$ in diam (Fig. 6a); cystidia not present; imbedded, elongated sterile elements abundant in hymenial region, very irregular in shape, 4–10 $\mu$ in diam. (Fig. 6b); basidia developing in a catahymenium, originating as imbedded spherical to pyriform basidioles (Fig. 6c), these giving rise to mature basidia that are utriform to clavate, elongated and often contorted, 4-sterigmate, 60–85 $\mu$ long and 8–12 $\mu$ wide at the expanded apex (Fig. 6d); basidiospores hyaline, smooth, negative in Melzer's reagent, ellipsoid to ovoid, some slightly curved, with a large blunt apiculus, highly variable in size 9–19 × 5–12 $\mu$ (Fig. 6e).

The basidiocarps of *C. lepidum* develop under snow in the winter or early spring in the mountains of southern Arizona and are associated with copious white mycelium growing over conifer needles and wood on the ground. They deteriorate rather rapidly and cannot be found by midsummer.

*Peniophora laurentii* Lundell, as discussed by Eriksson (1950), is very similar to our Arizona fungus but has incrusted cystidia. Eriksson states that *C. lepidum* is a synonym of *P. laurentii*. If this is the case, Romell's name would be the correct basionym. No incrusted cystidia could be found in our Arizona specimens. The catahymenial structure of *C. lepidum* and the large ellipsoid to ovoid basidiospores with larger apiculus are characters found in the genus *Laeticorticium* Donk. However, the absence of typical dendrohyphidia and clamp connections in *C. lepidum* mitigate against placing it in *Laeticorticium*.

SPECIMENS EXAMINED: RLG 7886, on base of living Douglas fir [*Pseudotsuga menziesii* (Mirb.) Franco], Treasure Park, Pinaleno Mts., Graham County, June 16, 1968; RLG 7883, on conifer needles on the ground, Riggs Flat Lake, Pinaleno Mts., June 15, 1968; RLG 9356, on Douglas fir twigs on ground, Summerhaven, Santa Catalina Mts., Pima County, May 18, 1970; RLG 9393, on base of living Douglas fir, Riggs Flat Lake, June 5, 1970; RLG 7839, on Douglas fir branches under snow, Bear Wallow, Santa Catalina Mts., April 29, 1968; ABB 1499, on quaking aspen (*Populus tremuloides* Michx.), Mt. Lemmon, Santa Catalina Mts., May 28, 1970.

BYSSOMERULIUS HIRTELLUS (Burt) Parm.—Fig. 7

*Merulius hirtellus* Burt *in* Ann. Mo. bot. Gdn **4**: 335. 1917. — *Byssomerulius hirtellus* (Burt.) Parm. *in* Eesti NSV Tead. Akad. Toim. (Biol.) **16**: 384. 1967.

Basidiocarps resupinate, soft, becoming widely effused; hymenial surface becoming distinctly merulioid, white to very pale pinkish or cinereous, distinctly cystidiate at 30 ×; sterile margin white to pale pinkish, soft, cottony; subiculum very thin, white, soft-cottony to almost arachnoid; basidiocarps associated with abundant sterile, pinkish (Rhodonite Pink to Pale Rhodonite Pink) cottony mycelium growing over twigs, leaves and other litter under snow.

Hyphal system monomitic; hyphae of sterile pink mycelium incrusted, 3–5 μ in diam., a few with constricted portions with greatly thickened to almost solid walls; subicular hyphae with abundant simple septa, thin- to moderately thick-walled, with occasional branching, 3–4 μ in diam., some lightly to heavily incrusted (Fig. 7a); cystidia abundant, cylindric, or rarely swollen at the apex, thin-walled, 3–4 μ in diam. and projecting to 35 μ (Fig. 7b); basidia clavate, 4-sterigmate, with a basal septum, in candelabrums, 20–25 × 3–4 μ (Fig. 7c); basidiospores hyaline, smooth, negative in Melzer's reagent, short-cylindric, slightly curved, 4–5 × 2–2.5 μ (Fig. 7d). Associated with a white rot. Gum guaiac reaction negative on fresh hymenial surface after 15 minutes.

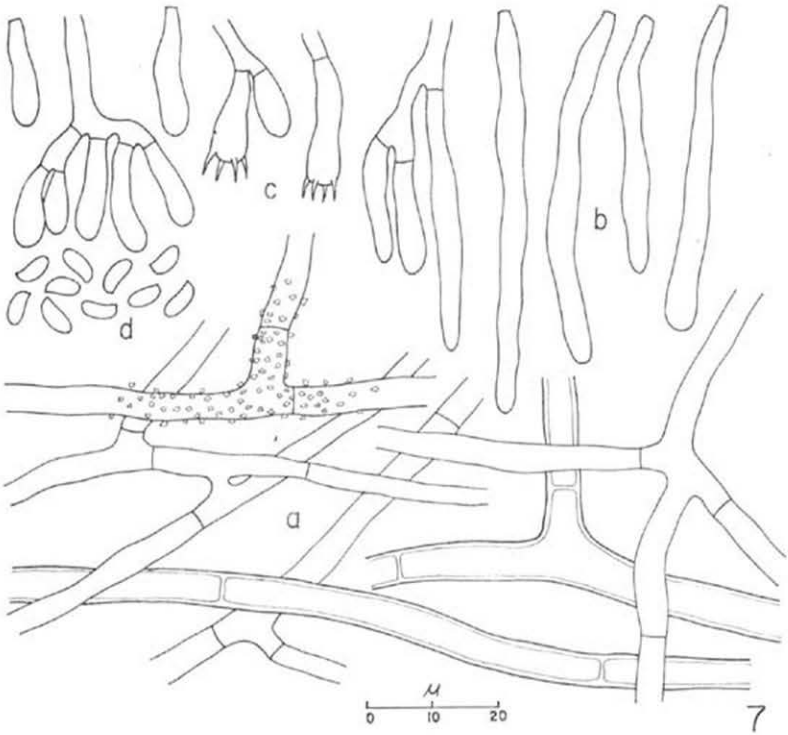


Fig. 7. Microscopic characters of *Byssomerulius hirtellus* (RLG 9375). — a. Subicular hyphae. — b. Cystidia. — c. Basidia. — d. Basidiospores.

The application of this name to the specimens cited is made with some reservations. Ginns (1968) has provided a description based on the holotype (BPI) and isotype (FH) of *M. hirtellus* and my observations of those specimens are in agreement with his. The basidiospores in our Arizona collections are slightly narrower and more distinctly curved than in the types of *M. hirtellus* and in a collection of mine from New York (RLG 5477, on *Picea rubens* Sarg., Saranac Lake, Sept. 11, 1965). The basidiospores as described and illustrated in this paper are more like those of *Merulius armeniacus* Bres., a species also placed in *Byssomerulius* by Parmasto. However, we have specimens of *M. armeniacus* in our Arizona collections that agree very well with the type of that species (BPI, Weir 15306). They differ from the specimens identified here as *M. hirtellus* in having a brightly colored hymenial surface (Vinaceous-Rufous to Hay's Russet) and a gelatinizing layer in the subhymenium. Until the range of variation in *B. hirtellus* and *B. armeniacus* is better understood, we will refer our Arizona specimens with pale pinkish to cinereous hymenial surface and non-gelatinized subhymenial layer to *B. hirtellus*.

*Byssomerulius hirtellus* also fruits in abundance in the summer rainy season in southern Arizona. The pinkish to gray colors and the strongly cystidiate hymenium are diagnostic characters.

SPECIMENS EXAMINED: RLG 9368 and 9375, on fallen twigs and branches of corkbark fir in snow, Mt. Lemmon, Santa Catalina Mts., Pima County, May 9, 1970; RLG 8375, on ponderosa pine, Long Park, Chiricahua Mts., Cochise County, Arizona, August 30, 1968; RLG 10626, on Douglas fir log, Mt. Bigelow, Santa Catalina Mts., July 26, 1972; RLG 10621, on Engelmann spruce log (*Picea engelmannii* Parry), Treasure Park, Pinaleno Mts., Graham County, Arizona, July 19, 1972.

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# BOTRYTIS AND BOTRYTIS-LIKE GENERA

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(With ten Text-figures)

Critical revision of *Botrytis*-like genera leads to recognition of *Botrytis*, *Chromelosporium*, *Glischroderma* and *Ostracoderma*. *Phymatotrichum* is synonymized with *Botrytis*, and previously assigned species are reconsidered. Six new genera are recognized: *Pulchromyces* (for *Phymatotrichum fimicola* Dring); *Phymatotrichopsis* (for *Phymatotrichum omnivorum* Duggar); *Streptobotrys*, *Amphobotrys*, and *Verrucobotrys* (for conidial states of the Sclerotiniaceae); *Dichobotrys* (for the conidial state of Operculate Discomycetes of the genus *Trichophaea*).

*Hyphelia terrestris* Fr. and related species, including conidial states of some Operculate Discomycetes of the genus *Peziza*, are placed in *Chromelosporium*. Peridiate fungi with a similar conidial apparatus, described in *Lycoperdellon*, are transferred to *Ostracoderma*, while *Glischroderma* is kept distinct.

Thirteen new species are proposed, and 16 new combinations are made for the species discussed.

The aim of this paper is to review the existing genera and to propose new ones in the classification of the *Botrytis*-like fungi. These fungi, including *Botrytis*, produce simultaneous, solitary, holoblastic conidia at the ends of conidiophore branches. All belong to Hughes' (1953) conidiogenetic section IB.

Micheli's old genus, validated[2] by Persoon (1801) under the name *Botrytis* Pers., and lectotypified by *B. cinerea* Pers. (Clements & Shear, 1931), has accommodated a still increasing number of related as well as unrelated fungi, exhibiting almost all of the kinds of conidiogenesis described by Hughes (1953) and Tubaki (1958). The number of taxa which have been assigned to the genus has increased from 5 originally (Persoon, 1801) to 128 (Saccardo, 1886), and has reached 380 today.

The need for a revision of the genus has been pointed out and initiated by several workers already. Even Nees (1817) described two new genera, *Virgaria* and *Cladobotryum*, to accommodate two species Link (1809) had erroneously referred to *Botrytis*. De Bary (1863) excluded from *Botrytis* most of the members that actually belong to

[1] Based in part on a paper presented in a symposium at the First International Mycological Congress, Exeter, September, 1971.

[2] I am reviving Hughes' (1958) proposal to begin nomenclature of the Hyphomycetes with Dec. 31, 1801, if May 1, 1753 is not te be chosen.

the Peronosporales that Persoon and others had included. He transferred them to *Peronospora* Corda and to *Phytophthora* De Bary. In more recent times, Hughes (1958) removed from the genus a number of species belonging to his sections II, III, and IV, and to section IX of Tubaki (1958).

The segregation of *Botrytis*-like fungi from *Botrytis* Pers. requires an exact understanding of the type species of that genus, *Botrytis cinerea*. De Bary (1864) demonstrated the connection of *B. cinerea* with its sclerotial state, *Sclerotium durum* Pers., and with its apothecial state, *Peziza fuckeliana* De Bary, a member of the Sclerotiniaceae. De Bary (1869) then provided the earliest complete description of the conidial apparatus, as well as of the other states. The same author (De Bary, 1884) finally pointed out the production by the same fungus of a spermatial state. Whetzel (1945, completed by Fitzpatrick) intended, on principle, to accept in *Botrytis* only those species which are, according to Smith's (1902) expression, "*Botrytis* of the *cinerea* type." He thus excluded intentionally from that restricted concept of *Botrytis* the group of "streptiform" *Botrytis* species and the "botryose conidiophores" of *Seaverinia*. Buchwald (1949) adopted almost exactly Whetzel's view, still calling for exclusion of any unrelated species, and particularly such species as *B. epigaea* Link (= *Hyphelia terrestris* Fr.).

From the early stage of development of its conidiophore to the point of full maturity, *Botrytis cinerea* presents many different aspects. These have even been taken for representatives of distinct genera. *Polyactis* Link and *Phymatotrichum* Bon. (lectotypified by *P. gemellum* Bon.) are both based on an immature stage of development of the first conidial head, still showing turgescent ampullae bearing conidia. *Haplaria* Link, on the contrary, is based on mature conidiophores, bifurcate or trifurcate by proliferation of branches from the first mature head, with several, successively developed clusters of conidia borne along these proliferations. *Haplaria* and *Polyactis* were correctly merged in *Botrytis* by Fries (1832), this synonymy confirmed by Hughes (1958) after study of the type material, and *Phymatotrichum* was correctly synonymized in *Botrytis* by Saccardo (1886). Since *Phymatotrichum* was recently revived by Bloss (1970), who seems to accept any assigned species, a critical consideration of the species formerly placed in that genus is also presented in this paper. Two of these serve as the type species of two new genera, *Phymatotrichopsis* and *Pulchromyces*.

Data published after De Bary's studies demonstrate that a number of other *Botrytis* and *Botrytis*-like fungi are states of Discomycetes. Here two groups are to be distinguished. In the first group, all members of the Sclerotiniaceae (Inoperculate Discomycetes), *Botrytis*, *Streptobotrys* and *Amphobotrys* produce true plano-convex sclerotia, while *Verrucobotrys* produces a substratal stroma. The other group is representative of the Pezizales (Operculate Discomycetes). Two kinds of conidial states are distinguished and connect to distinct perfect genera. The new genus *Dichobotrys*, with globose conidiogenous cells, has its perfect state in *Trichophaea* in the broad sense (Korf, 1972), inclusive of *Sphaerospora* (= *Sphaerosporella*), while

*Chromelosporium* Corda, with cylindrical conidiogenous cells, connects to some species of *Peziza*.[3]

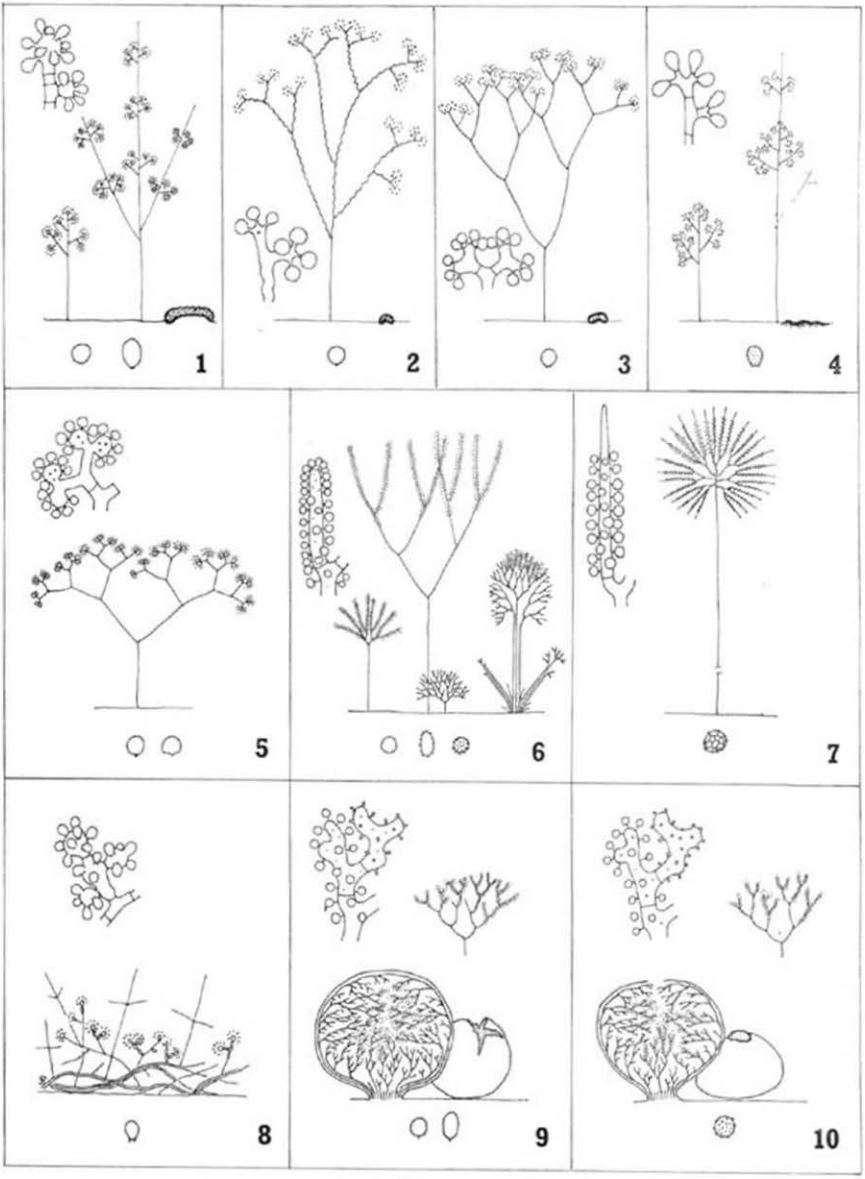
Those *Botrytis*-like fungi having a close similarity to *Chromelosporium* in producing numerous conidia on cylindrical, dichotomous conidiogenous cells have often been assigned to *Botrytis*, *Phymatotrichum*, *Hyphelia* Fr. 1825 or 1849, or *Ostracoderma* Fr. The genus *Hyphelia* Fr. 1825, based on *Trichoderma roseum* Pers., does not belong to this group. *Hyphelia* Fr. 1849 (lectotype, *H. terrestris* Fr.) and *Ostracoderma* (type, *O. pulvinatum* Fr.) are very close, having similar fertile hyphae, but are dissimilar in that the latter has a true peridiate fruitbody. This is precisely the distinction already made by Fries (1825, 1829, 1849). Juel (1920) merged the two genera under the name *Hyphelia* Fr. 1849, stressing the similarity in fertile hyphae. Hughes (1958) and Lundell & Nannfeldt (1959) adopted *Ostracoderma* as the correct name since *Hyphelia* Fr. 1849 is illegitimate. The oldest generic name available for *H. terrestris* and its non-peridiate allies is *Chromelosporium* Corda (type, *C. ochraceum* Corda). *Ostracoderma* is retained for the peridiate species, and *Lycoperdellon* Torrend is treated as a synonym of it. Another peridiate genus, *Glischroderma* Fuckel, though closely related to *Ostracoderma*, is provisionally kept separate.

Species of *Chromelosporium*, as understood here, have also been thought to be connected with Basidiomycetes of the genus *Tomentella* Bref. (Brefeld, 1888; von Höhnel, 1907). *Ostracoderma* (= *Lycoperdellon*) species have been presumed members of the Gasteromycetes (Heim & Malençon 1933; Heim, 1949), and *Glischroderma* was originally assigned to the Gasteromycetes by Fuckel (1870). *Phymatotrichum omnivorum* Duggar, here referred as *Phymatotrichopsis omnivora*, has been said to connect to *Hydnum omnivorum* Shear (Shear, 1925), or to *Trechispora brinkmannii* (Bres.) Rogers & Jackson (Baniecki & Bloss, 1970). None of these assumptions has been confirmed.

The segregation presented here of new form genera for the *Botrytis*-like fungi is primarily based on the morphology of the conidial state, in which sufficient diagnostic features can be observed even in the absence of other imperfect or perfect states. Such accompanying states (stromata, apothecia, spermatia), cultural characters, or any ecological features may serve, however, as additonal guides. These corroborate the classification to the point that, I believe, natural genera have been segregated. These genera can be grouped as follows, in part based on their connection to known perfect state families: —

I. Form genera of the family BOTRYTIDACEAE Lindley (Section IB)
   A. Genera connected to Inoperculate Discomycetes of the family SCLEROTINIACEAE Whetzel
      1. *Botrytis* Pers. — *Botryotinia* Whetzel
      2. *Streptobotrys* n.g. — *Streptotinia* Whetzel
      3. *Amphobotrys* n.g. — *Botryotinia* Whetzel
      4. *Verrucobotrys* n.g. — *Seaverinia* Whetzel

[3] Other *Peziza* species are known to produce an *Oedocephalum* conidial state; although it also belongs to Hughes' section IB, that genus is not considered here, the conidiophore being unbranched.




Figs. 1–10. Diagrammatic illustrations of the conidiophores (about × 5), of conidiogenous cells and conidia (about × 250), and of the sclerotium, stroma, or peridiate fruitbody when present (about × 3), numbered to correspond with the generic numbers used in the synoptic key and the arrangement in the text. — 1. *Botrytis*. — 2. *Streptobotrys*. — 3. *Amphobotrys*. — 4. *Verrucobotrys*. — 5. *Dichobotrys*. — 6. *Chromelosporium*. — 7. *Pulchromyces*. — 8. *Phymatotrichopsis*. — 9. *Ostracoderma*. — 10. *Glischroderma*.

B. Genus connected to Operculate Discomycetes of the family PYRONEMATACEAE Corda
   5. *Dichobotrys* n.g. — *Trichophaea* Boud.
C. Genus connected to the Operculate Discomycetes of the family PEZIZACEAE Fries
   6. *Chromelosporium* Corda — *Peziza* Pers.
D. Genera with no known perfect state
   7. *Pulchromyces* n.g.
   8. *Phymatotrichopsis* n.g.

II. Form genera of the family GLISCHRODERMATACEAE Rea (Section IB); with no known perfect state
   9. *Ostracoderma* Fries
   10. *Glischroderma* Fuckel

To aid in the rapid keying out of specimens to the correct genus, a synoptic key and a schematic chart (Figs. 1–10) are presented, based on the most useful generic characters. Korf (1972) indicated the way of using such a key. Each character is a possible first entry leading to candidate genera listed by the same numbers as above. The examination of additional characters finally selects one particular genus. I am following Leenhouts' (1973) modified method, in which boldface type is used to indicate genera showing only one of the alternatives in any character grouping.

SYNOPTIC KEY TO THE GENERA

*Criteria of the conidial state.*

| | |
|---|---|
| Peridium enclosing conidiophores: | present, non-ostiolate: **9** |
| | present, ostiolate: **10** |
| | absent: **1 2 3 4 5 6 7 8** |
| Arrangement of conidiophores: | mononematous, solitary or in groups: **1 2 3 4** 5 6 7 8 |
| | synnematous: 6 8 **9 10** |
| Branching of conidiophores: | alternate: **1 2 4** |
| | regularly dichotomous: **3 5** 6 **7** |
| | irregularly dichotomous or coralloid: 6 **9 10** |
| | absent to irregularly alternate: **8** |
| Contour of branches: | straight: **1 3 4 5 6 7 8 9 10** |
| | twisted: **2** |
| Proliferation of conidiophores: | present: **1 4** |
| | absent: **2 3 5 6 7 8 9 10** |
| Conidial shape: | globose: 1 **2 3** 4 5 6 **7** 8 9 **10** |
| | ovate or elliptical: 1 4 6 8 9 |
| | napiform: 5 |
| Conidial wall ornamentation: | absent: **1 2 3** 5 6 **8 9** |
| | verrucose or spinulose: **4** 6 **10** |
| | reticulate: **7** |
| Colour of spore mass: | grey turning brown: **1 2 3 4** |
| | white turning ochre-yellow to tawny or clay-brown: **5** 6 **7 8** 9 10 |
| | rose, violet or blue when young: 6 9 10 |

*Characters of the stromatal state.*

| | |
|---|---|
| Stroma: | sclerotial: **1 2 3** |
| | substratal: **4** |
| | absent: **5 6 7 8 9 10** |

Each generic name is provided below with its synonymy,[4] a description and a Latin diagnosis or a redescription, a list of selected known species, with Latin diagnoses if newly named, and finally a list of excluded species. These lists of excluded and accepted species, as well as the synonymies, do not pretend to be exhaustive now. More species of which I am aware have to be described or redescribed in most of these genera, and will be included in a more detailed monograph.

1. BOTRYTIS Pers., Syn. meth. Fung. 690. 1801.

*Botrytis* Micheli, Nov. Gen. Pl. 212. *t. 91 f. 1–4.* 1729 (pre-linnean name). ≡ *Botrytis* Micheli *in* Adanson, Familles plant. **2**: 3. 1763 (post-linnean, devalidated name). ≡ *Botrytis* Pers. subgen. *Eubotrytis* Buchw. *in* K. Vet.– og Landbohøjsk. Aarsskr. **1949**: 146. 1949 (no Latin diagnosis). ≡ *Botrytis* Pers. sect. *Macrosclerotiophorae* Buchw. *in* K. Vet.– og Landbohøjsk. Aarsskr. **1949**: 146. 1949 (no Latin diagnosis). — Type species: *B. cinerea* Pers. (lectotype, selected by Clements & Shear, 1931).

*Haplaria* Link *in* Mag. Ges. naturf. Freunde, Berlin **3**: 11. 1809. ≡ *Botrytis* Pers. 'tribus' *Spicatae* Fr., Syst. mycol. **3** (2): 396. 1832. — Type species: *H. grisea* Link (monotype) = *B. cinerea* Pers.

*Polyactis* Link *in* Mag. Ges. naturf. Freunde, Berlin **3**: 16. 1809; not *Polyactis* Link *in* L., Sp. Pl., Ed. 4, **6**(1): 62. 1824. ≡ *Monilia* Pers. [subgen.?] **Polyactis* (Link) Pers., Mycol. eur. **1**: 31. 1822. ≡ *Botrytis* Pers. 'tribus' *Cymosae* Fr., Syst. mycol. **3**(2): 397. 1832. ≡ *Botrytis* Pers. [subgen.?] B. *Polyactis* (Link) Sacc., Syll. Fung. **4**: 128. 1886. — Type species: *P. vulgaris* Link (monotype) = *B. cinerea* Pers.

*Phymatotrichum* Bon., Handb. Mykol. 116. *f.* 138. 1851. ≡ *Botrytis* Pers. [subgen.?] D *Phymatotrichum* (Bon.) Sacc., Syll. Fung. **4**: 134. 1886. — Type species: *P. gemellum* Bon. (lectotype, selected by Clements & Shear, 1931) = *B. cinerea* Pers.

*Botrytis* Pers. sect. *Microsclerotiophorae* Buchw., K. Vet.– og Landbohøjsk. Aarsskr. **1949**: 146. 1949 (no Latin diagnosis). — Type species: *B. tulipae* Lind (lectotype, selected here).

*Colonies* effuse, at first white to greyish, then dark brown; hyphae hyaline to brown, septate. *Conidiophores* erect, solitary or in groups of 2 to 5 borne on a cluster of hyphal cells, basal cell often inflated; stipe straight, subhyaline to brown, septate, branched towards the apex, branches lateral, alternate, at a wide angle to the axis, successively developed from the base to the apex, branching again alternately, forming at each end a globose, swollen conidiogenous cell bearing simultaneous conidia on pedicels, becoming septate and collapsing accordion-like at conidium maturity, after abscission leaving a prominent, flat, rounded scar at the apex of the stipe or the ends of the branch stumps; stipe and branch stumps proliferating from scars into new branches, septate, brown, producing new conidial heads; at maturity of these, proliferations occur again, making the resulting conidiophore monopodial, dichotomous or trichotomous, bearing one or more series of conidial clusters along the stalks. *Conidia* holoblastic, globose, obovate or elliptical, continuous, subhyaline to brown, with smooth walls, separated from the pedicel by a transverse septum, breaking off with a frill. Abnormal conidia with a median septum and a broadened base.

*Sclerotial state* referred to *Sclerotium* Pers. *Sclerotia* black, plano-convex, flattened or pulvinate or cerebriform, rounded, lobate or elongate, with the surface smooth,

[4] Rudakov's (1959) new infrageneric categories of *Botrytis* are not validly published, nor is it now possible to assign them their correct positions in the synonymies.

nodulose or echinulate; cortex of textura angularis, cells polygonal with walls thick and brown; medulla of textura intricata, interwoven hyphae with hyaline and gelatinous walls. *Appressoria* dark brown to black, developed by repeated division of the growing hyphae as a flat, palmate body of rectangular cells with walls becoming thick and brown, forming a cortex without a medulla.

*Spermatial state* referred to *Myrioconium* H. Sydow. *Spermodochium* developed from sclerotia or hyphae, sometimes in collapsed hyphal cells, white to isabellinous, typically composed of a sessile or stalked, compact, penicillate cluster of phialides or even of only a single phialide, phialides short, inflated towards the base, tapering at the apex, with or without a collarette; spermatia phialidic, hyaline, globose, minute, thick-walled, uniguttulate, developed in chains and forming mucilaginous masses.

*Perfect state* referred to *Botryotinia* Whetzel.

*Cultures* are readily obtained on standard culture media. Glucose favours stromatic production, while asparagine, hay extract, moderate temperature and near-ultraviolet light favour conidiogenesis. Apothecia form in culture under special conditions.

## SELECTED KNOWN SPECIES

*Botrytis aclada* Fresen., Beitr. Mycol. **1**: 16. 1850 = *Botrytis allii* Munn *in* Bull. N.Y. agric. Exp. Stn **437**: 396. 1917.

*Botrytis byssoidea* Walker *in* Phytopathology **15**: 709. 1925.

**Botrytis calthae** Hennebert, *sp. nov.*; Latin diagnosis in Hennebert & Groves *in* Can. J. Bot. **41**: 343. 1963; holotype: Herb. G.L.H. 3094; conidial state of *Botryotinia calthae* Hennebert & Elliott *in* Hennebert & Groves, *loc. cit.* 343. 1963.

*Botrytis cinerea* Pers., Syn. meth. Fung. 690. 1801 = *Haplaria grisea* Link *in* Mag. Ges. naturf. Freunde, Berlin **3**: 11. 1809. = *Polyactis vulgaris* Link, *loc. cit.* 16. 1809 = *Phymatotrichum gemellum* Bon., Handb. Mykol. 116. 1851 = *Botrytis fuckeliana* Buchw. *in* K. Vet.– og Landbohøjsk. Aarsskr. **1949**: 147. 1949; conidial state of *Botryotinia fuckeliana* (De Bary) Whetzel *in* Mycologia **37**: 679. 1945.

*Botrytis convoluta* Whetzel & Drayton *in* Mycologia **25**: 475. 1932, conidial state of *Botryotinia convoluta* (Drayton) Whetzel *in* Mycologia **37**: 679. 1945.

*Botrytis croci* Cooke & Massee *in* Cooke *in* Grevillea **16**: 6. 1887.

*Botrytis elliptica* (Berk.) Cooke *in* Grdnrs' Chron. **30**: 58. 1901.

*Botrytis fabae* Sárdiña *in* Mems R. Soc. esp. Hist. nat. **15**: 291. 1929.

**Botrytis ficariarum** Hennebert, *sp. nov.*; Latin diagnosis in Hennebert & Groves *in* Can. J. Bot. **41**: 355. 1963; holotype: Herb. G.L.H. 1114; conidial state of *Botryotinia ficariarum* Hennebert *in* Hennebert & Groves, *loc. cit.* 355. 1963.

*Botrytis galanthina* (Berk. & Br.) Sacc., Syll. Fung. **4**: 136. 1886.

*Botrytis gladiolorum* Timm. *in* Meded. Inst. Phytopath. Lab. BloembollOnderz. Lisse **67**: 15. 1941; conidial state of *Botryotinia draytonii* (Budd. & Wakef.) Seaver, North Am. cup-fungi (Inop.) 62. 1951 ("*draytoni*").

*Botrytis globosa* Raabe *in* Hedwigia **78**: 71. 1938; conidial state of *Botryotinia globosa* Buchw. *in* Phytopath. Z. **20**: 250. 1953.

*Botrytis hyacinthi* Westerd. & Beyma *in* Meded. phytopath. Lab. W. C. Scholten **12**: 15. 1928.

*Botrytis narcissicola* Kleb. *ex* Westerd. & Beyma *in* Meded. phytopath. Lab. W. C. Scholten **12**: 8. 1928; conidial state of *Botryotinia narcissicola* (Gregory) Buchw. *in* K. Vet.– og Landbohøjsk Aarsskr. **1949**: 137. 1949.

*Botrytis paeoniae* Oud. *in* Versl. gewone Verg. Afd. Natuurk. K. Ned. Akad. Wet. **1897**: 455. 1897.

*Botrytis perlargonii* Røed *in* Blyttia **7**: 77. 1949; conidial state of *Botryotinia perlargonii* Røed *in* Blyttia **7**: 77. 1949.

*Botrytis polyblastis* Dowson *in* Trans. Br. mycol. Soc. **13**: 102. 1928; conidial state of *Botryotinia polyblastis* (Gregory) Buchw. *in* K. Vet.– og Landbohøjsk. Aarsskr. **1949**: 137. 1949.

*Botrytis porri* Buchw. *in* K. Vet.– og Landbohøjsk. Aarsskr. **1949**: 147. 1949; conidial state of *Botryotinia porri* (Beyma) Whetzel *in* Mycologia **37**: 680. 1945.

**Botrytis ranunculi** Hennebert *apud* Hennebert & Groves *in* Can. J. Bot. **41**: 348. 1963; holotype: Herb. DAOM 57690; conidial state of *Botryotinia ranunculi* Hennebert & Groves, *loc. cit.* 348. 1963.

*Botrytis sphaerosperma* Buchw. *in* K. Vet.– og Landbohøjsk. Aarsskr. **1949**: 148. 1949; conidial state of *Botryotinia sphaerosperma* (Gregory) Buchw., *loc. cit.* 137. 1949.

*Botrytis squamosa* Walker *in* Phytopathology **15**: 710. 1925; conidial state of *Botryotinia squamosa* Viennot-Bourgin *in* Annls Epiphyt. **4**: 38. 1953.

*Botrytis tulipae* Lind, Danish fungi 650. 1913 (often erroneously cited as "(Lib.) Lind") ≡ *Botrytis parasitica* Cavara *in* Atti Ist. bot. Univ. Pavia **2**(1): 432. 1888, not. *B. parasitica* Pers., Mycol. eur. **1**: 35. 1822; sclerotial state: *Sclerotium tulipae* Lib., Crypt. ard. **36**. 1830 ≡ *Botrytis tulipae* (Lib.) Hopkins *in* Mem. Cornell Univ. agric. Exp. Stn **45**: 331. 1921 (later homonym).

### Some names to be excluded

*Botrytis carnea* Schum., Enum. Pl. Saell. **2**: 278. 1803 is *Chromelosporium carneum* (Pers.) Hennebert.

*Botrytis carnea* (Ehrenb.) Spreng. *in* L. Syst. Veg., Ed. 16, **4**(1): 551. 1827 (later homonym) is *Chromelosporium carneum* (Pers.) Hennebert.

*Botrytis crystallina* (Bon.) Sacc., Syll. Fung. **4**: 135. 1886 is *Chromelosporium ollare* (Pers.) Hennebert.

*Botrytis dichotoma* Corda, Icon. Fung. **1**: 18. 1837 is *Chromelosporium ochraceum* Corda.

*Botrytis epigaea* Link *in* L., Sp. Pl., Ed. 4, **6**(1): 53. 1824 is *Chromelosporium tuberculatum* (Pers.) Hennebert.

*Botrytis epigaea* Link var. *ochracea* D. Sacc., Mycoth. ital. *1178*. 1903 is *Chromelosporium ochraceum* Corda.

*Botrytis fulva* Link *in* L., Sp. Pl., Ed. 4, **6**(1): 58. 1824 is *Chromelosporium ollare* (Pers.) Hennebert.

*Botrytis luteo-brunnea* Krem. & Bad. *in* Acta Soc. Bot. Pol. **23**: 727. 1954 is *Chromelosporium ollare* (Pers.) Hennebert.

*Botrytis spectabilis* Harz *in* Bull. Soc. imp. Sci. nat. Moscou **44**(1): 114. 1871 is *Chromelosporium ochraceum* Corda.

*Botrytis terrestris* (Link) Pers., Mycol. eur. **1**: 38. 1822 is *Costantinella terrestris* (Link) Hughes.

*Botrytis terrestris* Brunaud *in* Annls. Acad. Sci. nat. Char. Inf. **24**: 71. 1888 (later homonym) is *Chromelosporium tuberculatum* (Pers.) Hennebert.

*Botrytis terrestris* Jensen *in* Bull. Cornell agric. Exp. Stn **315**: 489. 1912 (later homonym) is *Chrysosporium pannorum* (Link) Hughes.

### A taxonomic redisposition of the species assigned to *PHYMATOTRICHUM* Bon.

*Phymatotrichum baccarum* Oud. *in* Versl. gewone Vergad. Afd. Natuurk. K. Ned. Akad. Wet. **1900**: 392. 1900 is *Aureobasidium pullulans* (Berkh.) Arnaud.

*Phymatotrichum compactum* Pat. *in* Bull. Soc. mycol. Fr. **7**: 162. 1891 ≡ *Botrytis compacta* (Pat.) Sacc., Syll. Fung. **10**: 536. 1892 is **Nodulisporium compactum** (Pat.) Hennebert, *comb. nov.*

*Phymatotrichum doryphorum* (Pound & Clem.) Lindau *pro synon. in* Rabenh., KryptogFl., Ed. 2, **1**(8): 116. 1904 ≡ *Botrytis doryphora* Pound & Clem. *in* Pound, Rep. Bot. Surv. Nebr. **3**: 11. 1894 is a *Botryosporium* species.

*Phymatotrichum epigaeum* (Link) Oud. *in* Verh. K. Akad. Wet. (Nat. II) **11**: 493. 1904 ≡ *Botrytis epigaea* Link 1824 is *Chromelosporium tuberculatum* (Pers.) Hennebert.

*Phymatotrichum fimicola* Dring *in* Trans. Br. mycol. Soc. **42**: 406. 1959 is *Pulchromyces fimicola* (Dring) Hennebert.

*Phymatotrichum fungicola* Zeller *in* Mycologia **21**: 110. 1929 is **Aegerita fungicola** (Zeller) Hennebert, *comb. nov.*

*Phymatotrichum gemellum* Bon., Handb. Mykol. 116. 1851 ≡ *Botrytis gemella* (Bon.) Sacc. *in* Michelia **2**: 258. 1881 (iconotype: Bon., *loc. cit.* f. 138; lectotype species of *Phymatotrichum*) is *Botrytis cinerea* Pers.

*Phymatotrichum gossypinum* (Bres.) Trotter *in* Sacc., Syll. Fung. **25**: 697. 1931 ≡ *Botrytis gossypina* Bres. *in* Annls mycol. **18**: 57. 1920 is *Trichoderma polysporum* (Link) Rifai.

*Phymatotrichum hamatum* (Bon.) Oud. *in* Ned. Kruidk. Arch. III **2**: 908. 1903 ≡ *Verticillium hamatum* Bon., Handb. Mykol. 97. 1851 is *Trichoderma hamatum* (Bon.) Bainier.

*Phymatotrichum laneum* Bon., Handb. Mykol. 116. 1851 ≡ *Botrytis lanea* (Bon.) Sacc., Syll. Fung. **4**: 136. 1886 is *Chromelosporium tuberculatum* (Pers.) Hennebert.

*Phymatotrichum omnivorum* Duggar *in* Ann. Mo. bot. Gdn **3**: 22. 1916 is *Phymatotrichopsis omnivora* (Duggar) Hennebert.

*Phymatotrichum paeoniae* (Oud.) Oud. *in* Verh. K. Akad. Wet. (Nat. II) **11**: 493. 1904 ≡ *Botrytis paeoniae* Oud., an accepted species of *Botrytis*.

*Phymatotrichum pyramidale* Bon., Handb. Mykol. 116. 1851 ≡ *Botrytis pyramidalis* (Bon.) Sacc., Syll. Fung. **4**: 135. 1886 ≡ *Botryosporium pyramidale* (Bon.) Cost., Muced. simpl. 45. 1888 is *Botryosporium pulchrum* Corda.

*Phymatotrichum silvicola* Tabenh. & Watkins *in* Am. J. Bot. **24**: 390. 1937 ("*silvicolum*") is *Chromelosporium tuberculatum* (Pers.) Hennebert.

*Phymatotrichum tilletii* (Desm.) Oud. *in* Verh. K. Akad. Wet. (Nat. II) **11**: 493. 1904 ≡ *Botrytis tilletii* Desm. *in* Annls Sci. nat (Bot.) II **10**: 308. 1838 ("*tilletei*") is *Costantinella terrestris* (Link) Hughes.

## 2. **Streptobotrys** Hennebert, *gen. nov.*

Type species: *S. streptothrix* (Cooke & Ellis) Hennebert.

Coloniae effusae, griseae deinde brunneae, hyphis hyalinis seu brunneis, septatis, ramosis. Conidiophori erecti, solitarii vel caespitosi, magni, laxos racemos conidiorum ferentes; stipites cylindrici, brunnei, septati, stricti, sursum ramosi, ramis longis, tortilibus, iterum ramosis, ramulis extremis in apice conidiogenis, non inflatis, simul conidia ad pediculos producentibus, tarde dilabentibus. Conidia holoblastica, globosa, subhyalina vel brunnea, laevia, cum basali vestigio pediculi. Sclerotia minuta. Spermatia phialidica hyalina. Species typica, *Streptobotrys streptothrix* (Cooke & Ellis) Hennebert.

*Colonies* effuse, grey turning soon to dark grey and dark brown; hyphae hyaline to brown, septate, branched and anastomosing. *Conidiophores* erect, single or in groups of 2 or 3, tall, with large, lax conidial heads; stipe cylindrical, brown, septate, often with a slightly swollen basal cell, wall straight, at about half height alternately branched at a wide angle, branches long, with the wall tightly twisted and branched again several times, the last branchlets at right angles near the ends, each apical cell of branches and branchlets delimited by a septum, remaining unswollen, conidiogenous, producing 2 to 6 simultaneous conidial buds on short pedicels, and collapsing at maturity, leaving the branches with terminal, perpendicular stumps which do not proliferate. *Conidia* holoblastic, regularly globose, subhyaline to brown, smooth, bearing an inconspicuous frill at the basal septum.

*Sclerotial state* referred to *Sclerotium* Pers. *Sclerotia* of small size and similar to those of *Botrytis*.

*Spermatial state* referred to *Myrioconium* Sydow. *Spermodochium* similar to that of *Botrytis*.

*Perfect state* referred to *Streptotinia* Whetzel.

*Cultures* are readily obtained, fast growing, developing both conidia and sclerotia on most standard media under daylight or near-ultraviolet light and moderate temperature. Perfect states have been obtained in culture (Elliott 1962, 1969).

DESCRIBED SPECIES

**Streptobotrys arisaemae** Hennebert, *sp. nov.*; Latin diagnosis in Whetzel *in* Mycologia **37**: 686. 1945; holotype: Herb. CUP 8377; conidial state of *Streptotinia arisaemae* Whetzel, *loc. cit.*

**Streptobotrys caulophylli** Hennebert *sp. nov.*; Latin diagnosis in Elliott *in* Can. J. Bot. **40**: 1200. 1962; holotype: Herb. DAOM 75514; conidial state of *Streptotinia caulophylli* Elliott, *loc. cit.*

**Streptobotrys streptothrix** (Cooke & Ellis) Hennebert, *comb. nov.* ≡ *Polyactis streptothrix* Cooke & Ellis *in* Grevillea **7**: 39. 1878 ≡ *Botrytis streptothrix* (Cooke & Ellis) Sacc., Syll. Fung. **4**: 127. 1886.

## 3. **Amphobotrys** Hennebert, *gen. nov.*

*Botrytis* Pers. subgen. *Sphaerobotrytis* Buchw. *in* K. Vet.– og Landbohøjsk. Aarsskr. **1949**: 146. 1949 *pro parte typica* (no Latin diagnosis). — Type species: *Amphobotrys ricini* (Buchw.) Hennebert.

Coloniae effusae, ochro-griseae deinde brunneae, hyphis hyalinis, septatis, ramosis. Conidiophori erecti, solitarii, magni, laxos racemos conidiorum ferentes; stipites cylindrici, pallide brunnei, septati, sursum dichotomice bifurcati, ramis symmetricis, divaricatis, longis, cylindricis, repetito bifurcatis, in apice geminatis globosis, inflatis cellulis conidiogenis, simul conidia ad pediculos ferentibus et deinde dilabentibus. Conidia holoblastica, globosa, subhyalina vel brunnea, laevia, cum basali vestigio pediculi. Sclerotia media et spermatia phialidica hyalina. Species typica, *Amphobotrys ricini* (Buchw.) Hennebert.

*Colonies* effuse, white turning grey-ochraceous to brown, hyphae hyaline, septate, branched. *Conidiophores* erect, single, tall, with large, lax conidial heads; stipe cylindrical, light brown, septate, at about half height bifurcate at a wide angle, branches almost symmetrical, long, cylindrical, repetitively bifurcating at shorter intervals to produce groups of paired, globose, inflated, terminal conidiogenous cells, each developing simultaneous conidial buds on short pedicels, then collapsing at maturity. *Conidia* holoblastic, regularly globose, subhyaline to brown, smooth, bearing an inconspicuous frill at the basal septum.

*Sclerotial state* referred to *Sclerotium* Pers. *Sclerotia* of small size, similar to those of *Botrytis*.

*Spermatial state* referred to *Myrioconium* Sydow, similar to that of *Botrytis*.

*Perfect state* referred to *Botryotinia* Whetzel.

*Cultures* readily obtained on standard culture media. Perfect state unknown in culture.

DESCRIBED SPECIES

**Amphobotrys ricini** (Buchw.) Hennebert, *comb. nov.* ≡ *Botrytis ricini* Buchw. *in* K. Vet.– og Landbohøjsk. Aarsskr. **1949**: 148. 1949 (Latin diagnosis by reference to Godfrey, 1919) = *Botrytis bifurcata* Miller, Giddens & Foster *in* Mycologia **49**: 789. 1957; conidial state of *Botryotinia ricini* (Godfrey) Whetzel *in* Mycologia **37**: 680. 1945.

## 4. **Verrucobotrys** Hennebert, *gen. nov.*

*Botrytis* Pers, subgen. *Verrucobotrytis* Buchw. *in* K. Vet.– og Landbohojsk. Aarsskr. **1949**: (no Latin diagnosis). — Type species: *Verrucobotrys geranii* (Seaver) Hennebert.

Coloniae effusae, brunneae, hyphis subhyalinis vel brunneis, septatis, ramosis. Conidiophori erecti, singuli, apice ramosi; stipes cylindrici, septati, brunnei, crasso pariete; rami racemum conidiorum formantes laterales, alternati, terminalibus cellulis non inflatis, conidiogenis, simul pauca conidia ad pediculos producentibus, rami tarde pro magna parte dilabentes, stipites e cicatricibus apicalibus et lateralibus deinde proliferantes. Conidia holoblastica, pyriformia vel subglobosa, brunnea, basi applanata, crasso et interno valde punctato pariete, cum obscuro vestigio pediculi dilabentia. Stromata in substrato delineata. Species typica, *Verrucobotrys geranii* (Seaver) Hennebert.

*Colonies* effuse, white turning brown, hyphae subhyaline to brown, branched, septate. *Conidiophores* erect, single, stipe cylindrical, septate, brown, thick-walled, with lateral, alternate branches near the apex, forming a tree-like conidial head, successively developed from the base to the apex and branched again as in *Botrytis*, each terminal cell of branches unswollen, conidiogenous, producing 2 to 3 simultaneous conidial buds on short pedicels, the greater part of the branches collapsing and breaking off at conidium maturity leaving scars on the main axis, which may proliferate axially and laterally to produce new conidial heads. *Conidia* holoblastic, pyriform to subglobose, with a flattened base, mostly without a frill, brown, with thick walls, an inner wall layer heavily punctate.

*Stromatal state* not a true sclerotium but a substratal stroma, delimited by a black line formed of rind-like, dark, thick-walled cells and filled with medullary, interwoven, thin-walled hyphae mixed with host tissues; developing *in vitro* in irregular large areas of subhyaline to brown hyphae delineated with a dark line of compacted, thick-walled, brown hyphal cells.

*Spermatial state* not observed.

*Perfect state* referred to *Seaverinia* Whetzel.

*Cultures* readily obtained on standard culture media. Perfect state unknown in culture.

### DESCRIBED SPECIES

**Verrucobotrys geranii** (Seaver) Hennebert, *comb. nov.* ≡ *Botrytis geranii* Seaver *in* Mycologia **39**: 116. 1947; conidial state of *Seaverinia geranii* (Seaver & Horne) Whetzel *in* Mycologia **37**: 705. 1945.

## 5. **Dichobotrys** Hennebert, *gen. nov.*

Type species: *D. abundans* Hennebert.

Coloniae effusae, ochraceae hyphis hyalinis, laxis. Conidiophori erecti, magni, repetito dichotomice furcati; rami longi, divaricati, sursum curtiores, terminalibus geminatis globosis inflatis conidiogenis cellulis, simul conidia producentes, demum collabentibus. Conidia holoblastica, singula, sessilia vel pedunculata, subglobosa vel napiformia, laevia, superne saepe crassiori parite, inferne tenui pariete, cum vestigio pediculi dilabentia. Species typica, *Dichobotrys abundans* Hennebert.

*Colonies* large, effuse, pale to dark ochraceous, creeping hyphae hyaline, loose. *Conidiophores* erect, tall, dichotomously furcate at about half height, branches long, symmetrical, divergent, and furcating symmetrically several times at shorter lengths

up to the apex, terminal branches each bearing paired, round, inflated conidiogenous cells developing simultaneous conidial buds, then collapsing at maturity. *Conidia* holoblastic, single, sessile or on pedicels, subglobose to napiform with an equally thick wall or with a thicker wall on the upper half than on the lower half, wall smooth, with the basal septum often at some distance down in the pedicel, breaking off at maturity by rupture of the pedicel under the septum, leaving a conspicuous frill.

*Perfect state* referred to *Trichophaea* Boudier.

*Cultures* readily obtained on standard culture media, both conidial and perfect states being produced.

DESCRIBED SPECIES

**Dichobotrys abundans** Hennebert, *sp. nov.*; conidial state of *Trichophaea abundans* (Karst.) Boud., Hist. class. Discomyc. Eur. 61. 1907.

Coloniae effusae, primum albae, demum ochraceae, hyphis hyalinis, prostratis. Conidiophori erecti, 7 – 10 µm crassi, septati, dichotomice furcati, ramis primis 100 – 200 µm longis, secondariis 50 – 65 µm, tertiis 20 – 30 µm, apicalibus cellulis rotundis inflatis, conidiogenis, 10 – 15 µm diametro, usque 10 vel 15 conidia ferentes. Conidia ad pediculum 2–3 µm longum, 1 µm crassum ennata, subglobosa vel napiformia, laevia, superno pariete parce crassiori, ochracea, pedicellata, cum pediculi vestigio liberata, (5–) 8–11 (–15) × 7–9 µm. Holotypus: Herb. G.L.H. 3168, in sterilisato humo, Salinas, California, 1. III. 1963, leg. E. E. Butler.

**Dichobotrys brunnea** Hennebert, *sp. nov.*; conidial state of *Trichophaea brunnea* (Alb. & Schw.) Batra *in* Batra & Batra *in* Kansas Univ. Sci. Bull. **44**: 167. 1963.

MISAPPLIED NAME. — *Sphaerospora hinnulea* (Berk. & Br.) Massee *sensu* Wolf *in* J. Elisha Mitchell scient. Soc. **79**: 159. 1963 (fide R. P. Korf., *pers. comm.*).

Coloniae effusae, floccosae, primum albae, demum griseo-brunneae, hyphis hyalinis, septatis, ramosis. Conidiophori magni, erecti, parce ramosi, 2-3-repetite dichotomici, cellulis apicalibus ramorum inflatis rotundis, geminatis, 6–12 simul ennata conidia ferentibus. Conidia hyalina, globosa, 12–15 µm diametro. Habitat in humo in viridicario. Holotypus (iconotypus); Wolf *in* J. Elisha Mitchell scient. Soc. **79**: 157. *f.* 1*F*. 1963.

**Dichobotrys parvispora** Hennebert, *sp. nov.*; conidial state of **Trichophaea saccata** (Evans) Korf, *comb. nov.* ≡ *Sphaerospora saccata* Evans *in* Trans. Br. mycol. Soc. **57**: 244. 1971.

Coloniae effusae, primum albae, demum ochraceae, hyphis hyalinis, prostratis, septatis. Conidiophori erecti, cylindrici, 8–10 µm crassi, parce septati, dichotomice ramosi, ramis primariis 100–500 µm longis, secondariis et posterioribus curtioribus ultimis 15–40 µm, pluries septatis, terminalibus cellulis rotundis inflatis, conidiogenis, 10–14 µm diametro, numerosa conidia ferentibus. Conidia singula ad 1 µm crassum pediculum ennata, napiformia vel subglobosa, raro cordata vel obovata, e visu laterali, circularia e visu apicali, tarde superne crassiori pariete, inferne depresso pariete, laevia, 4–6 µm alta × 4–8 µm lata, cum vestigio pediculi dilabentia. Habitat prope thermis in cumulo deiecto carbonariorum. Holotypus: Herb. G.L.H. 11949, ex CBS 804.70, Staffordshire, Anglia, Maio 1968, leg. H. C. Evans.

**Dichobotrys sessilispora** Hennebert, *sp. nov.*; Latin diagnosis in Cain & Hastings *in* Can. J. Bot. **34**: 360. 1956; holotype: Herb. TRTC 30102; isotype: Herb. G.L.H. 2221; type maintained as living culture, ATCC 18897, MUCL 2221; conidial state of **Trichophaea minuta** (Cain) Korf, *comb. nov.* ≡ *Sphaerospora minuta* Cain *in* Cain & Hastings, *loc. cit.*

6. CHROMELOSPORIUM Corda *in* Sturm, Deutschl. Fl. III (Pilze), **3**(13): 81. *t. 41.* 1833. — Type species: *C. ochraceum* Corda (monotype).

*Hyphelia* Fr., Summa Veg. Scand. 447. 1849; not *Hyphelia* Fr., Syst. Orb. Veg. 149. 1825 [holotype species, *Trichoderma roseum* Pers. ≡ *H. rosea* (Pers.) Fr.]. ≡ *Hyphelia* Fr. [subgen.?]** *Hyphomycetoidea* Fr., Syst. mycol. **3**(1): 213. 1829. ≡ *Hyphelia* Fr. [subgen.?] *Geohypha* Fr., Summa Veg. Scand. 447. 1849. — Type species: *H. terrestris* Fr. (lectotype, selected by Juel, 1920). (Later homonym by exclusion of holotype: see Donk, 1962a.)

*Botrytis* Pers. 'tribus' *Paniculatae* Fr., Syst. mycol. **3**(2): 405. 1832. ≡ *Botrytis* Pers. [subgen.?] A. *Eubotrytis* Sacc. Syll. Fung. **4**: 116. 1886. — Type species: *Botrytis carnea* Schum. (lectotype selected here for both taxa).

*Colonies* effuse or in small patches, velvety or tufted, at first white, then diversely coloured, rose, purple, violet, lilac, blue, yellow, ochraceous, grey or brown, developing on the substratum either a dense subiculum or a loose network of creeping, hyaline to fulvous, often broad, thin-walled, simple or aggregated, fast growing hyphae, soon collapsing at maturity. *Conidiophores* erect, either mononematous, solitary or caespitose, or in fasciculate synnemata, very short to long, apically developing small, individual, radiate or pulvinate to larger, compacted conidial heads; stipes hyaline to ochraceous fulvous, cylindrical, septate, thin-walled, anastomosing when synnematous, dichotomously furcate at the apex; branches short or longer, repeatedly branched, regularly dichotomous to irregularly coralloid, with or without symmetrical septation, parallel or divergent, cylindrical, straight, or slightly inflated with blunt tips, hyaline, thin-walled, conidiogenous either on their terminal cell or along several dichotomies backwards, producing numerous, simultaneous, well-spaced conidial buds on conspicuous pedicels, collapsing almost entirely at conidium maturity. *Conidia* holoblastic, borne singly on pedicels, globose, subglobose or ovate, at first smooth and hyaline, diversely coloured in mass, with the inner wall finely punctate, verrucose, echinulate or coarsely warted, ornamentation cyanophilic, and external wall smooth and translucid.

*Perfect state* referred to *Peziza* Pers.

*Cultures* readily obtained from ascospores, conidia and hyphae on standard media from species with known perfect states; from most unconnected species, germination of conidia fails to occur, as also reported by Brefeld (1888), but growth from hyphal transfers has been obtained.

NOTES: Brefeld (1888) described and illustrated basidial fungi observed by Johan-Olsen, his assistant, in connection with some of the species assigned here. *Tomentella flava* Bref. [= *Botryohypochnus isabellinus* (Fr.) J. Erikss.] was said to be associated with *Botrytis argillacea* Cke. or *B. gemella* (Bon.) Sacc. *sensu* Sacc. (i.e. *Chromelosporium carneum* of this treatment), and *T. granulata* Bref. with *B. epigaea* Link (i.e., *C. tuberculatum*). He confessed explicitely not to have seen conidial and basidial states in direct connection on the same hypha, but assumed their mutual relationship from the striking similarities of their hyphae and spores and from their regular concomitance in nature. Von Höhnel (1907) added to these observations, connecting *B. isabellina* Preuss (i.e. *C. ochraceum*) to *T. isabellina* (Fr.) Höhn. (= *T. flava*), and *B. carnea* Schum. (≡ *C. carneum*) with *T. fusca* (Pers.) Höhn. No demonstration of these connections has ever been provided.

However, several authors have assumed the correctness of Brefeld's and von

Höhnel's assertions. Juel (1920), while describing the similar conidial apparatus in *Chromelosporium* (as *Hyphelia*) and in *Ostracoderma* (also as *Hyphelia*) indicated the presumed basidial state, following Brefeld. Heim & Malençon (1933), and Malençon (1960), with the same faith in Brefeld's statements, concluded these fungi were basidiomycetous.

As Lohwag (1934) already foresaw, it is now established that a number of species of this genus are conidial states of Operculate Discomycetes. All fall in the genus *Peziza* in its broad sense, including spherical- and elliptical-spored species (Schneider, 1954; Wolf, 1955, 1958; Korf, 1961; Paden, 1972).

Details of the conidial apparatus as seen under the electron microscope have been provided for *Chromelosporium ollare* (conidial *Peziza ostracoderma*) by Hughes & Bisalputra (1970).

## Described species

**Chromelosporium arenosum** Hennebert, *sp. nov.*

Fungus imperfectus. Coloniae pellucidae, sporulantes arenosae, primum albae, demum cretaceae, hyphis teneribus, sparsis, araneosis, parce septatis, 7–9 $\mu$m crassis, facile evanescentibus, saepe regenerantibus. Conidiophori mononemati, brevissimi, erecti, sparsi, solitarii, stipes 70–100 $\mu$m longi, 8–9 $\mu$m crassi, basi inflata, cylindracei sed ad septos constricti, 2 septati, in apice 1–3-dichotomice furcati; rami breves, intermedii 10–15 $\mu$m longi, 6–7 $\mu$m crassi, terminales usque ad 50 $\mu$m longi, 13 $\mu$m crassi, in tota longitudine conidiogeni. Conidia singula ad denticulum, globosa vel ovata, 3.5–5.5 × 3.5–6.5 $\mu$m, crasso pariete, externo laevi et hyalini, interno tuberculato cum 6–10 rotundis cyanophilis verrucis in mediano visu. Habitat in putrido ligno. Holotypus: Herb. K., Flora Venezuelae 2474, ad lignum putridum *Espeletiae*, 3550 m. alt., Mucudaji, Sanide Santo Domingo, Estado Mesida, Venezuela, 22 Julio 1958, leg. R. W. G. Dennis; isotypus: Herb. G.L.H. 2298, DAOM 83359.

**Chromelosporium canadense** Hennebert, *sp. nov.*

Fungus imperfectus. Coloniae effusae, laxae, primum albae, demum fulvae vel cinnamomeae, hyphis crassis, teneribus, evanescentibus. Conidiophori mononemati, erecti, singuli, fulvi, parce septati, stipites 200–300 $\mu$m longi, cylindrici, 8–10 $\mu$m crassi, regulariter et repetite dichotomici, ramis vere divaricatis, longis, primariis 160–200 $\mu$m longis, terminalibus conidiogenis, brevibus, continuo geminatis vel quaternis, symmetricis, 16–48 $\mu$m longis, 10–12 $\mu$m crassis. Conidia singula ad denticulum, fulva, globosa, 4–6.6 $\mu$m diametro, verrucosa, 10–20 verrucis in mediano visu. Habitat in putrescentibus muscis et ligno, autumno. Holotypus: Herb. DAOM 71947, and lignum putridum in sylvis, Gatineau Park, Gatineau, Quebec, Canada, 25 Nov. 1960, leg. S. J. Hughes socio G. L. Hennebert; isotypus: Herb. G.L.H. 1689-A.

NOTE: The fungus has been obtained several times in culture on Hagem's Medium, but remained sterile.

**Chromelosporium carneum** (Pers.) Hennebert, *comb. nov.* ≡ *Isaria carnea* Pers., Syn. meth. Fung. 698. 1801. — Neotype specimen, designated here: Herb. G.L.H. 1208, on leaves of *Quercus pedunculatus* and *Fagus sylvatica*, Forêt de Soignes, Tervueren, Belgium, 18 Aug. 1960, leg. G. L. Hennebert.

NOTE: This species forms synnematous conidiophores, and commonly develops on dead leaves in Europe, more rarely in America. A perfect state is unknown.

**Chromelosporium coerulescens** (Bon.) Hennebert, *comb. nov.* ≡ *Polyactis coerulescens* Bon. *in* Fresen., Beitr. Mykol. **1**: 14. 1850 ≡ *Botrytis coerulescens* (Bon.) Sacc., Syll. Fung. **4**: 132. 1886. — Neotype specimen, selected here: Herb. G.L.H. 2323, on rotting leaves and humic debris of *Acer saccharum*, *Betula lutea* and *Tsuga canadensis* in mixed woods, Bell's Corners, Ontario, Canada, 30 July 1961, leg. G. L. Hennebert.

NOTES: This species is synnematous, and is intermediate between *C. carneum* and *C. tuberculatum*. It is remarkable for its bright, crystal blue color, turning rose violet. It grows in large patches on decayed wood and mosses in the forest, and is common in America, rare in Europe. A perfect state is unknown.

**Chromelosporium macrospermum** Hennebert, *sp. nov.* '

Coloniae arancosae, albae, demum sporulantes ferrugineae, hyphis teneribus, laxis, intricatis, prostratis, hyalinis vel subhyalinis, producentibus laterales cellulas magnas, sphaericas, 40–50 μm diametro, tenui pariete. Conidiophori mononemati, erecti, pallidi vel ferruginei, cylindrici, septati, stipites 400–600 × 15–18 μm, apice bis usque quater dichotomice furcati; rami cylindrici, 20 μm crassi, parce septati, terminales erecti, radiati, cylindrici vel clavati, 130–160 μm longi, 20 μm crassi, conidiogeni, tarde evanescentes. Conidia singula ad pediculum, globosa, laevia, ferrugineae, 15–23 μm diametro. Status perfectus: *Peziza* sp. indet. Holotypus: Herb. G.L.H. 1116, cultura sicca ex ascosporis *Pezizae*, in sterilisata terra in caldo viridicario, Heverlee, Belgio, 2 Aprili 1960, leg. G. L. Hennebert.

NOTES: This species differs from *C. ollare* in having conidia twice the diameter of those in that species. The perfect state material represents an apparently undescribed species, but is perhaps too fragmentary to serve as a type specimen (R. P. Korf, *pers. comm.*).

*Chromelosporium ochraceum* Corda *in* Sturm, Deutschl. Fl. III (Pilze), **3**(13): 81, *t. 41*. 1833.

NOTES: The species is characterized by mononematous conidiophores with long, dichotomous branches and verrucose conidia. It commonly develops on litter materials in deciduous forests. A perfect state is unknown, and attempts to culture it have failed.

**Chromelosporium ollare** (Pers.) Hennebert, *comb. nov.* ≡ *Dematium ollare* Pers., Syn. meth. Fung. 697. 1801; conidial state of *Peziza ostracoderma* Korf *in* Mycologia **52**: 650. 1961 ("1960"). — Neotype specimen, designated here: Herb. G.L.H. 1112, on damp, sterilized soil in greenhouse, Berlin, March 1953, leg. R. Schneider; type maintained as a living culture, CBS 382.54, MUCL 1112.

NOTE: The conidial state of this common greenhouse fungus has, following the classification of Hughes (1958), been assigned to *Ostracoderma* (Korf, 1961; Fergus, 1961; Barron, 1968; von Arx, 1970).

**Chromelosporium trachycarpum** Hennebert, *sp. nov.* = ? *Rhinotrichum trachycarpum* Wolf *in* J. Elisha Mitchell scient. Soc. **74**: 166. 1958 (type not indicated); conidial state of *Peziza trachycarpa* Currey.

Coloniae pellucidae, primum albae, demum ochroleucae vel ochraceae, velociter crescentes, hyphis teneribus, prostratis, intricatis, aggregatis, hyalinis. Conidiophori erecti, breves, 50–100 μm longi, in apice multiplice dichotomice furcati; rami cylindracei, breves, 20–55 μm longi, 8–10 μm crassi, aperte divaricati, conidiogeni toti, capita compacta pulvinata formantes. Conidia singula ad pediculum, pallide luteo-ochracea, globosa vel breve ovata, externa laevia, interne granulata vel verruculosa, 10–15 verrucis in mediano sectione, 5–9 × 5–7 μm. Habitat in foci locis, in sylvis. Holotypus: Herb. G.L.H. 2197, cultura sicca ex ascosporis *Pezizae trachycarpae* in foci loco in sylva, Campo undecimo, Alleghany State Park, N.Y., America sept., 11 Juno 1961, leg. G. L. Hennebert; ascophoro stato adjunte preservato (Herb. DAOM 83.324, G.L.H. 2197; det. confirm. R. P. Korf).

**Chromelosporium tuberculatum** (Pers.) Hennebert, *comb. nov.* ≡ *Trichoderma tuberculatum* Pers., Syn. meth. Fung. 234. 1801 = *Hyphelia terrestris* Fr., Syst. mycol. **3**(1): 213. 1829.

NOTES: This common species develops byssoid patches on naked, loamy soil in the forest, and is characterized by synnematous, compacted conidiophores of variable colour, bearing verrucose conidia. A perfect state is unknown.

*Chromelosporium* state of *Peziza endocarpoides* Berk. *in* Hook. f., Fl. Nov. Zeal. **2**: 199. 1855 = *Peziza leiocarpa* Curr. *in* Trans. Linn. Soc. Lond. (Bot.) **24**: 493. 1864.

NOTE: The state developed in artificial culture consists of compacted patches of conidiophores bearing globose to obovate, verruculose conidia in strains received from Dr. J. W. Paden.

### 7. **Pulchromyces** Hennebert, *gen. nov.*

Type species: *P. fimicola* (Dring) Hennebert.

Fungi imperfecti. Coloniae effusae, primum albae, sporulantes ferrugineae, velociter crescentes, petaliformes vel zonatae, hyphis hyalinis. Conidiophori mononemati, erecti, magnissimi, singuli vel caespitosi, hyalini demum brunnescentes, parce septati, crasso pariete, ex apice stipitis spiraliter numerosos laterales ramos formantes; rami aequales, radiati, 2–4-fide dichotomice furcati, terminalibus cellulis longis, cylindricis, conidiogenis, fere simultanea conidia ad pediculos producentibus, praeter sterilem attenuatam et acutam apicalem partem, totis ramis evanescentibus et cadentibus a stipite in maturitate. Conidia holoblastica, singula ad pediculum, sphaerica, juvenia hyalina et laevia, matura ferruginea et reticulata, crasso pariete, prominente basi praedita. Habitat in rosoris fimo, Africa, America. Species typica, *Pulchromyces fimicola* (Dring) Hennebert.

*Colonies* effuse, at first white, then ferrugineous when sporulating, fast growing, petaloid to zonate, hyphae hyaline, septate, often aggregated. *Conidiophores* mononematous, erect, very tall, single or caespitose, hyaline turning brown, sparingly septate, thick-walled, producing spirally at the apex of the stipe numerous lateral branches; branches of equal length, radiate, 2 to 4 times dichotomously furcate, with terminal cells longer, cylindrical, conidiogenous, producing almost simultaneous conidia on pedicels, except at the sterile, tapered and acute end, branches collapsing and breaking off from the stipe at conidium maturity. *Conidia* holoblastic, single on a pedicel, spherical, hyaline and smooth when young, then ferrugineous and reticulate, with a prominent base. Habitat in rodent dung.

*Perfect state* unknown.

*Cultures* readily obtained on standard media.

DESCRIBED SPECIES

**Pulchromyces fimicola** (Dring) Hennebert, *comb. nov.* ≡ *Phymatotrichum fimicola* Dring *in* Trans. Br. mycol. Soc. **42**: 406. 1959.

8. **Phymatotrichopsis** Hennebert, *gen. nov.*

Type species: *P. omnivora* (Duggar) Hennebert

Fungi imperfecti. Coloniae araneosae, floccosae, hirsutae, implexae vel compactae, luteo-ochraceae vel brunneae, persistentes. Mycelium ex hyphis septatis, fibulis destitutis, ramosis, saepe anastomosis et multiseptatis in funiculos aggregatis, cum aerialibus cruciatis hirsutis setis praeditis. Conidiophori laterales in hyphis ennati, simplices vel ramosi, moniliformes, terminalibus et subterminalibus cellulis inflatis, globosis, conidiogenis, fere simultaneiter sessilia conidia producentibus. Conidia holoblastica, globosa vel ovata, laevia, tenui pariete, ampla basi cum vestigio praedita. Habitat ad vivendarum plantarum basim in terra. Perfectus status incognitus. Species typica, *Phymatotrichopsis omnivora* (Duggar) Hennebert.

*Colonies* araneose, floccose, bristly, matted or compacted, yellow-ochraceous to brown, persistent. Mycelium composed of septate hyphae, without clamps, branched, often anastomosing, more closely septate and aggregated into funicles, provided with aerial, cruciate, hair-like setae. *Conidiophores* borne laterally on hyphae, simple or branched, moniliform, with terminal and subterminal cells inflated, globose, conidiogenous, producing almost simultaneously sessile conidia. *Conidia* holoblastic, globose or ovate, smooth, thin-walled, with a broad base and a frill of attachment. Habitat at the base of living plants in soil.

*Perfect state* unknown.

*Cultures* are readily obtained from hyphae, but sporulate sparsely on artificial media.

DESCRIBED SPECIES

**Phymatotrichopsis omnivora** (Duggar) Hennebert, *comb. nov.* ≡ *Phymatotrichum omnivorum* Duggar *in* Ann. Mo. bot. Gdn **3**: 11. 1916; mycelial state: *Ozonium omnivorum* Shear *in* Bull. Torrey bot. Club **34**: 305. 1907 = *Hydnum omnivorum* Shear *in* J. agric. Res. **30**: 476. 1925 (illegitimate, perfect state name based on an imperfect state type).

NOTES: A "perfect state" has been described by Shear (1925) as being produced by *Ozonium omnivorum*, and was referred to as *Hydnum omnivorum* only on the basis of the external, hydnoid aspect of the mycelial state. No basidia or basidiospores were observed by Shear, nor by Dr. L. K. Weresub and myself when we studied the type collection. Another basidial state, associated with bulbils and identified as *Trechispora brinkmannii* [i.e., *Sistotrema brinkmannii* (Bref.) J. Erikss.], has been indicated by Banieki & Bloss (1970) as being connected to *Phymatotrichum omnivorum*. Comparison of pure cultures of *S. brinkmannii* and *Phymatotrichopsis omnivora* makes evident, as suggested by Weresub & Leclair (1972), that the connection of these two fungi is most doubtful.

9. OSTRACODERMA Fries, Syst. Orb. Veg. **1**: 150. 1825.

Type species: *O. pulvinatum* Fries (monotype).

*Lycoperdellon* Torrend *in* Broteria (Bot.) **11**: 92. 1913. — Type species: *L. torrendii* (Bres.) Torrend.

*Fruitbodies* solitary or gregarious, variable in size, emerging from a subiculum of septate hyphae, expanding from hemispherical to subglobose or globose, sessile or subpedicellate, covered with a crustaceous, diversely coloured peridium from pale grey to testaceous brown, and with a gleba composed of conidiophores which are white, rose, grey or ochre-yellow in mass. *Peridium* glabrous, pellicular, brittle, entirely covering the fruitbody, splitting or breaking down at maturity, composed of interwoven, septate, branched hyphae, the most external ones thick-walled and encrusted with some cementing material, the internal ones with a thinner wall and developing fertile granches inwards. *Gleba* composed of a subperidial layer of branched hyphae developed from the base of the fruitbody and producing apically numerous, dichotomous to coralloid branches filling the central cavity; branches cylindrical to slightly swollen and sinuous, sparingly septate, conidiogenous much of their length, producing simultaneously numerous, well-spaced conidia on pedicels. *Conidia* holoblastic, single on each pedicel, globose, ovate or elliptical, hyaline or pale coloured, with an external, smooth, transparent wall, the inner wall not ornamented but cyanophilic, breaking off with a scar of attachment. Habitat on soil surface.

*Perfect state* unknown.

*Cultures* were not established when conidia were placed on artificial media; no germination occurred.

NOTES: The question has been raised, for the species of *Lycoperdellon*, as to whether these fungi belong to the Basidiomycetes or the Ascomycetes. Since that genus is synonymous, the question now applies to *Ostracoderma*. Heim & Malençon (1933) first described the conidial nature of the spores in *Lycoperdellon*. They argued, however, in favour of its assignment to the Gasteromycetes, a position which was opposed by Lohwag (1933) who favoured the Ascomycetes. While Fischer (1933), Heim (1949) and Malençon (1960, 1964a, 1964*b*) were still inclined to regard them as Basidiomycetes, Zeller (1948) simply suggested to keep them in the Fungi Imperfecti, as long as basidia or asci had not been found. Donk (1962a, 1962b) implied from the similarities between the conidial apparatus of *Lycoperdellon* and that of *Peziza ostracoderma* that *Lycoperdellon* might well prove to be the conidial state of a Discomycete.

Recent electron microscopic studies carried out by R. Bronchart and V. Demoulin of the Botany Department, University of Liège, Belgium, on *Ostracoderma torrendii* demonstrated in this fungus the existence of a septal pore characteristic of the Ascomycetes (V. Demoulin, *pers. comm.*). The paired bodies observed near the septa in *O. pulvinatum* by Juel (1920) and in *L. torrendii* by Malençon (1960) are presumably Woronin bodies like those accompanying the septal pore in Bronchart and Demoulin's unpublished photographic documents.

DESCRIBED SPECIES

**Ostracoderma minutum** (Heim) Hennebert, *comb. nov.* ≡ *Lycoperdellon minutum* Heim *in* Treb. Mus. Ci. nat., Barcelona (Bot.) **15**: 138. 1934.

*Ostracoderma pulvinatum* Fr., Syst. mycol. **3**(1): 214. 1829.

**Ostracoderma sphaerosporum** (Dissing & Lange) Hennebert, *comb. nov.* ≡ *Lycoperdellon sphaerosporum* Dissing & Lange *in* Bull. Jard. bot. État Brux. **32**: 408. 1962.

**Ostracoderma torrendii** (Bres.) Hennebert, *comb. nov.* ≡ *Lycogala torrendii* Bres. *in* Torrend *in* Broteria (Bot.) **7**: 28. 1908 ≡ *Lycoperdellon torrendii* (Bres.) Torrend *in* Broteria (Bot.) **11**: 92. 1913.

NAMES TO BE EXCLUDED

*Ostracoderma carneum* (Ehrenb.) Hughes *in* Can. J. Bot. **36**: 792. 1958 is *Chromelosporium carneum* (Pers.) Hennebert.

*Ostracoderma epigaeum* (Link) Hennebert *ex* Hellmers *in* Horticultura **19**(5): 72. 1965 belongs in the synonymy of *Chromelosporium tuberculatum* (Pers.) Hennebert. The combination was made by Hellmers against my wishes, and misapplied by him to the conidial state of *Peziza ostracoderma* Korf, which he erroneously cited as a synonym of *P. atrovinosa* Cooke & Gerard.

*Ostracoderma fossarum* (Fautrey) Hughes *in* Can. J. Bot. **36**: 792. 1958 is *Chromelosporium tuberculatum* (Pers.) Hennebert.

*Ostracoderma isabellinum* (Preuss) Hughes *in* Can. J. Bot. **36**: 792. 1958 is *Chromelosporium ochraceum* Corda.

*Ostracoderma linkii* (Duby) Hughes *in* Can. J. Bot. **36**: 792. 1958 is *Chromelosporium carneum* (Pers.) Hennebert.

*Ostracoderma ochraceum* (Corda) Hughes *in* Can. J. Bot. **36**: 792. 1958 is *Chromelosporium ochraceum* Corda.

*Ostracoderma spadiceum* Schw. *in* Trans. Am. phil. Soc. II **4**: 262. 1832 is *Dictydiaethalium plumbeum* Rost.

*Ostracoderma terrestre* (Fr.) Nannf. *in* Lundell & Nannf., Fungi exs. suecici, Fasc. 53–54, Schedae 40. 1959 is *Chromelosporium tuberculatum* (Pers.) Hennebert.

*Ostracoderma* state of *Peziza ostracoderma* Korf is *Chromelosporium ollare* (Pers.) Hennebert.

11. GLISCHRODERMA Fuckel *in* Jb. nassau. Ver. Naturk. **23–24**: 34. 1870.—Type species: *G. cinctum* Fuckel (monotype).

NOTES: This genus is provisionally accepted for the only species to be described, *G. cinctum*. As far as I can understand from an examination of the type material (Fuckel, Fungi rhen. **162**. 1863, as "? *Ostracoderma pulvinatum* Fr.," Herb. G), it differs from *Ostracoderma* mainly if not solely in the ornamentation of the conidial wall. Malençon (1964b), describing a recent collection as *G. cinctum*, pointed to the presence of an apical ostiole in the peridium, a character that Fuckel denied for his fungus. A perfect state is unknown, and cultures have apparently never been attempted.

*Glischroderma*, *Lycoperdellon*, and *Ostracoderma* have also served as the bases for families and orders. Rea (1922) erected the family Glischrodermataceae to include *Glischroderma*. Heim (1934) proposed the family name Lycoperdellaceae for *Lycoperdellon*. Malençon (1964b) synonymized the two families, choosing the oldest, Glischrodermataceae, to include both genera. At the same time he erected a new family, Ostracodermataceae, for non-peridiate species which are now to be classified in *Chromelosporium*; since the genus *Ostracoderma* does have a peridium, Malençon's second family is clearly synonymous with Glischrodermataceae. In the meanwhile, Zeller (1948) accepted the family Lycoperdellaceae, even though no family diagnosis has apparently ever been published, excluded it from the Gasteromycetes, and added the genus *Leucophlebs* Harkn. He then proposed a new order for these fungi, Lycoperdellales, which he placed in the Fungi Imperfecti. Malençon's (1964b) order Glischrodermatales will fall in synonymy if such orders were to be recognized.

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# ON BOUDIER'S GENUS LEPIDOTIA (PEZIZACEAE)

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(With two Text-figures and Plates 17–19)

A stipitate Operculate Discomycete with asci that blue in iodine, *Lepidotia hispida*, has been rediscovered growing on *Sphagnum*-pots in North America. The species was first found nearly a century earlier by Quélet in France, and has not been reported since. It is the type species of the nearly forgotten generic name *Lepidotia*, which is not accepted here but placed in synonymy with *Peziza*. An unnamed imperfect state is formed, and apothecia are quickly and easily produced in pure culture. When treated as a species of *Peziza*, a new name is required, *P. quelepidotia* Korf & O'Donnell, nom. nov.

The genus *Lepidotia* Boudier (1885) was erected for one species (and possibly a second) of Operculate Discomycetes referred to the family Pezizés, "groupe" Aleuriés. Boudier characterized the group by asci blueing in iodine at the apex, and by apothecia having furfuraceous or somewhat filamentose, but never hairy, outer surfaces. Four of the six genera he included were characterized by ellipsoidal ascospores; among these, *Lepidotia* was distinguished by its ascospores lacking oil guttules and by distinctly stipitate or obconic apothecia bearing triangular, submembranaceous scales.

Boudier's (1907) later treatment of these genera with iodine-positive asci did not differ significantly, except in the exclusion of *Sphaerosoma* Klotzsch in Dietr. and the inclusion of *Pachyella* Boud. in what he now termed the tribe Aleuriées. Two species were listed under *Lepidotia*, *L. hispida* (Quél.) Boud. and *L. subrepanda* (Cooke & Phill.) Boud., neither combination having been formally proposed earlier. These were the same species originally mentioned by Boudier (1885), where in the notes under the generic name *Lepidotia* he wrote, "Comme espèces, la *Peziza hispida* Quel.[2] et peut-être *subrepanda* Phill." His expressed doubt about the assignment of *P. subrepanda* to the genus automatically fixes *P. hispida* as the only possible type (i.e., originally designated type) of the generic name. When Eckblad (1968) listed *Lepidotia*

[1] Completed while holding a Fulbright/Hays Senior Research Scholarship in Belgium, 1972–73. The study was begun in the Plant Pathology Herbarium, Cornell University, Ithaca, New York, and was supported in part by (U.S.) National Science Foundation grant GB-8548.

[2] Neither Boudier nor Cooke used the accent mark on Quélet's name in their published accounts, spelling it "Quelet." I do not feel the accent marks should be restored while quoting these authors.

under "Insufficiently known and excluded genera" (because he did not know of the Quélet specimen discussed below), he 'selected' *Lachnea hispida* as the type of the generic name.

Neither species of *Lepidotia* appears to have been reported as being collected again after both were illustrated by Cooke (1877, 1879) nearly a century ago. And thus Boudier's genus has remained forgotten, or at least doubtful. Mme Le Gal (1947) excluded it from her tribe Aleurieae as a doubtful genus: "N'ayant pu examiner aucune des deux espèces que BOUDIER y fait rentrer, nous ne saurions prendre position à leur sujet."

In the absence of specimens, *L. subrepanda* seems indeed to be a 'lost' species, known only from Cooke's (1877: fig. 260) description and drawing reproduced here (Plate 17). The triangular scales are shown to be composed of cohering, septate hyphae, and the spores are illustrated as smooth, and without guttules. Whether or not the asci blue in iodine is not known.

The other original species, *Lepidotia hispida*, is more critical, since the generic name *Lepidotia* is tied to it nomenclaturally. Quélet (1879) described it at the 'séance' of December 13, 1878, of the Société Botanique de France. Actual publication of the species, under the name *Lachnea hispida* Quél., could not have appeared in print before June of the following year (see Bull. Soc. bot. Fr. **25**: 317. "1878", where there is a "Note ajoutée pendant l'impression, juin 1879" referring to the same 'séance'). In Quélet's description he refers specifically to "Cooke, *Peziz.* f. 402," which identifies Cooke's (1879: fig. 402) plate published in March, or earlier, 1879. This drawing (reproduced here, Plate 17) is described on the accompanying page of the text, with the notations "*Peziza hispida* Quelet, in litt." and "Figured from specimens communicated by Dr. Quelet."

Since Quélet published *Lachnea hispida* later than Cooke had published *Peziza hispida* Quél. *ex* Cooke, one might consider the Quélet name to be a new combination, i.e., one would cite it as *Lachnea hispida* (Quél. *ex* Cooke) Quél. However, *Peziza hispida* Quél. *ex* Cooke is a later homonym of *P. hispida* Huds. per Purton, validly published in 1821, and is thus an invalid name. There being no obstacle to the use of the epithet 'hispida' in the genus *Lachnea*, Quélet's transfer should instead be treated as the proposal of a *nomen novum* (Art. 72, International Code of Botanical Nomenclature) and he alone should be cited as the author of the name *Lachnea hispida*.

Some twenty years ago, when I began my studies of generic names in the Pezizales that are only now reaching fruition (Korf, 1972), I obtained the Quélet specimen from which Cooke had drawn up his diagnosis and illustration of *Peziza hispida* on loan from the Herbarium of the Royal Botanic Gardens, Kew. I found that the asci indeed blued in iodine, and that there were few if any characters to separate it generically from *Peziza* St-Amans.

## AN AMERICAN COLLECTION

Approximately two years ago, Mr. Kerry O'Donnell, a graduate student at Michigan State University, sent me an interesting Operculate Discomycete for identification. The stipitate apothecia (Plate 18 Fig. a) and yellow-green colors exhibited by the fungus were unusual, and recalled to me the genus *Gelatinodiscus* Kanouse & Smith, where I tentatively assigned it. Mr. O'Donnell correctly pointed out to me features in which his fungus differed from the only species of that genus, *G. flavidus* Kanouse & Smith. He noted that the ascospores of his fungus were lightly marked (Fig. 1) and that the paraphyses were unbranched, as opposed to the smooth ascospores and branching paraphyses of *G. flavidus*.[3] Eventually I advised him that his fungus could best be referred to the very large and difficult genus *Peziza*. I had,

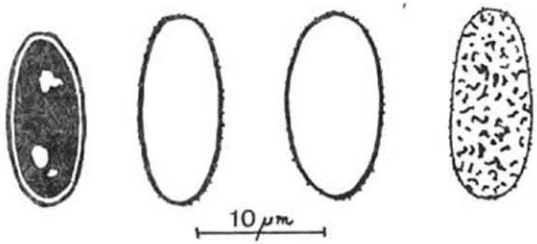


Fig. 1. *Peziza quelepidotia* ascospores; at left, young ascospore with cyanophilic perispore and cyanophilic cytoplasm, with polar granules and spore wall not taking up cotton blue dye; in center, two mature ascospores devoid of guttules, viewed in optical section; at right, mature ascospore in face view. — All from mounts in cotton blue dye in lactic acid, Specimen No. *Korf 4074*, drawn with the aid of a Wild drawing tube, × 1900.

at that time, little hope of being able to put a specific epithet on his fungus in view of our chaotic state of knowledge of the species of this genus.

Quite as an afterthought, I remembered having examined the type specimen of *Lepidotia hispida* many years earlier. I consulted the slide I had prepared from that specimen, and to my surprise found that the spores of *L. hispida* were not smooth, as reported by Cooke and by Quélet, but were lightly though densely marked and wholly indistinguishable from those of Mr. O'Donnell's collection. Likewise the hairs and scales on the apothecium are indistinguishable between collections (Fig. 2).

Two characters of the recent collection seem irreconcilable with Cooke's drawings (Plate 17): the presence of a distinct stipe, and the yellow-green colors recalling not only *Gelatinodiscus* but such Inoperculate Discomycetes as '*Rutstroemia*' *luteovirescens* (Rob.) White and its allies. Scarcely any stipe is visible in Cooke's drawing, who

[3] I have since had opportunity to examine a recent collection of *G. flavidus*, which demonstrated to me that it is not at all closely related to the Pezizaceae where I had assigned it (Korf, 1972).

in fact clearly indicated that the species was sessile. The colors of the plate, rendered in the description as "incarnato-pallida," scarcely agree at all with the O'Donnell fungus when it produces its apothecia in culture.

It was particularly instructive for me to examine Quélet's (1879) description, and to compare it with Cooke's (1879) description and drawings. At once it becomes apparent that Cooke knew the fungus only from dried and rehydrated material. The stipe is easily broken off in dried specimens, and at the time I examined the Cooke Herbarium specimen, I made no note of the presence of any stipe. The very characteristic colors of the living fungus are lost on drying, and a rehydrated apothecium might indeed look as devoid of yellow or green tones as does the original Cooke plate. On the other hand, Quélet's description, drawn up from living material (probably the same collection), agrees remarkably well with the American collection in all respects except for the initial color of the apothecium, "blanche" according to Quélet. Ours, as it grows in culture, is initially yellow-green, but of course our substrate is not a natural one, which might influence the colors. Quélet's description of the final color, "jaune sale", is not inappropriate for the colors we see; old apothecia in culture are olive-brown. The two conflicting diagnoses are reprinted here to facilitate the reader's understanding:—

Cooke (1879: 238):

Sessilis, sparsa, incarnato-pallida, demum explanata, extus marginique squamulis acutis obsita. Ascis cylindraceis. Sporidiis ellipticis, hyalinis. Paraphysibus gracilibus.

*Peziza hispida* Quelet, in litt.

Attached to mosses.

France.

Cups 1 cm. diam. Sporidia .015 × .008 mm. Scales triangular, composed of parallel hyaline connate hairs.

Figured from specimens communicated by Dr. Quelet.

Quélet (1879: 291):

Cupule épaisse, globuleuse puis cyathiforme (0m,01) et *stipitée*, charnue, fragile, blanche puis jaune sale, hérissée de poils *sétacés et rameux*, souvent connés en écaille. Hyménium opalin. Spore ellipsoïde allongée (0mm,015), hyaline. (Cooke, *Peziz.* f. 402).

*Printemps.*—Sur l'humus marécageux des forêts de la plaine.

Quélet italicized features which he considered diagnostic, notably that the apothecia were stipitate (Cooke, it should be recalled, described them as sessile) and that the apothecia were clothed with branching, setaceous hairs that were often grouped into scales. Cooke, on the contrary, only illustrated hairs that were cemented together to form scales, not mentioning nor illustrating any separate hairs or any branching of these. In Mr. O'Donnell's fungus, not all of the hairs are cemented into teeth, and branching of these also occurs (Fig. 2). I have no hesitancy in identifying the recent collection with Quélet's species.

Most of my observations on *Lepidotia hispida* have been made on apothecia produced in culture in the laboratory in petri dishes on a medium concocted by Mr.

O'Donnell, and which we call "Jiffy-7 Pellet agar." This is easily constituted by suspending two 'Jiffy-7 Pellets,' a commercially available peat-moss product,[4] in a liter of water, to which is added 30 to 50 g agar, the mixture being autoclaved for fifteen to twenty minutes at 117 °C. The suspension is poured into petri dishes, and on solidification is seeded with a bit of the agar or a portion of an apothecium from a previous culture. If the dishes are placed under constant fluorescent lights at normal laboratory temperature, apothecia begin development within four days to a week, and are mature within ten days to two weeks.

Jiffy-7 pellets consist of a compacted *Sphagnum*-moss mixture which when placed in water expands to form a spongy mass held in place by a mesh net on the outside; they are then ready for planting seeds for eventual transfer to the garden. Mr. O'Donnell's collection of *L. hispida* was originally brought into the laboratory at Michigan State University by a homeowner, who found a crop of apothecia developing on his planted Jiffy-7 pellets. We believe that the original source of the Jiffy-7 pellet material is in Scandinavia, but whether *L. hispida* was imported along with the pellets or came from spores in America is impossible to ascertain. Quélet indicated that his species grew on swampy humus, while Cooke indicated that the apothecia of Quélet's specimen were attached to mosses. Our assumption is that Quélet's specimen grew on some decaying *Sphagnum*-like moss in a swampy area, surely a habitat not too dissimilar from a moistened Jiffy-7 pellet.

Mr. O'Donnell successfully isolated the fungus, and developed the Jiffy-7 Pellet agar as a fruiting medium (O'Donnell & Beneke, 1973). He was later able to isolate single ascospores and to prove that the species is homothallic (capable of developing apothecia from a single ascospore), and to demonstrate that the ascospores are uninucleate (Plate 18 Fig. e).

My studies of *L. hispida* in culture confirm my earlier conclusion that the genus *Lepidotia* cannot satisfactorily be separated from *Peziza*, which I take in the broad sense (Korf, 1961) to include *Aleuria* sensu Boudier (non Fuckel), *Galactinia* (Cooke) Boud., and *Plicaria* Fuckel.[5] The presence of a stipe does not appear to be of generic significance among these iodine-positive species. Boudier (1904–11: pl. 266) illustrated the distinctly stipitate *Aleuria asterigma* Vuill. (a *Peziza* in my sense) among the many sessile species he assigned to that genus. A portion of his plate is reproduced here (Plate 19). The illustration immediately recalls the gross morphology of *L. hispida*. Here, however, the squamules on the outer surface are composed of globose

[4] The product is listed in the catalogues of all major seedsmen in the U.S., and is also available at garden supply stores. I found it also in the garden department of a supermarket in Belgium, marketed by the Jiffy-Pot Benelux S.A. company. It is said to consist of compacted peat-moss and added fertilizer.

[5] This is the same taxonomic group which Mme Le Gal (1953) tentatively proposed and later adopted (Le Gal, 1962) as *Galactinia* (Cooke) Boud. emend. Le Gal. *Peziza* as conceived by Eckblad (1968) differs in including two genera I consider amply distinct, *Sarcosphaera* Auersw. and *Pachyella* Boud. emend. Pfister. On the other hand, he recognized *Plicaria* for species of *Peziza* which essentially differ only in having spherical ascospores.

cells (Plate 19 Fig. m) and not of triangular scales composed of filaments, characters upon which Boudier (1885) had established *Lepidotia*. While the apothecia of *L. hispida* do possess hyphae which are sometimes glued into more or less triangular scales, best seen in dried specimens and overemphasized in Cooke's drawing, the hyphae are very similar to those present in a number of species of *Peziza*, and recently described well and in some detail by Svrček (1970). The structure of the apothecium is much as in other species of *Peziza*, with the outermost layers composed mainly of greatly enlarged, subglobose to pyriform cells (Fig. 2; Plate 18 Fig. d). The asci are typically operculate (Plate 18 Fig. c), and the spores, though devoid of oil drops and with essentially homogeneous cytoplasm at maturity, do have small droplets and granulations aggregated into two polar groups at an early stage of development (Fig. 1; Plate 18 Fig. b). The cytoplasm of young ascospores is cyanophilic, as is the perispore, but at maturity the cytoplasm no longer stains blue and distinct, closely spaced, cyanophilic spore markings, scarcely visible in optical section but obvious in face view, develop (Fig. 1).[6]

Some of the species of *Peziza* have been shown to produce an imperfect state. These are usually of the *Botrytis*-like genera *Oedocephalum* Preuss or *Chromelosporium* Corda [earlier called *Ostracoderma* Fr., but see the paper by Hennebert (1973) in which the status of *Ostracoderma* as a peridiate genus — more recently called *Lycoperdellon* — is at last made clear]. *Lepidotia hispida* also produces an imperfect state under certain conditions, but it is not of this type, and belongs perhaps to an undescribed genus according to Prof. Hennebert (Plate 18 Figs. f, g).

It is impossible to transfer the epithet of *Lepidotia hispida* to *Peziza*, or to accept

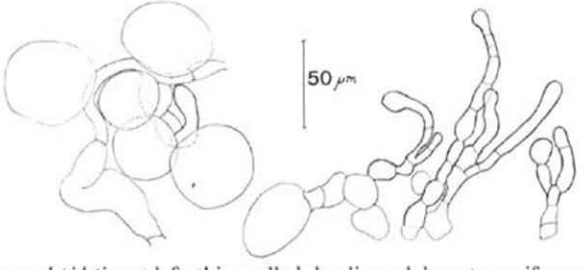


Fig. 2. *Peziza quelepidotia*; at left, thin-walled, hyaline, globose to pyriform cells of the ectal excipulum a few cells in from the surface, interspersed with hyphal elements; at right, pale brown excipular cells giving rise to darker brown, hair-like processes, some of which branch, that make up the tomentum and which cohere to form the scales on the apothecial surface. — From mounts in 50 percent aqueous glycerine, Specimen No. *Korf* 4074, drawn with the aid of a Wild drawing tube, × 250.

[6] Mr. O'Donnell is proceeding with his Ph. D. studies on this fungus, at the completion of which cultures will be deposited in the American Type Culture Collection and in the 'Centraalbureau voor Schimmelcultures' for the use of others. It grows so easily in culture that its adaptability for use in class work for students of mycology or even of general botany is readily apparent.

Cooke's name in that genus, because of the existence of an earlier homonym. Since we are unaware of any earlier epithet which can be applied, a new name for the species is hereby proposed:—

**Peziza quelepidotia** Korf & O'Donnell, *nom. nov.*

Figs. 1—2, Plate 18

[*Peziza* (*Sarcoscypha*) *hispida* Quél. *ex* Cooke, Mycographia **1**: 238. 1879, March or earlier (basionym); non *Peziza hispida* Huds. *per* Purton, Append. Midl. Flora **3**: 462. 1821.] — *Lachnea hispida* Quél. *in* Bull. Soc. bot. Fr. **25**: 291. ["1878"] 1879, June or later [*nom. nov.*, see Art. 72, Int. Code Bot. Nomencl.]. — *Neottiella hispida* (Quél.) Sacc., Syll. Fung. **8**: 192. 1889. — *Lepidotia hispida* (Quél.) Boud., Hist. classif. Discom. d'Eur. 43. 1907.

ETYMOLOGY: From Quélet and the generic name *Lepidotia*.

ILLUSTRATION: Cooke, Mycogr. **1**: pl. 112, fig. 402. 1879.

HOLOTYPE: *Quélet*, sine no., sine dat., Hérimoncourt, Doubs, France, Herb. M. C. Cooke (K)

ACKNOWLEDGEMENTS

I wish to thank Prof. G. L. Hennebert for graciously providing space and facilities in his laboratory during my sabbatical leave from Cornell University. Thanks are also due to the Director of the Royal Botanic Gardens, Kew, for the loan of the type material of *Peziza hispida*. Mr. H. Lyon of Cornell's Department of Plant Pathology copied the original illustrations for Plates 17 and 19, and made the photograph of apothecia from material in culture (Plate 18 Fig. a). All the remaining figures on Plate 18 were made by Mr. Kerry L. O'Donnell, Michigan State University, who offered them for use in this publication.

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## EXPLANATION OF PLATES 17–19

### PLATE 17

Cooke's (1877, 1879) illustrations of *Peziza subrepanda* (Fig. 260) and of *P. hispida* (Fig. 402).

### PLATE 18

*Peziza quelepidotia* from specimens grown on agar. — a. Apothecia in various stages of development. — b. Young ascospores in glycerine-Melzer's Reagent mount (1 : 1) showing polar aggregations of globules and granules. — c. Empty asci with the opercula thrown back. — d. Vertical section through a portion of an apothecium. — e. Young ascospores stained in propionic iron haematoxylin demonstrating the single nucleus in each spore. — f, g. Conidia and conidiophores. (Fig. a: × 3.8; Fig. b: × 1000; Figs. c, e: × 1330; Fig. d: × 20; Figs. f, g: × 535.)

### PLATE 19

Boudier's (1904–1911) illustration of *Aleuria asterigma*, only a portion reproduced showing apothecia (*a, b, d, e, f*) and globose cells which make up the squamules (*m*). The apices of two paraphyses are shown between *m* and *f*.

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# DONKIOPORIA KOTL. & POUZ., A NEW GENUS FOR PORIA MEGALOPORA (PERS.) COOKE

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A new genus of resupinate polypores, *Donkioporia* Kotl. & Pouz., is proposed for the fungus chiefly known under the name of *Poria megalopora* (Pers.) Cooke. Since the oldest name of the species appears to be *Boletus expansus* Desm., the new combination *Donkioporia expansa* (Desm.) Kotl. & Pouz., is proposed. The genus is characterized microscopically by a trimitic hyphal system possessing both thin- and thick-walled generative hyphae with clamp-connections. The internal layer of the walls of some of the thick-walled generative hyphae gives an amyloid reaction.

*Poria megalopora* (Pers.) Cooke, a resupinate polypore, has also been reported in mycological literature under various other names, such as *Boletus expansus* Desm., *Polyporus expansus* (Desm.) Desm., *Phellinus cryptarum* (Bull. ex Fr.) P. Karst. sensu Cartwr. & Findl., *Fomitiporia ohiensis* Murrill, etc. This interesting polypore, which clearly prefers worked oak timbers, is a well-known inhabitant of structural members in houses, as well as in outside wooden structures such as bridges, fences etc.

This fungus presents a taxonomic problem as regards its position in the natural system for this group of fungi. The genus *Poria* sensu lato is an artificial aggregate of unrelated species and there have been several attempts to reassess it in more natural genera. Nevertheless, even in the more natural genera no position for *Poria megalopora* can be found. Some attempts have been made by several authors to insert this species into the group of perennial xanthochroic polypores. In this connection mention should be made of Murrill (1907), who erected a new genus for this and similar polypores, describing the species under discussion anew as *Fomitiporia ohiensis* Murrill. *Fomitiporia*, which embraces various resupinate xanthochroic polypores, is now usually referred, together with the pileate species, to *Phellinus* Quél. Heim (1942) transferred *Poria megalopora* to this genus, making the new combination *Phellinus megaloporus* (Pers.) Heim; this recombination was also made by Bondarcev (1953), who does not appear to have been aware of Heim's earlier binomial. However, as correctly noted by Jahn (1967: 103), this polypore does not belong in *Phellinus* Quél. because of the presence of clamp-connections. Jahn (l.c.) left this species in the artificial genus *Poria* s.l., leaving its correct position for future study.

Another attempt to place this species was made by Domanski & Orlicz (1967) who transferred it to the genus *Fomes* (Fr.) Fr. em. Teix. However, we are unable

to substantiate this transfer because the species of this genus are characterized by having thick-walled spores, whereas the spores of *Poria megalopora* (= *P. expansa*) are thin-walled. Another distinguishing character is the generative hyphae which are all thin-walled in the species of *Fomes* but are both thin- and thick-walled in the species under discussion.

For this reason, we now return to the problem of the generic position of *Poria megalopora* (= *P. expansa*). As our search for a suitable genus proved unsuccessful, we propose to establish a new genus, taking the liberty to name it in honour of the late Dr. M. A. Donk, who has contributed very considerably to the knowledge of polypores, and particularly to the present species.

**Donkioporia** Kotl. & Pouz., *gen. nov.*

Carposomata resupinata, perennia, hymenophoro poroideo instructa, tramate tenui, obscure brunnea, cum strato nigro inter carpophoro et substrato seu inter contextu novo et carpophoro vetusto. Systemate hypharum trimitico: hyphis generativis copiosis, ramificatis, tum tenuiter tunicatis, hyalinis, fibulatis, inamyloideis acyanophilisque, tum crasse tunicatis, brunneis usque obscure brunneis, fibulatis, cum lamina pariete interiori saepe amyloidea; hyphis sceleticis haud ramificatis absque fibulis, moderatim crasse tunicatis, flavoferrugineis; hyphis ligativis abundante ramificatis, tenuiter tunicatis, hyalinis, haud septatis absque fibulis, saepe modo dichotomico ramificatis. Basidia clavata, tetrasterigmatica. Sporae breviter ellipsoideae, haud truncatae, tenuiter tunicatae, laeves, hyalinae, inamyloideae, indextrinoideae et acyanophilae.

TYPUS: *Poria expansa* (Desm.) H. Jahn.

Fruitbodies resupinate, perennial, with poroid hymenophore, thin or thick dark brown context, and a thin black layer (i.e. appearing in section as a black line) between the carpophore and the wood or between the new context and the old carpophore. Hyphal system trimitic: generative hyphae abundant, branched, with clamp connections, some thin-walled, hyaline, inamyloid and acyanophilous, others thick-walled, brown to dark brown, with the internal layer of the walls often amyloid; skeletal hyphae often with simple, secondary septa, slightly thick-walled, rusty yellow; ligative (binding) hyphae richly, often dichotomously, branched, thin to thick-walled, hyaline, not septate and clampless. Basidia clavate, tetrasterigmatic. Spores short-ellipsoid, not truncate, with thin, smooth, hyaline, inamyloid, indextrinoid, acyanophilous walls.

TYPE: *Poria expansa* (Desm.) H. Jahn.

At the present time, this genus contains only one species, which thus far is known in the mycological literature chiefly as *Poria megalopora* (Pers., 1825) Cooke, 1885. However, the oldest known name for this fungus is *Boletus expansus* Desm., 1823, as ascertained by Donk (1933) and confirmed by the study of the original material by Jahn (1967). Therefore, we propose the following new combination:—

**Donkioporia expansa** (Desm.) Kotl. & Pouz., *comb. nov.* Basionym: *Boletus expansus* Desmazières, Catalogue des plantes omises, pl. 18, 1823 (for other synomyms, see Jahn, 1967: 100).

SPECIMENS STUDIED:—

BELGIUM

Chateau de Bormenville (Condroz), on wood within house, 1. VII. 1962, V. Demoulin, det. H. Jahn (PR).

CZECHOSLOVAKIA

Prenčov (Central Slovakia), on rotten oak wood of bridge in front of the parsonage, VII. 1888, A. Kmeť (BRA); ibid., in the parish barn on dry wood of *Quercus*, IX. 1891, A. Kmet (BRA, 2×). — Babiná near Krupina (Central Slovakia), on fallen trunk of *Quercus cerris*, 7. VI. 1965, Z. Pouzar, det. F. Kotlaba & Z. Pouzar (herb. Kotlaba & Pouzar). — Praha near Lučenec (Southern Slovakia), on *Quercus* wood in cave, VI. 1954, A. Príhoda, det. Z. Pouzar & F. Kotlaba (PR 607, 130).

GERMANY

Remmighausen near Detmold (Westphalia), on an old oak pole (*Quercus*) taken from the framework of a house, 5. XII. 1966, H. Jahn (herb. Kotlaba & Pouzar); ibid., road to the cemetery on a fence post near meadow (oak wood from an old house), 29. XII. 1966 and 16.I.1967, H. Jahn (PR 654,346). – Mosel, castle Eltz near Moselkern (Rheinland), on a ceiling beam (probably *Quercus*) in an old half-ruined stable, 31.III.1967, M. A. & H. Jahn, det. H. Jahn (herb. Kotlaba & Pouzar).

ITALY

Vittorio (Treviso), on a pole of *Abies* ("ad asseres abietinos") IX.1900; D. Saccardo, Mycotheca italica, 606, *Poria ferruginosa* (PR 704, 485).

The genus *Donkioporia* does not seem to be closely related to any other resupinate polypores. However, we would like to place it in proximity to *Fomes* (Fr.) Fr. em. Teix. because of the trimitic hyphal system with clamped generative hyphae, the brownish trama, and the amyloid internal layer of certain generative hyphae confined chiefly to the encrusted layer of the carpophores. The amyloidity of the hyphae forming the encrusted layer is rather widely distributed among the fungi of the fomitoid group (excluding xanthochroic *Phellinus* species). Another interesting feature also connecting *Donkioporia expansa* with the species of *Fomes* is the rudimentarily developed granular core which, however, we have only seen in one specimen of *D. expansa*. In this instance we also found that the internal wall of the ligative hyphae in the granular core gave an amyloid reaction. However, this seems to be quite an accidental phenomenon because normally these ligative (binding) hyphae are consistently inamyloid.

Species of the genus *Fomes* differ from *Donkioporia expansa* by the absence of thick-walled generative hyphae, so characteristic of the latter. These hyphae are of special interest because, in cases when they are in or near the encrusted layer of the fungus, the internal layer of the hyphal walls is often amyloid. Thick-walled hyphae with an amyloid internal layer also occur in species of the genus *Fomes* (being confined exclusively to the encrusted layer of the pileus) but, contrary to those of *D. expansa*, they are not provided with clamp-connections.

*Donkioporia expansa* is macroscopically similar to some species of the genus *Gloeophyllum* (P. Karst.) P. Karst., especially to the resupinate form of *Gloeophyllum trabeum* (Pers. ex Fr.) Murrill = *Phaeocoriolellus trabeus* (Pers. ex Fr.) Kotl. & Pouz. Nevertheless, the members of this genus differ in at least two important characters: (i) absence of thick-walled hyphae provided with clamp-connections, and (ii) absence of amyloidity of the hyphal walls.

Whilst describing this new genus for *Poria expansa*, we would also like to discuss briefly the genus *Spongioides* Lázaro é Ibiza (1916), to which our attention was drawn by Dr. M. A. Donk (personal communication). According to his opinion, Lázaro's description possibly covers two polypores: one pileate and one resupinate. After studying Lázaro's generic description of *Spongioides*, we reached the conclusion that the major part of the description concerns a pileate fungus which may very well be either *Heterobasidion annosus* (Fr.) Bref. or, better, *Trametes serialis* (Fr.) Fr. = *Antrodia serialis* (Fr.) Donk, whilst a minor part could easily also cover *Poria megalopora* = *Donkioporia expansa*. For this reason, it is in our opinion impossible to use the generic name *Spongioides* Lázaro é Ibiza to accommodate *Poria megalopora*. We made an attempt to obtain for study Lázaro's original material of *Spongioides cryptarum* but Dr. F. Diego Calonge of Madrid kindly informed us that there are no specimens of this fungus in Lázaro's herbarium. In consequence, we recommend that *Spongioides* Lázaro é Ibiza be typified by the pileate part of the description, and placed in the synonymy of either *Heterobasidion* Bref. or *Trametes* Fr. (possibly *Antrodia* P. Karst.)

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# ARCHITECTURE DE LA PAROI SPORIQUE DES HYMÉNOMYCÈTES ET DE SES DIFFÉRENCIATIONS

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(Planches 20 à 23)

Mise au point critique des connaissances actuelles acquises grâce à la microscopie photonique et à la microscopie électronique par transmission.

## I—INTRODUCTION

Les mycologues ne disposant que du microscope à lumière ont depuis longtemps distingué deux couches dans la paroi de nombreuses spores, couches qui ont été baptisées *endospore* et *épispore* ou *exospore* pour rappeler leurs positions respectives. Il est rare que l'endospore soit facilement visible sur la spore fraîche; elle est naturellement indiscernable dans ces conditions lorsque l'épispore est noirâtre.

Dans quelques cas on a pu distinguer, à l'extérieur de l'épispore, une couche que l'on a appelée *périspore*. *Coprinus narcoticus* (Batsch ex Fr.) Fr. montre, autour de la couche noire généralement considérée comme épispore, une périspore beaucoup plus pâle, épaisse, qui, par dessiccation, se ratatine en se fripant. Chez d'autres Agaricales à spores noirâtres la périspore passe généralement inaperçue lors des observations courantes. V. Fayod, à qui revient le mérite d'avoir démontré son existence, l'a appelée exospore, parce que, n'ayant pas vu l'endospore cachée par l'épispore noirâtre, il a été conduit à considérer cette dernière comme étant l'endospore.

Les recherches précises faites en photonique dans la période moderne ont conduit à l'idée que, dans bien des cas, la paroi sporique comprend plus de trois couches; la terminologie ancienne que nous venons de rappeler est alors trop pauvre. Pour créer le moins possible de termes nouveaux on peut, comme l'ont fait M. Locquin et J. Perreau-Bertrand par exemple, utiliser le mot exospore pour désigner une couche située entre l'épispore et la périspore, et non plus comme synonyme d'épispore. Des néologismes sont cependant indispensables. L'observation attentive de la périspore de *Coprinus narcoticus* montre qu'elle comprend, outre une épaisse couche interne, une fine pellicule qui la limite du côté externe. En microscopie électronique, cette pellicule tranche brutalement sur les parties sous-jacentes de la périspore par sa très grande opacité; c'est *l'ectospore* de R. Heim.

De grands progrès dans la connaissance de l'architecture de la paroi sporique ont été réalisés grâce à la microscopie électronique. Encore peu nombreux sont cependant les mémoires où la paroi sporique des Hyménomycètes est étudiée avec cette tech-

nique sur des espèces suffisamment nombreuses et variées dans leurs affinités pour qu'on ait pu tenter de dégager des idées générales et d'aborder les délicats problèmes d'homologies.

On doit tout d'abord citer trois thèses: celle de H. A. P. Burge, malheureusement restée inédite, portant sur la paroi des Russulacées et de genres supposés affines, celle de J. Perreau-Bertrand consacrée à la paroi d'espèces à spores ornées, enfin celle de L. M. Meléndez-Howell centrée sur l'étude des pores germinatifs. Les recherches qui ont conduit à l'élaboration des deux derniers mémoires ont été effectuées sous la direction du Professeur Roger Heim.

Parmi les travaux plus récents, il faut citer une publication de H. Clémençon, qui étudie la paroi, non seulement chez des espèces à spores ornées, mais aussi chez des espèces à spores lisses, et les nombreuses notes de Mlle M. Besson, devenue Mme Antoine, dont l'ensemble constitue la partie fondamentale d'une Thèse où sont étudiées les parois et leurs différenciations dans une centaine d'espèces.

Il est évident qu'au fur et à mesure que s'accumulaient de nouveaux résultats, certaines idées ont évolué. Il était impossible qu'il en fût autrement; la série de notes de M. Besson, dont la publication s'est échelonnée de 1969 à 1972, en fournit un exemple typique, qui montre la nécessité d'une synthèse de l'ensemble des résultats. Si nous nous décidons aujourd'hui à présenter un raccourci des connaissances actuelles sur l'architecture de la paroi sporique des Hyménomycètes, c'est d'abord qu'ayant été le Directeur des recherches de M. Besson-Antoine, nous avons pu suivre pas à pas le déroulement de ses recherches d'électronique, mais c'est aussi parce que, parallèlement, nous avons poursuivi des investigations en microscopie photonique sur le même thème.

Le pouvoir de résolution du microscope à lumière étant beaucoup plus faible que celui du microscope électronique, on est tenté de penser qu'il ne peut être d'un grand secours lorsqu'il s'agit d'étudier un ensemble aussi peu épais que l'est souvent une paroi sporique.

Il faut pourtant reconnaître que, dans une foule de cas, la microscopie photonique a fourni d'importantes indications, plus particulièrement sur des spores soumises à des traitements convenables. Un traitement à chaud (120 °C par exemple) par une lessive de base forte (par ex. KOH) s'est révélé particulièrement utile dans une foule de cas (M. Besson & R. Kühner, 1972a). Pour une concentration suffisante en KOH les spores des chromosporés sont plus ou moins décolorées, ce qui permet alors de bien voir des couches profondes qui, dans la spore non traitée, peuvent être difficilement visibles, voire totalement invisibles au travers de couches pigmentées plus externes.

Il ne faut cependant pas oublier que les traitements alcalins violents, tels que ceux qui décolorent les spores de chromosporés lysent souvent plus ou moins certains constituants morphologiques de la paroi; il est facile de constater, par exemple, que pour des concentrations assez fortes le traitement potassique élimine souvent complètement les épines ou verrues qui ornent la surface de nombreuses spores. Aussi,

pour tirer le meilleur parti de cette technique, est-il recommandé d'essayer des lessives de concentrations variées, entre 0,5 % et 10 % par exemple.

Même si la couche externe de la paroi est incolore ou n'est que faiblement colorée sous le microscope, elle peut empêcher de bien voir les couches situées au-dessous d'elle lorsque son indice de réfraction est particulièrement élevé. Si V. Fayod a considéré que la paroi sporique des *Rhodophyllus* est simple, c'est qu'il n'a vu que la couche superficielle, polyédrique, de la paroi, parce qu'elle est si réfringente que, malgré sa teinte à peine rosée sous le microscope, elle empêche de bien voir la ou les couches qui sont au-dessous. Des traitements alcalins convenables mettent facilement ces dernières en évidence, soit, s'ils sont violents, en les dégageant par suite de l'élimination de la couche polyédrique qui les enveloppait (R. Kühner, 1948), soit s'ils sont plus modérés en gonflant celle-ci, en l'hydratant, et par suite en abaissant son indice de réfraction (M. Besson & R. Kühner, 1972c). D'une façon générale, chez les Hyménomycètes, les couches profondes de la paroi sont plus résistantes aux traitements alcalins violents que les couches superficielles.

Il est évident que tout traitement qui, à l'image du traitement potassique, gonfle exclusivement certaines couches ou les gonfle plus que d'autres, est susceptible de créer entre couches contiguës des différences d'indices de réfraction, parfois considérables, qui facilitent l'étude de la paroi. C'est ainsi, par exemple, qu'en soumettant les spores des Lépiotes de la section *Procerae* à l'action de l'ammoniaque puis à celle de l'acide acétique (traitement ammoniaco acétique), on gonfle bien plus certaines couches de la paroi que d'autres, comme M. Locquin l'a reconnu le premier, ce qui permet de distinguer des détails structuraux indiscernables en photonique sans ce traitement.

Il ne faut pas oublier que certains traitements hydratants sont susceptibles de provoquer d'importantes déformations lorsqu'ils gonflent de façon inégale différentes couches de la paroi. Si par exemple la paroi gonfle moins dans la région externe que dans sa région interne, les couches internes pourront se plisser; en examinant par un bout, en microscopie photonique, des spores ayant subi l'action de la potasse à l'autoclave, on remarque souvent que la face interne de la paroi, du côté du protoplasme, présente quelques gros plis longitudinaux dont la formation ne peut être due qu'à des inégalités de gonflement alcalin.

Il est clair que la déshydratation exigée par l'inclusion dans les résines pratiquée en vue des observations en électronique peut également donner à certaines structures une allure fort différente de celle qu'elles ont sur le frais. On sait que la périspore de *Coprinus narcoticus* se contracte en séchant, de sorte que sur matériel d'herbier l'ectospore est ratatinée contre l'épispore noire, fripée-plissée contre elle. Il est certain que les ondulations que montre, en électronique, l'ectospore de *Coprinus cineratus* Quél. var *nudisporus* Kühner (M. Besson & R. Kühner, 1972b: Pl 1 fig. 1), ont une origine analogue, à savoir la contraction, par déshydratation, de l'épaisse couche sous-jacente.

Des éléments morphologiques de la paroi, qui n'ont que 0,1 $\mu$, voire que 0,05 $\mu$ d'épaisseur sur les ultracoupes de matériel inclus dans les résines, peuvent être très

facilement discernés en microscopie photonique lorsqu'ils sont plus ou moins gonflés d'eau d'imbibition, au moins s'ils tranchent alors sur leur environnement par une réfringence plus forte ou si l'on parvient à les colorer électivement.

En ce qui concerne les colorations la microscopie électronique est d'ailleurs très en retard sur la microscopie ordinaire, les soi-disant colorations réalisées pour l'électronique se situant uniquement dans une gamme de gris (du gris clair au noir), dont les tonalités traduisent une plus ou moins grande transparence ou opacité aux électrons. Finalement c'est uniquement par une propriété de cet ordre qu'en électronique on peut distinguer directement l'une de l'autre deux couches contiguës.

Les colorations utilisées en photonique relevant pour la plupart de mécanismes fort différents de ceux qui permettent les "colorations" d'électronique, et les différences d'indices de réfraction ne se manifestant pas en électronique, on comprend qu'il soit parfois délicat de faire le raccord entre les données fournies par ces deux techniques d'étude.

Quoi qu'il en soit l'expérience montre que les résultats de la microscopie photonique complètent fort utilement ceux de l'électronique; il n'est même pas rare que plusieurs distinctions qui s'imposent en photonique soient beaucoup plus subtiles en électronique.

La microscopie photonique présente d'ailleurs sur l'électronique un avantage évident, la simplicité de nombre de ses techniques, simplicité telle qu'il est possible d'examiner un grand nombre d'espèces en un temps court. Nous en avons très largement profité, et grâce aux techniques évoquées ci-dessus, nous avons étudié la paroi sporique dans d'innombrables Agaricales de groupes variés, ce qui a permis à M. Besson-Antoine d'entreprendre ses recherches d'électronique, non sur des espèces prises au hasard, mais bien sur des espèces choisies en fonction des résultats qu'elles avaient fourni en photonique.

Parmi les auteurs ayant utilisé la microscopie électronique, l'accord est loin d'être réalisé au point de vue terminologique. J. Perreau-Bertrand a repris les termes: endospore, épispore, exospore, périspore, issus de la microscopie photonique. R. Singer a proposé une modification légère de cette terminologie, consistant à remplacer la terminaison *spore* par la terminaison *sporium* car, selon lui, il n'est pas logique d'utiliser le même mot endospore pour désigner, tantôt une spore née à l'intérieur d'un article, comme l'ascospore des Ascomycètes, tantôt une couche interne de la paroi sporique. L'abandon du terme endospore pour désigner celle-ci s'impose particulièrement aux auteurs qui, comme H. Clémençon, pensent que la basidiospore est, comme l'ascospore, une endospore, et qu'elle comprend de ce fait, outre la paroi qui appartient en propre à la spore, une enveloppe externe qui n'est que le prolongement, autour d'elle, de la paroi de la baside; de fait, cet auteur a remplacé tous les termes repris par J. Perreau-Bertrand par des mots nouveaux. Nous reviendrons plus bas sur les changements terminologiques proposés par H. Clémençon d'une part, par M. Besson-Antoine et nous-mêmes d'autre part.

## II—LES GRANDS ENSEMBLES DE LA PAROI SPORIQUE

A la suite de recherches effectuées en microscopie électronique par M. Besson-Antoine et en photonique par l'auteur de ces lignes, nous distinguons (M. Besson-Antoine & R. Kühner, 1972b) dans la paroi sporique deux couches principales: le *myxosporium* à l'extérieur, l'*eusporium* à l'intérieur, chacune de ces couches comportant assez souvent plusieurs feuillets.

La couche que nous appelons myxosporium correspond indiscutablement à la périspore de certains auteurs, et si nous avons proposé un nom nouveau pour elle, c'est uniquement parce que le mot périspore a été utilisé pour désigner, soit notre myxosporium dans son entier, soit seulement telle ou telle de ses différenciations possibles, par exemple l'ectospore ou, dans la terminologie de J. Perreau-Bertrand et de L. M. Meléndez-Howell, ce qui se trouve sous l'ectospore. Le mot myxosporium a été choisi pour rappeler qu'à l'origine cette couche offre, au moins dans nombre de familles, une consistance mucilagineuse, consistance qui se traduit par le fait que, chez plusieurs espèces, lorsque des spores entrent accidentellement en contact au cours de leur développement, leurs myxosporiums confluent. L'un de nous (R. Kühner, 1934 a) l'a montré en photonique et a figuré un résultat d'une telle confluence chez *Coprinus narcoticus*: les quatre spores issues d'une même baside peuvent se trouver groupées dans une enveloppe commune. Dans plusieurs espèces, un feuillet, généralement très mince, semble séparer le myxosporium de l'eusporium; pour rappeler cette situation intermédiaire nous avons proposé (M. Besson & R. Kühner, 1972a) de l'appeler *médiostratum*.

## III—LA PAROI SPORIQUE ET SES DIFFÉRENCIATIONS SOMMITALES CHEZ LES HYMÉNOMYCÈTES À SPORES BLANCHES, OCRACÉES, BRUNES, NOIRES OU VIOLACÉES

### A—Les feuillets de l'eusporium

Dans l'eusporium, des différences d'opacité aux électrons permettent souvent de distinguer deux ou trois feuillets principaux.

Comme l'a fait remarquer pour la première fois J. Perreau-Bertrand, on trouve, chez plusieurs espèces, un feuillet qui se distingue de ceux placés en dehors de lui par sa grande transparence aux électrons et l'absence de structure apparente; on le voit bien, par exemple, sur des clichés publiés par M. Besson & R. Kühner (notamment 1972a: Pl. 2 fig. 3, ou, ici même, Pl. 20 fig. 1; Pl. 21 fig. 2; Pl. 23 fig. 1 et 2). H. Clémençon l'appelle *corium*; il correspond indiscutablement à l'*endospore* de J. Perreau-Bertrand. Comme nous avons longtemps cru, avec ces auteurs, que ce feuillet est toujours au contact du protoplasme il nous a paru possible de conserver pour lui le mot endospore ou d'utiliser son dérivé *endosporium*.

Nous nous demandons aujourd'hui s'il est vrai que l'endosporium se trouve toujours au contact du protoplasme; un cliché de M. Besson-Antoine (1972: Pl. 10 fig. 3 et ici même Pl. 21 fig. 2) relatif à *Hebeloma radicosum* (Bull. ex Fr.) Ricken, montre en effet, en dedans de l'endosporium transparent, un très mince feuillet

opaque, qui ne peut correspondre à une différenciation externe du protoplasme puisqu'il conflue avec la partie interne du bouchon qui obture l'appendice apiculaire; c'est en somme un *endocorium*.

Quoiqu'il en soit, au cours du développement de la paroi sporique, l'endosporium s'édifie plus ou moins tardivement, toujours après la couche située en dehors de lui; il peut donc manquer chez les spores immatures. Il semble que chez nombre d'espèces il n'y ait jamais d'endosporium, même à maturité. A. P. Burge n'a jamais vu d'endosporium chez les Russulacées qu'elle a étudiées; c'est pourquoi, étiquetant les feuillets de la paroi sporique de A à F, en partant de l'intérieur, elle a désigné par A le feuillet qui, chez les espèces édifiant un endosporium, se situe immédiatement en dehors de ce dernier. Ce feuillet A, généralement épais, est limité du côté externe par un feuillet au contraire très mince, mais particulièrement opaque aux électrons, le feuillet B de Burge, la *tunica* de Clémençon (Voir par exemple: M. Besson, 1970b: Pl. 2 fig. 3; M. Besson-Antoine, 1972: Pl. 16 fig. 1 ou, ici même, Pl. 20 fig. 1 et Pl. 21 fig. 1).

Le feuillet qui se trouve entre la tunica et le corium (ou, lorsque celui-ci manque, entre la tunica et le protoplasme) est caractérisé par la coexistence de substance transparente et de substance opaque, comme on le voit sur la fig. 17 du mémoire de H. Clémençon. Cet auteur l'appelle *coriotunica*, parce qu'il croit que la substance transparente et la substance opaque sont respectivement de nature coriale et de nature tunicale. La couche pour laquelle J. Perreau-Bertrand a repris le terme *épispore*, issu des vieilles observations en photonique, correspond à la coriotunica ou à l'ensemble coriotunica + tunica. Il est difficile de lui conserver la dénomination épispore, d'abord parce que, chez les espèces qui n'ont pas d'endospore, c'est la couche interne de la paroi, ensuite parce que ce que nombre d'auteurs n'utilisant que la microscopie photonique ont appelé épispore est souvent un feuillet plus proche de la surface, puisque nombre d'entre eux ont considéré que, chez les spores ornées, les ornements sont d'origine épisporique alors que les chercheurs qui ont travaillé en électronique s'accordent pour considérer, depuis Burge et Perreau-Bertrand, qu'ils naissent d'une couche placée à l'extérieur de ce que ce dernier auteur appelle épispore. C'est pourquoi, avant que H. Clémençon n'ait proposé sa nomenclature, M. Besson avait suggéré (1970a) pour l'épispore de J. Perreau-Bertrand l'étiquette *sclérospore*, que M. Besson & R. Kühner (1972a) ont transformée en *sclérosporium*; ces étiquettes nous semblent avoir le double avantage de ne rien préjuger quant à la situation de cette couche et d'exprimer sa fermeté par rapport à la consistance initialement mucilagineuse du myxosporium proche.

L'importance prise par la substance opaque dans la constitution de la coriotunica et sa répartition dans celle-ci varient beaucoup d'une espèce à l'autre. Il peut arriver que la substance opaque soit également abondante dans toute l'épaisseur de la coriotunica (Clémençon, fig. 20), mais il n'est pas rare qu'elle soit inégalement répartie; elle peut être plus abondante du côté interne (Clémençon, fig. 23), mais chez nombre d'espèces l'importance qu'elle prend croît de l'intérieur vers l'extérieur; elle le fait souvent si progressivement (par ex. M. Besson & R. Kühner, 1972b: Pl. 3

fig. 1), que l'individualité de la tunica peut être mise en doute. Enfin, dans des cas plus rares, la coriotunica montre une alternance de zones opaques et de zones transparentes; une telle zonation, frappante chez *Coprinus silvaticus* Peck (M. Besson & R. Kühner, 1972b: Pl. 1 fig. 2), complique l'interprétation de la structure de l'eusporium.

Sur des spores ayant subi un traitement convenable la microscopie photonique permet souvent, elle aussi, de reconnaitre une structure stratifiée de l'eusporium. Chez les espèces de Naucoriacées, Coprinacées et Lepiotacées qui possèdent un *endosporium*, celui-ci est en général facile à reconnaitre sur des spores ayant subi un traitement par la potasse à l'autoclave; il tranche sur le sclérosporium qui l'entoure, par sa réfringence alors beaucoup plus forte (M. Besson-Antoine & R. Kühner, 1972a), ce qui tend à prouver que le corium ne correspond pas simplement à la partie interne de la coriotunica d'où la substance opaque aux électrons serait totalement absente. S'il est vrai que le feuillet réfringent, toujours très mince, que l'on observe souvent à l'extérieur du sclérosporium de spores traitées par KOH à l'autoclave, correspond à la *tunica* et à elle seulement, la différence d'indice entre ce feuillet externe et le sclérosporium plaide en faveur de l'idée que la tunica est un feuillet individualisé de l'eusporium, au même titre que le corium.

Chez certaines leucosporées à paroi sporique épaisse, le feuillet interne de la spore se distingue de ceux situés en dehors par le fait qu'il est le seul de la paroi à se colorer en pourpre au Giemsa. *Laccaria tortilis* (Bolt. ex S. F. Gray) Cooke et les Lépiotes à pore germinatif sont dans ce cas (R. Kühner, 1972); il semble que, chez ces dernières, ce soit le même feuillet que le bleu de crésyl colore en rouge-pourpre (R. Kühner, 1934b et 1972). Chez les Lépiotes où il est particulièrement épais, l'utilisation de ces teintures montre qu'il est en réalité double, constitué de deux minces couches se colorant de façon un peu différente (M. Locquin, 1943; R. Kühner, 1972).

Lorsque le sclérosporium est épais il n'est pas rare qu'après gonflement on y distingue en photonique deux couches différant par leur indice de réfraction et parfois aussi par leurs affinités tinctoriales. On peut reconnaitre ces deux couches sur matériel de diverses chromosporées traité par KOH à l'autoclave, mais elles ont été tout d'abord mises en évidence par M. Locquin sur des spores de Lépiotes de la section *Procerae*, gonflées par le procédé ammoniaco-acétique. Cet auteur appelait *épispore* et *exospore* les couches de la paroi sporique des *Procerae* que nous avons considérées depuis (R. Kühner, 1972) comme représentant respectivement la *sclérospore interne* et la *sclérospore externe*, et dont divers réactifs, iode ou bleu coton par exemple, confirment l'individualité, de façon parfois très brillante. Il est possible qu'*endo*- et *exosclérosporium* puissent être encore distingués l'un de l'autre par des différences d'opacité aux électrons; c'est ce que suggère par exemple un cliché de M. Besson-Antoine (1972: Pl. 1 fig. 1 ou, ici même Pl. 23 fig. 2) relatif à *Lepiota procera* (Scop. ex Fr.) S. F. Gray, mais nous ne pensons pas que chaque fois que des différences d'opacité permettent de distinguer deux couches dans un sclérosporium ces deux couches méritent respectivement les étiquettes endo- et exosclérosporium; pour nous

elles ne les méritent pas si le passage d'une opacité à l'autre est progressif car, en photonique, endo- et exosclérosporium paraissent brutalement limités l'un par rapport à l'autre.

### B—MYXOSPORIUM ET MÉDIOSTRATUM CHEZ LES ESPÈCES À SPORES ORNÉES

#### 1. Le sporothécium et ses différenciations

Dans les spores ornées, la disposition de l'ectospore par rapport aux ornements peut varier d'une espèce à une autre et deux dispositions extrêmes doivent être distinguées: ou bien l'ectospore est tendue au-dessus du sommet des ornements, ou bien elle est comme moulée sur eux.

Les Ganodermes et *Fayodia bisphaerigera* (J. E. Lange) Sing. illustrent le premier cas. En raison de l'opacité plus ou moins grande de la substance des ornements de ces champignons, il est facile de voir que l'ectospore est doublée intérieurement par un mince feuillet transparent; c'est ce dernier qui repose sur le sommet des ornements; il est évident sur un cliché de Furtado, relatif à un Ganoderme, et sur les clichés de *Fayodia bisphaerigera* publiés par M. Besson (1969a: Pl. 1 fig. 2 et 4 ou, ici même, Pl. 21 fig. 3).

Là où l'ectospore opaque, au lieu d'être tendue au-dessus des ornements, est comme moulée sur eux, on ne la distingue bien que chez les espèces où la substance des ornements est plus ou moins transparente aux électrons et chez celles, à ornements opaques, qui possèdent un mince feuillet transparent doublant l'ectospore du côté interne. Comme l'a montré M. Besson (1969b: Pl. 2 fig. 1 à 4), *Rhodotus palmatus* (Bull. ex Fr.) Maire illustre ce cas de façon spectaculaire, car on y distingue, sans la moindre difficulté, sous l'ectospore opaque, un mince feuillet transparent qui la double. Selon H. A. P. Burge, M. Besson et H. Clémençon les Russulacées sont dans le même cas; le feuillet transparent est toutefois si mince, qu'indiscutable sur certains clichés (Clémençon, fig. 14), il est beaucoup moins évident sur d'autres.

Clémençon a proposé les termes *ectosporothécium* et *endosporothécium* pour désigner respectivement le feuillet externe opaque, correspondant à l'ectospore de Heim, et le feuillet interne transparent qui le double intérieurement. Là où seul le feuillet opaque peut être distingué, par exemple chez les espèces où la substance des ornements est transparente, Clémençon parle seulement de *sporothécium*.

#### 2. Le médiostratum

Le feuillet que M. Besson & R. Kühner (1972a) ont proposé de nommer ainsi ressemble à l'endosporothécium par sa grande transparence aux électrons et généralement par sa minceur, mais au lieu d'être situé à l'extérieur des ornements, il est situé sous eux, immédiatement à l'extérieur de la tunica opaque ou, si celle-ci n'est pas différenciée, de la coriotunica. Le médiostratum n'est évidemment reconnaissable que là où une opacité plus ou moins grande de la couche myxosporiale qui le recouvre permet d'en tracer la limite externe. Cette condition est réalisée au plus

haut degré chez les Russulacées et l'on comprend que ce soit dans des représentants de cette famille et dans des types réputés affines que le médiostratum ait été reconnu pour la première fois; la découverte revient à Burge, qui désignait par la lettre C le feuillet que nous appelons médiostratum (voir par ex. M. Besson, 1970a: Pl. 1 fig. 1 ou, ici même, Pl. 22 fig. 2).

Il est certain que le feuillet pour lequel H. Clémençon a proposé, dès 1970, le nom *tectum* correspond à notre *médiostratum* ou le comprend; il est par exemple évident que le feuillet des Russulacées que cet auteur appelle tectum secondaire, et dont il précise que c'est le tectum proprement dit, correspond exactement à la couche C de Burge et à notre médiostratum.

Après avoir pensé que le médiostratum constitue un feuillet indépendant de l'eusporium et du myxosporium, nous croyons aujourd'hui qu'il ne constitue, au même titre que le sporothécium, qu'une différenciation de ce dernier; nous le croyons, non seulement que nous n'avons pu reconnaitre son existence chez diverses espèces à spores ornées, mais aussi parce que, chez nombre d'espèces à spores lisses, on ne trouve, à l'extérieur de la tunica, qu'un (mince) feuillet transparent dont il est difficile de dire s'il correspond plutôt à un médiostratum qu'à un endosporothécium; ce problème sera envisagé plus loin. Dans cette optique, nous proposons d'appeler *Eumyxosporium* la partie du myxosporium qui ne correspond, ni au sporothécium, ni au médiostratum.

### 3. Origine myxosporiale des ornements

Concernant l'origine des ornements, l'accord est loin d'être réalisé entre les chercheurs ayant utilisé l'électronique. H. Clémençon pense que la transparence ou l'opacité électronique de la masse fondamentale d'un ornement peut renseigner sur l'identité de la couche dont il dépend; lorsque la matière fondamentale d'un ornement est transparente aux électrons (fig. 1 à 5) comme le feuillet qu'il appelle *tectum*, il estime qu'il doit être rattaché à ce feuillet; il rattache à une couche différente qu'il appelle *épitunica*, les ornements opaques aux électrons des *Galerina* et des *Cortinarius* (fig. 19). Nous ne pouvons partager cette opinion. Nous ferons remarquer que les ornements transparents en électronique sont généralement incolores en photonique alors que les ornements colorés en photonique apparaissent généralement opaques en électronique; ce dernier cas est illustré, non seulement par les *Cortinarius* et les *Galerina*, mais également par les *Hebeloma*, les *Coprinus*, etc . . . Il est vraisemblable que l'opacité d'un ornement, au lieu d'être le signe d'une origine particulière, n'est due qu'à une quelconque imprégnation naturelle.

Pour J. Perreau-Bertrand, les ornements sont des épaississements, vers l'extérieur, d'un feuillet basal continu, qu'elle appelle *exospore* et qui, selon elle, se distingue de la *périspore* transparente aux électrons située immédiatement en dehors par son opacité. De fait les ornements apparaissent opaques aux électrons sur les clichés de J. Perreau-Bertrand, et ceci dans les genres les plus variés. Il est certain que les ornements ne sont pas toujours reliés les uns aux autres par leurs bases, comme le croyait

cet auteur. H. A. P. Burge avait déjà reconnu que les épines des *Laccaria* sont indépendantes les unes des autres. Avant de considérer ce dernier cas, nous examinerons celui de quelques espèces qui présentent un feuillet basal continu, dont les ornements ne sont que des épaississements vers l'extérieur; on verra que, sur plusieurs points, nous sommes en désaccord, soit avec J. Perreau-Bertrand, soit avec H. Clémençon.

Chez les Russulacées, la matière fondamentale des ornements est en partie remarquablement opaque aux électrons, comme l'est la couche continue tout autour de la spore, qui réunit les ornements par leurs bases; cette couche basale opaque tranche brutalement sur le mince médiostratum (ou tectum secondaire) transparent situé au-dessous (par ex. M. Besson, 1970a: Pl. 1 fig. 1), H. A. P. Burge, M. Besson et H. Clémençon ont montré que, du côté externe, un mince sporothécium tapisse étroitement la masse fondamentale des ornements et, entre eux, la couche continue qui les réunit par leurs bases. Ce sporothécium n'est bien reconnaissable que parce que l'ectosporothécium opaque est séparé de la masse opaque du reste de l'ornement par un mince endosporothécium transparent (par ex. Clémençon, fig. 11). Il est donc évident que l'eumyxosporium des Russulacées est entièrement utilisé à la formation des ornements et de la couche qui les porte.

Mais il ets non moins évident, comme les auteurs cités et J. Perreau-Bertrand l'ont montré, que la masse fondamentale de chaque ornement apparait électroniquement très hétérogène; outre une partie très opaque, située juste sous le sporothécium, et qui se poursuit dans le feuillet qui réunit les ornements par leurs bases, partie étiquetée D par Burge et nommée *interstratum* par Clémençon, elle comporte une partie profonde très transparente (E de Burge, qui étiquetait F le sporothécium; *tectum primaire* de Clémençon).

Plusieurs auteurs n'ayant utilisé que la microscopie photonique, M. Josserand par exemple, avaient remarqué que, chez diverses Russulacées, on voit émerger, çà et là, de l'ornementation amyloïde, des saillies qui ne le sont pas. C'est pourquoi il est tentant de penser, avec J. Perreau-Bertrand et H. Clémençon, que la matière opaque aux électrons est la matière amyloïde. Il faut cependant reconnaitre que cette hypothèse est assez gratuite si l'on considère que les verrues amyloïdes des *Leucopaxillus* et des *Melanoleuca* sont assez transparentes aux électrons pour que H. Clémençon les aient rattachées à son tectum (Clémençon, fig. 2 et 5).

Les mycologues n'ayant utilisé que la photonique pensaient que les saillies non amyloïdes sont des épaississements d'une couche continue à la surface de la spore. J. Perreau-Bertrand pensait de même que la partie des ornements transparente aux électrons est en continuité avec une fine couche basale continue, également transparente, couche qu'elle appelle exospore; à l'origine de la partie opaque des ornements serait une autre couche, extérieure par rapport à la précédente, la périspore. Ces vues, que J. Perreau-Bertrand a illustrées par un schéma très explicite, sont en contradiction avec un passage des conclusions du mémoire de cet auteur, selon lequel "la périspore non pigmentée s'oppose à l'exospore pigmentée"; elles sont par ailleurs en désaccord avec les clichés de H. A. P. Burge, M. Besson, H. Clémençon, et même

avec certaines des photographies J. Perreau-Bertrand, qui montrent que, très souvent, les parties transparentes des ornements sont entourées de toutes parts, même en dessous, par de la matière opaque.

Une lecture superficielle du travail de H. Clémençon pourrait laisser croire que, comme J. Perreau-Bertrand, il faisait dériver la matière transparente et la matière opaque d'un ornement de deux couches distinctes; il désigne en effet ces deux matières, respectivement par les termes *tectum* et *interstratum*. Ce serait certainement mal interprèter sa pensée puisque d'une part il précise que l'interstratum n'est pas à proprement parler une couche de la paroi sporique et que d'autre part, ayant suivi les premiers stades du développement de la paroi (fig. 11 à 13), il écrit que la synthèse de l'interstratum et du tectum primaire est soumise à des variations locales, de sorte que des morceaux de substance tectale primaire arrivent à se trouver sur et dans l'interstratum. La totalité des ornements des Russulacées et de la couche qui les porte dérive donc d'une seule et même véritable couche de la paroi, pour nous l'eumyxosporium.

En dehors des Russulacées on connait bien des espèces dont les ornements se présentent, au moins à un âge convenable de la spore, comme des épaississements localisés d'une mince couche continue tout autour de la spore, l'exospore au sens de J. Perreau-Bertrand.

Pour cet auteur l'exospore est une couche distincte de la périspore qui la surmonte, bien que les ornements exosporiques croissent à l'intérieur de cette dernière. Pour M. Besson-Antoine et l'auteur de ces lignes l'exospore n'existe pas, du moins en tant que couche distincte de la périspore; l'exospore et les ornements dérivent tous deux d'une même couche myxosporiale et, en dehors d'eux, il n'y a rien autre que le sporothécium qui les tapisse éventuellement. Pour justifier notre interprétation nous allons examiner le cas de quelques Hyménomycètes à spores incolores sous le microscope, amyloïdes, (*Melanoleuca*, *Leucopaxillus*, *Dentipellis*, *Gloeocystidiellum*) ou non (*Lepista*).

L'ornementation de *Lepista panaeola* (Fr.) Karst. rappelle celle des Russulacées en ce sens qu'à maturité de la spore, la masse fondamentale de chaque verrue est électroniquement hétérogène, comprenant une partie profonde que coiffe une couche plus opaque, la limite entre les deux étant brutale. Ceci a été reconnu, de façon indépendante, par M. Besson (1970b: Pl. 1 fig. 1) et par H. Clémençon. Le premier de ces auteurs a montré qu'une telle hétérogénéité n'apparait que secondairement; les verrues de la spore jeune sont électroniquement homogènes (M. Besson, 1970b: Pl. 1 fig. 2 ou, ici même, Pl. 20 fig. 4).

M. Besson et H. Clémençon ont reconnu que la couche la plus opaque de la spore mûre se poursuit entre les ornements, qu'elle réunit les uns aux autres par leurs bases. H. Clémençon a été tenté de l'assimiler à l'interstratum des Russulacées, mais il faut remarquer que chez le *Lepista* elle n'est pas amyloïde et que, contrairement à l'interstratum des Russulacées, cette couche ne passe pas sous la couche plus transparente.

Sur la fig. 1, Pl. 1 de M. Besson, on distingue, sous la couche aux ornements, un

médiostratum qui tranche sur elle aussi nettement que chez les Russulacées; par sa transparence remarquable il contraste, non seulement avec la partie la plus opaque de la verrue, mais aussi avec la masse profonde de celle-ci, dont la transparence est beaucoup moins grande.

Si les verrues sont unies les unes les autres par leur couche la plus opaque, le noyau moins opaque de chaque verrue est indépendant de celui de chaque verrue voisine, comme chez les Russulacées.

Dans les clichés de Clémençon (Fig. 3 et 4) le noyau de chaque verrue est beaucoup plus transparent que dans celui de Besson; de ce fait il tranche mieux sur la couche opaque qui le coiffe, mais il se confond avec le médiostratum (tectum de Clémençon), ce qui explique que Clémençon ait considéré que le noyau de chaque verrue de *Lepista panaeola* n'est qu'un épaississement du tectum, ce qu'il est difficile d'admettre lorsqu'on jette un coup d'oeil, même rapide, au cliché de Besson.

Clémençon admet que, chez les *Leucopaxillus* également, la masse fondamentale de chaque verrue n'est qu'un épaississement du tectum; M. Besson a montré (1970a) que si l'on a parfois cette impression sur la spore mûre (Pl. 4 fig. 1), les coupes de spores jeunes (Pl. 4 fig. 2) prouvent qu'il n'en est rien. Les coupes de jeunes spores de *Leucopaxillus amarus* (A. & S. ex Fr.) Kühner montrent clairement un fin médiostratum transparent, à l'extérieur duquel se trouve une couche grise continue, mince par endroits, épaisse au niveau des verrues.

C'est une structure du même type que M. Besson a retrouvée chez *Gloeocystidiellum furfuraceum* (Bres.) Donk (1970a: Pl. 4 fig. 3 ou, ici même, Pl. 22 fig. 2), *G. porosum* (Berk. et Curt.) Donk (ici même Pl. 20 fig. 6) et chez un *Dentipellis* indéterminé (1970a: Pl. 4 fig. 5), trois espèces à spores amyloïdes comme celles des *Leucopaxillus*.

Clémençon pense que, chez les espèces à verrues sporiques amyloïdes que sont les *Melanoleuca*, les verrues sont des fragments de tectum séparés les uns des autres (Fig. 5). Les photographies de M. Besson (1970a: Pl. 3 fig. 7 et 8) conduisent à penser que le cas des *Melanoleuca* n'est pas fondamentalement différent de celui des genres examinés plus haut. H. Clémençon a d'ailleurs précisé que, chez les *Melanoleuca*, un sporothécium continu tapisse extérieurement les ornements et, entre eux, la couche sur laquelle ils reposent.

Alors que dans les types précédents la masse fondamentale du myxosporium (ou eumyxosporium) est entièrement utilisée à l'édification des ornements et de la couche, de même nature, qui les réunit par leurs bases, dans d'autres espèces une partie seulement de cette masse sert à construire les ornements; on peut en effet voir entre eux, au moins au début, une épaisseur importante, parfois aussi grande que leur hauteur, de *substance myxosporiale résiduelle*.

Bien souvent les ornements se présentent dans ce cas comme des piliers. S'il arrive qu'ils soient réunis par leurs bases, il n'est pas rare qu'ils le soient alors également par leurs sommets, par une couche continue tapissant le sporothécium, comme on peut le voir sur des clichés de M. Besson, par exemple chez *Coprinus verrucispermus* Joss. (M. Besson, 1972: Pl. 1 fig. 6 ou, ici même, Pl. 20 fig. 3), chez *Fayodia bis-*

*phaerigera* (M. Besson: 1969a ou, ici même, Pl. 21 fig. 3) ou, encore mieux, chez *Hebeloma calyptrosporum* Bruchet (M. Besson & G. Bruchet, Pl. 1 fig. 4).

Chez *Tubulicium clematidis* (B. & G.) Oberw., les piliers semblent plus indépendants les uns des autres; leur indépendance vis à vis d'une couche sous-jacente est apparue avec une évidence particulière sur certaines coupes ultrafines de spores où le myxosporium avait été arraché accidentellement de l'eusporium, entrainant les ornements formés en son sein (M. Besson, 1969c: Pl. 2 fig. 2).

Chez certaines espèces il arrive qu'à maturité ne subsistent du myxosporium que les ornements formés en son sein, le reste ayant diffluć; celà arrive chez le *Tubulicium* cité. Dans de tels cas une troncature des ornements à leur extrémité devenue libre trahit leur naissance au sein d'une couche myxosporiale d'épaisseur égale.

Une indépendance des ornements les uns par rapport aux autres se retrouve dans le genre *Laccaria*, où elle a été tout d'abord signalée par H. A. P. Burge. M. Besson (1971) a confirmé le fait, précisant en outre que la matière des ornements présente une infrastructure longitudinalement fibrillaire. Elle a en outre montré que, malgré leur forme conique-pointue, qui en fait de véritables épines, les ornements des *Laccaria* naissent au sein d'un myxosporium dont une partie seulement est utilisée à leur édification (Pl. 2 fig. 1); ce qui reste du myxosporium disparait ici très rapidement sans laisser de traces.

La hauteur des ornements d'origine myxosporiale dépend naturellement de l'épaisseur du myxosporium. Dans bien des spores dont le sommet est largement arrondi, les ornements du dôme apical ont même hauteur que ceux de la région équatoriale; ils sont même parfois plus élevés que ceux-ci. Par contre, on a depuis longtemps remarqué que lorsque le sommet de la spore est atténué ou étiré en papille, la hauteur des ornements diminue souvent (progressivement) à l'approche de la papille, qui peut parfois paraître lisse en microscopie photonique; c'est que l'épaisseur du myxosporium diminue dans la région apicale de ces espèces (par ex: M. Besson-Antoine & R. Kühner, 1972b: Pl. 3 fig. 1).

### C—Myxosporium et médiostratum chez les espèces à spores lisses

De ce qui vient d'être dit du rapport entre la hauteur des ornements et l'épaisseur du myxosporium, il ne faudrait pas conclure que chez les espèces dont la spore est dépourvue d'ornements le myxosporium est forcément mince. Son épaisseur peut même être suffisamment grande pour qu'il puisse être facilement mis en évidence, en photonique; c'est le cas par exemple chez des *Panaeolus*; s'il est difficile de voir le myxosporium sur des spores isolées dans l'eau pure, parce qu'il est incolore et dépourvu de pellicule limitante visible, on peut déjà se douter de son existence en constatant que dans une suspension assez dense de spores fraîches dans l'eau, les parties noires de la paroi sporique ne se touchent jamais; si l'eau renferme, avec les spores, de très fines particules en suspension, par exemple celles d'un fin précipité de colorant neutre, on voit celles-ci marquer la limite extérieure du myxosporium.

Sur un cliché d'électronique de M. Besson & R. Kühner (1972a: Pl. 1 fig. 1)

relatif à *Panaeolus campanulatus* (Bull. ex Fr.) Quél., on voit que, même à l'état déshydraté, le myxosporium a encore une épaisseur importante, puisqu'elle se situe entre 0,3 et 0,4$\mu$. Le même cliché montre que l'épaisseur du myxosporium diminue, progressivement mais rapidement, à l'approche du pore et qu'au dessus de celui-ci elle est très faible, de l'ordre de 0,02$\mu$.

De telles différences d'épaisseur du myxosporium d'une région à l'autre d'une même spore ne sont sans doute pas fréquentes chez les espèces à spores lisses, même chez les espèces à pore germinatif. Le myxosporium de *Coprinus cineratus* est aussi épais au-dessus du pore qu'ailleurs (M. Besson & R. Kühner 1972; Pl. 1 fig. 1). Celui des Lépiotes porées, des *Procerae* par exemple, apparait partout mince en électronique; tout au plus est il un peu moins mince au-dessus du pore (M. Besson-Antoine, 1972: Pl. 16 fig. 1).

Comme le montrent les photographies d'électronique de M. Besson & R. Kühner (1972a) le myxosporium de *Panaeolus* ne montre, à l'extérieur du fin médiostratum, aucune différenciation sur la spore immature (Pl. I fig. 1), alors que plus tard une mince couche de substance opaque se dépose à sa base, contre le médiostratum (Pl. 2 fig. 3), couche que nous avons rapportée à l'*épitunica* de H. Clémençon; son appartenance au myxosporium est bien visible sur cette dernière figure où l'on voit confluer les épitunicas appartenant à deux spores proches.

Dans de nombreux Hyménomycètes à spores lisses on ne trouve, à l'extérieur de la tunica opaque ou, si celle-ci n'est pas distincte, de la coriotunica, que deux minces feuillets dont l'ensemble correspond à notre myxosporium: l'interne transparent, l'externe, superficiel, opaque; ces deux feuillets, que L. M. Meléndez-Howell appelle respectivement *périspore* et *ectospore*, se voient bien par exemple sur des clichés de cet auteur (Pl. 37 fig. 2 et 4) relatifs à de grandes Lépiotes; leur ensemble repose ici sur une *tunica* opaque (que Meléndez-Howell appelle *exospore*) particulièrement reconnaissable au-dessus du bouchon qui obture le pore germinatif de ces espèces. Les feuillets reconnus par Meléndez-Howell au-dessus du bouchon porique sont encore plus frappants, car plus contrastés, sur un cliché inédit de M. Besson-Antoine (1972: Pl. 16 fig. 1, ou, ici même, Pl. 20 fig. 1) relatif à *Lepiota procera*.

Un myxosporium constitué seulement de deux minces feuillets, l'interne transparent, l'externe opaque, a été reconnu chez bien d'autres Agaricales que les Lépiotes, notamment chez de nombreuses espèces sans pore. H. Clémençon a figuré un tel myxosporium, aussi bien chez des chromosporées, comme par exemple *Flammula carbonaria* (Fr. ex Fr.) Kummer (fig. 2) que chez des leucosporées des genres *Mycena* (fig. 6) ou *Collybia* (fig. 7). M. Besson-Antoine (1972) a mis en évidence, avec beaucoup de netteté, les deux minces feuillets myxosporiaux chez deux espèces à spores blanches d'affinités fort différentes: *Aspropaxillus giganteus* (Sow. ex Fr.) Kühner & Maire (Pl. 6 fig. 6 ou, ici même, Pl. 20 fig. 5), proche des *Clitocybe* et *Amanita vaginata* (Bull. ex Fr.) Vitt. (Pl. 6 fig. 1 ou, ici même, Pl. 20 fig. 2); chez cette dernière espèce une tunica sombre, limitant l'eusporium du côté externe, souligne nettement la mince couche transparente qui revêt celui-ci.

L'ensemble de ces deux minces feuillets: un opaque à la surface, un transparant

le doublant vers l'intérieur et accolé d'autre part à l'eusporium, constitue donc une structure extrêmement répandue chez les Hyménomycètes à spores lisses et sur l'interprétation de laquelle il importerait de se mettre d'accord.

Le feuillet externe, de par sa situation et son opacité, ne semble pas avoir posé jusqu'ici de difficulté majeure; L. M. Meléndez-Howell le nomme *ectospore* et H. Clémençon *sporothécium*, mais on sait que ces deux termes peuvent être synonymes.

Le feuillet sous-jacent ressemble par sa transparence aux deux feuillets connus, chez les espèces à spores ornées, sous les étiquettes respectives: *endosporothécium* et *médiostratum*. H. Clémençon pense que le feuillet transparent des espèces à spores lisses ne peut être un endosporothécium; c'est pourquoi il a proposé pour le désigner une dénomination nouvelle: *tectum*.

Les raisons invoquées par cet auteur pour éliminer l'interprétation endosporothécium sont fort loin de nous convaincre. Elles sont basées sur l'hypothèse selon laquelle lorsqu'un sporothécium est différencié en deux feuillets (ectosporothécium opaque et endosporothécium transparent), ces deux feuillets correspondent aux deux feuillets qui constitueraient la totalité de la paroi de la baside, donc que tout feuillet plus interne de la spore lui appartient en propre, c'est à dire ne se poursuit pas de la spore dans le stérigmate. Selon Clémençon le feuillet qu'il appelle tectum diffère du feuillet interne de la paroi de baside par son épaisseur et sa tonalité en électronique; cet auteur en tire la conclusion qu'il ne peut s'agit d'un feuillet commun à la spore et à la baside, c'est à dire d'un endosporothécium. Un tel raisonnement nous parait absolument sans valeur parce qu'on peut fort bien imaginer qu'un feuillet commun à la spore et à la baside subisse dans la spore des différenciations qui n'ont pas lieu dans la baside. Si l'épaisse couche opaque qui limite à l'extérieur le myxosporium de *Coprinus cineratus* appartient au sporothécium, ce qu'il parait difficile de nier, il faut bien reconnaitre qu'on ne trouve rien qui lui ressemble, par l'épaisseur et l'opacité, dans la paroi de la baside; un cliché de M. Besson-Antoine & R. Kühner (1972b: Pl. 1 fig. 3) montre que les différenciations qui rendent si frappant le sporothécium de cette espèce cessent brutalement dès la région apiculaire et ne se poursuivent donc pas sur la baside. De même si la pellicule tendue au-dessus des ornements de la spore de *Fayodia bisphaerigera* est un sporothécium, ce qu'il est d'autant plus difficile de nier qu'elle montre en électronique une différenciation en feuillet externe opaque et feuillet interne transparent (M. Besson, 1969a), il faut reconnaitre qu'elle diffère de la paroi de la baside parce qu'elle est amyloïde contrairement à celle-ci (R. Kühner, 1930). Ces deux exemples montrent que ce n'est pas en comparant les caractères d'un feuillet de la spore avec ceux des feuillets de la paroi basidiale qu'on peut espérer décider qu'un feuillet observé dans la spore est ou non le prolongement d'un feuillet de la baside; le seul moyen de trancher la question est de voir, en électronique, s'il y a ou non continuité du feuillet de la spore au feuillet de la baside au travers de la paroi du stérigmate, ce qui apparemment n'a été réalisé jusqu'ici que de façon très exceptionnelle.

A l'occasion de l'étude de la région apiculaire de la spore, nous reviendrons sur ce problème et nous verrons que plusieurs travaux récents ne sont pas en accord

avec l'hypothèse sur laquelle est basée l'interprétation de Clémençon. Remarquons cependant que d'autres arguments pourraient être invoqués à l'appui de la manière de voir de cet auteur, selon laquelle le feuillet transparent qui, chez les espèces à spores lisses, se trouve immédiatement à l'extérieur de la tunica, ne peut être un endosporothécium.

Les deux Corticiacées: *Gloeocystidiellum furfuraceum* et *Scytinostroma hemidichophyticum* Pouz. ont des spores apparemment très comparables, tant en photonique (elles sont amyloïdes dans les deux espèces) qu'en électronique comme le montrent les clichés de M. Besson-Antoine (1972); la seule différence apparente sur ces clichés réside dans le fait que la première espèce a les spores verruqueuses (Pl. 12 fig. 5 ou, ici même, Pl. 22 fig. 2) alors que la seconde a les spores lisses (Pl. 12 fig. 6 ou, ici même, Pl. 22 fig. 1). Les verrues du *Gloeocystidiellum* se présentent comme des épaississements d'une mince couche continue reposant sur un médiostratum particulièrement tranché; il n'y a pas de sporothécium visible. Il est difficile d'échapper à l'idée que le feuillet myxosporial transparent du *Scytinostroma* correspond au médiostratum du *Gloeocystidiellum*. Mais cette comparaison pose un autre problème: le feuillet myxosporial superficiel opaque de l'espèce à spore lisse, qui aurait certainement été considéré comme ectospore par L. M. Meléndez-Howell, ou comme sporothécium par H. Clémençon, ne correspond-il pas plutôt à tout ce qui reste du myxosporium après différenciation du médiostratum, c'est à dire à l'ensemble de la couche aux verrues du *Gloeocystidiellum*?

Ce que l'on sait de la spore de *Panaeolus campanulatus* (M. Besson & R. Kühner, 1972a) plaide encore en faveur de la manière de voir de Clémençon. Nous avons admis que la mince couche transparente qui, chez cette espèce, tapisse l'extérieur de la tunica, est un médiostratum et non un endosporothécium, d'abord parce que la couche d'un gris uniforme qui la recouvre au début (Pl. 1 fig. 1) a une épaisseur beaucoup trop grande pour être considérée comme un exosporothécium, ensuite parce que s'individualise plus tard, au plancher de cette couche grise, une épitunica bien plus sombre (Pl. 2 fig. 3). L'épaisse couche grise est un Eumyxosporium typique. Or, à l'approche du pore, elle s'amincit rapidement et, au-dessus du pore, son épaisseur n'est guère supérieure à celle du médiostratum. A ce niveau l'aspect est proche de celui rencontré chez *Lepiota procera*. Si la couche grise qui recouvre le médiostratum transparent de ce *Panaeolus* n'était pas plus épaisse sur le reste de la spore qu'elle ne l'est au-dessus du pore, le mince feuillet transparent que nous appelons médiostratum nous aurait posé les mêmes problèmes pour son interprètation que le mince feuillet transparent de *Lepiota procera* par exemple.

Mais si ce dernier est bien un médiostratum, c'est à dire si la comparaison entre le Panaeole et la Lépiote est valable, le feuillet sombre qui revêt ce feuillet transparent chez la Lépiote et les espèces à spores lisses d'autres genres citées plus haut, doit il être toujours considéré comme un sporothécium? N'est-ce pas plutôt tout ce qui reste du myxosporium après différenciation du médiostratum? Comme on le voit l'interprétation du feuillet myxosporial externe mince et opaque de nombre d'espèces

à spores lisses qui semblait à première vue ne poser aucun problème est en réalité fort délicate.

Quant au problème que nous nous sommes posés au sujet de l'identité du feuillet interne transparent des espèces à spores lisses, on peut se demander s'il ne s'agit pas d'un faux problème. Il est en effet bien possible que la distinction entre endosporothécium et médiostratum chez plusieurs espèces à spores ornées ne soit due qu'au développement de la couche aux ornements plus ou moins opaque au sein d'un myxosporium transparent: c'est ce que suggère le cas de *Coprinus cineratus*; dans cette espèce à spores lisses se différencie en effet, entre l'ectospore et la tunica opaques, une mince couche grise, plus ou moins confusément limitée, qui scinde le myxosporium transparent en deux parties, l'une externe, l'autre interne (M. Besson & R. Kühner, 1972b: Pl. 1 fig. 1). Nous assimilons cette couche grise à la couche opaque qui se dépose à la base du myxosporium de *Panaeolus campanulatus*, y formant une épitunica qui n'est séparée de la tunica que par un médiostratum ténu.

Chez les *Coprinus* à spores ornées, comme *C. verrucispermus*, la substance épitunicale opaque s'accumule dans toute l'épaisseur du myxosporium et y forme les ornements, ou ne ménage que deux feuillets transparents ténus, l'un sous l'ectospore, l'autre au-dessus de la tunica.

## D—Les différenciations sommitales de l'eusporium et celles qui les accompagnent éventuellement

### 1. Le pore germinatif

L'électronique montre de façon indiscutable que ce qu'on appelle pore germinatif n'est pas une cavité; à l'emplacement du soi disant pore se trouve ce que nous appelons la *médulla* (M. Besson & R. Kühner, 1972a), qui est une colonne d'une substance plus ou moins différente par son aspect de celle qui constitue l'eusporium environnant et qui "traverse" ce dernier, au moins sur une partie de son épaisseur. Bien que le mode de développement de la médulla n'ait été élucidé que dans de très rares cas, on sait déjà qu'il peut varier beaucoup d'une espèce à une autre. Chez les *Panaeolus* (M. Besson & R. Kühner, 1972a) l'eusporium reste mince au sommet de la spore, alors que partout ailleurs il s'épaissit fortement en direction centripète; ainsi nait une excavation, d'abord occupée par du protoplasme (Pl. 1 fig. 1) et que viendra remplir la matière constituant la médulla (Pl. 1 fig. 3); cette dernière a une origine comparable à celle que nous décrirons plus loin pour le bouchon apiculaire, en ce sens qu'elle est formée de matériel comblant une excavation.

Il n'y a jamais d'excavation interne au sommet de la spore de *Coprinus cineratus* parce que, lorsque l'eusporium s'épaissit, il le fait autant au sommet qu'ailleurs; la colonne médullaire correspond ici à une différenciation de l'eusporium dans la région du dôme apical; elle s'allonge vers l'intérieur de la spore au fur et à mesure que les autres parties de l'eusporium s'épaississent (R. Hugueney); au niveau de la

médulla, l'épaississement de l'eusporium peut même être un peu en avance sur ce qu'il est ailleurs.

Chez les espèces à pore germinatif il y a très souvent un endosporium ou corium distinct. Il arrive, par exemple chez des Lépiotes de la section *Annulosae*, que la différenciation d'une colonne médullaire se poursuive jusque dans ce feuillet, par exemple chez *Lepiota brebissonii* Godey apud Gillet (M. Besson-Antoine, 1972: Pl. 16 fig. 3 ou, ici même, Pl. 23 fig. 1; R. Kühner, 1972). Mais il semble que, dans la plupart des espèces à pore germinatif, la matière de l'endosporium ne présente aucune hétérogénéité dans la région sommitale, contrairement à la matière du sclérosporium; alors, comme ce dernier, la médulla porique finit par être séparée du protoplasme par l'endosporium.

La colonne médullaire peut être à peu près cylindrique, mais dans nombre d'espèces, elle s'épaissit ou, si l'on préfère s'élargit, dans sa partie externe. Cet épaississement peut être léger, comme par exemple chez *Coprinus cineratus* (M. Besson & R. Kühner, 1972b: Pl. 1 fig. 1), mais il peut être beaucoup plus accusé dans certaines espèces où la médulla prend la forme de la chair d'un champignon, avec un chapeau plus ou moins large, très large par exemple chez *Coprinus silvaticus* (Ibid, Pl. 1 fig. 2), porté par un pied tantôt court comme chez cette espèce, tantôt plus allongé, chez *Lepiota brebissonii* et *L. naucina* (Fr.) Kummer par exemple. C'est à Meléndez-Howell que revient le mérite d'avoir mis en évidence, pour la première fois, la diversité des formes que peut affecter la médulla.

L'allure de la matière de la médulla en électronique semble varier passablement d'une espèce à l'autre. Meléndez-Howell a montré (Pl. 37 fig. 2 et 3) que, chez les Lépiotes de la section *Procerae*, la médulla qui obture le pore et qu'elle appelle *bouchon porique* est fortement hétérogène en électronique, étant constituée par un mélange de parties transparentes et de parties franchement opaques; ce bouchon porique tranche alors avec l'endosporium sur lequel repose sa base, l'endosporium étant homogène, ne comprenant que du matériel transparent aux électrons. Toutes ces particularités se voient particulièrement bien sur un cliché de M. Besson-Antoine (1972: Pl. 16 fig. 1 ou, ici même, Pl. 20 fig. 1) relatif à *Lepiota procera*.

Selon D. A. Griffiths comme selon M. Besson & R. Kühner (1972a: Pl. 1 fig. 2 et 3) la médulla des *Panaeolus* est également hétérogène, se montrant spongieuse ou maculée de flocons opaques sur fond transparent, alors que l'endosporium est entièrement transparent. Mais parmi les espèces qui édifient un endosporium, on en connait pas mal chez lesquelles la substance médullaire se présente, en électronique, avec un aspect au moins très voisin de celui de l'endosporium (par ex. M. Besson-Antoine & R. Kühner, 1972b: Pl. 1 fig. 2); la médulla se présente alors comme un *prolongement endosporique* au travers du sclérosporium, et Meléndez-Howell l'a considérée comme telle chez une foule de champignons.

Cet auteur pense donc que le pore est obturé, chez certaines espèces, par un *bouchon porique*, chez d'autres par un *prolongement endosporique*; elle a même signalé de rares cas où la partie proximale du pore serait obturée par un prolongement endosporique alors que la partie distale le serait par un bouchon porique.

C'est parce que Meléndez-Howell a utilisé l'expression bouchon porique dans un sens qu'elle croyait très spécial que nous avons renoncé à utiliser cette dénomination simple et évocatrice pour désigner ce que nous avons appelé médulla. Précisons que nous ne croyons pas cependant à l'opposition bouchon porique/prolongement endosporique, essentiellement pour la raison que dans trop de cas où l'électronique nous présente la médulla comme un prolongement endosporique, le photonique nous a permis de voir qu'il n'en est rien.

Chez plusieurs des espèces où la forme de la médulla évoque celle de la chair d'un champignon à chapeau, la substance du chapeau est différente de celle du stipe, pouvant être par exemple bien plus transparente aux électrons, comme le montrent notamment des clichés de M. Besson & R. Kühner (1972b) relatifs à *Lacrymaria pyrotricha* (Holmsk. ex Fr.) Konr. & Maubl. (Pl. 2 fig. 1) et à *Coprinus picaceus* (Bull. ex Fr.) S. F. Gray (Pl. 2 fig. 3).

Chez la dernière espèce cette différenciation semble en rapport étroit avec la différenciation de deux couches dans le sclérosporium environnant. Lorsque, comme dans les deux exemples cités, on passe assez brutalement de la substance du chapeau à celle du stipe, il peut être commode de parler respectivement de *piléomédulla* et de *caulomédulla*.

La différenciation piléomédulla/caulomédulla s'impose encore davantage chez certains Coprins, *Coprinus verrucispermus* par exemple, où un feuillet très opaque, la *néotunica*, sépare la piléomédulla, qui a la forme d'une épaisse lentille biconvexe, de la caulomédulla (M. Besson & R. Kühner, 1972b: Pl. 3 fig. 1).

Meléndez-Howell a montré que le feuillet opaque qu'elle nomme *exospore* et que nous appelons *tunica* se poursuit sans modification au-dessus de la médulla; nous l'avons maintes fois vérifié. Il arrive que la substance médullaire subisse à son extrémité externe, juste sous la tunica, et sur une très faible longueur, des différenciations particulières. Par exemple, chez *Coprinus cineratus*, M. Besson & R. Kühner (1972b: Pl. 1 fig. 1) ont figuré un feuillet assez clair puis, un peu plus profondément un feuillet opaque; un ensemble analogue a été figuré par Meléndez-Howell chez *Lacrymaria velutina*.

Nous avons dit plus haut que l'ensemble situé à l'extérieur de la tunica opaque et que nous considérons ici comme myxosporium au sens large, est, chez une foule d'Agaricales à spores lisses, réduit à deux minces feuillets: l'intérieur transparent (Périspore de Meléndez-Howell. Tectum de Clémençon), le superficiel opaque (Ectospore de Meléndez-Howell. Sporothécium de Clémençon). Meléndez-Howell a montré que ces deux feuillets se retrouvent au-dessus du pore germinatif. Chez plusieurs Lépiotes à pore germinatif, cet auteur a décrit une lentille "formée par la périspore et l'ectospore", dont l'ensemble serait un peu plus épais au-dessus du pore que sur le reste de la spore. L'épaississement du feuillet transparent semble surtout notable chez les *Annulosae*. Dans l'étude des pores germinatifs, comme dans celles des autres parties de la spore, l'apport de la microscopie photonique est loin d'être négligeable. La médulla porique est remarquablement mise en évidence chez diverses Lépiotes par le Giemsa qui la colore en rouge-pourpre (R. Kühner, 1972).

Cette particularité tinctoriale est peut-être largement répandue puisque R. Hugueney (inédit) l'a retrouvée sur les spores immatures de plusieurs Coprins.

Chez les Lépiotes de la section *Procerae* la différence d'infrastructure mise en évidence par Meléndez-Howell entre le bouchon porique et l'endosporium est à mettre en parallèle avec la différence de colorabilité au bleu de crésyl, l'endosporium seul se colorant en rouge-pourpre (R. Kühner, 1934b).

Chez les Lépiotes de la section *Annulosae* la ressemblance infrastructurale entre l'endosporium et la médulla, qui a conduit Meléndez-Howell à la conclusion que la médulla n'est ici qu'un prolongement endosporique, est à mettre en parallèle avec le fait que la médulla se colore en rouge-pourpre par le bleu de cresyl tout comme l'endosporium (R. Kühner, 1934b).

L'accord entre électronique et photonique est loin d'être toujours aussi parfait. Par exemple, en électronique la médulla porique de *Coprinus sterquilinus* (Fr.) Fr. se présente comme un prolongement endosporique (M. Besson Antoine & R. Kühner, 1972b: Pl. 1 fig. 2). Le photonique, sur spores décolorées par KOH à l'autoclave, montre que ce n'est qu'illusion; l'endosporium tranche brutalement sur la médulla qui le surmonte par sa réfringence beaucoup plus forte; il peut d'ailleurs en être séparé mécaniquement, à la fois facilement et nettement. Chez diverses Naucoriacées porées le traitement par KOH à l'autoclave révèle également des différences entre médulla et endosporium (M. Besson Antoine & R. Kühner, 1972a); dans certaines espèces la médulla est alors beaucoup moins réfringente que l'endosporium, comme chez *Coprinus sterquilinus*; dans d'autres elle est entièrement lysée à des concentrations pour lesquelles l'endosporium semble intact.

Sur du matériel traité par KOH à l'autoclave où la médulla porique a subsisté, on reconnait chez certaines espèces un mince disque beaucoup plus réfringent qu'elle et qui en recouvre l'extrémité externe nous l'avons nommé *opercule* (M. Besson & R. Kühner, 1972a). R. Hugueney pense que l'opercule correspond à la couche différenciée que révèle l'électronique entre l'extrémité de la médulla et la tunica de certaines espèces, comme *Coprinus cineratus*, c'est à dire à l'ensemble de l'hypotunica et de l'intertunica de M. Besson & R. Kühner (1972b); l'opercule de ce Coprin doit sans doute être rattaché à la médulla puisque R. Hugueney a reconnu (inédit) que sur des spores immatures il se colore en rouge-poupre par le Giemsa, à peu près comme la médulla. L'opercule que le Giemsa met plus ou moins en évidence au-dessus du pore de *Lepiota procera* ne peut guère être qu'une différenciation du feuillet superficiel opaue du myxosporium. Il faudrait donc distinguer entre opercules profonds et opercules superficiels.

L'emploi du bleu de crésyl ou du Giemsa permet, dans certains cas, de préciser l'architecture de la mince couche séparant l'extrémité de la médulla de la surface de la spore. Nous avons obtenu des résultats particulièrement brillants avec les Lépiotes de la section *Annulosae* (R. Kühner, 1972), en observant les préparations colorées par ces teintures, soit dans l'ammoniaque, soit dans de l'eau acétifiée et légèrement iodée, ce dernier milieu d'observation faisant virer au noirâtre les colorations pourpres communiquées par le bleu de crésyl ou le Giemsa. Grâce à ces

techniques nous avons pu reconnaître qu'au delà de la médulla métachromatique, la paroi sporique de ces Lépiotes comprend deux minces feuillets: l'interne non colorable, le superficiel métachromatique comme la médulla. Nous avons été tentés de penser que la partie non colorable représente un très mince bouchon porique au sens de L. M. Meléndez-Howell, mais, si l'on en croit cet auteur, il n'y a pas de bouchon porique chez les Lépiotes de la section *Annulosae*. S'il en est bien ainsi les deux minces feuillets reconnus par nous en photonique au-dessus de la médulla de ces espèces correspondraient à la périspore et à l'ectospore de Meléndez-Howell ou ce qui revient au même au tectum et au sporothécium de Clémençon.

Aux différenciations dans l'épaisseur de la paroi sporique de la région sommitale de la spore correspondent souvent, dans la même région, des particularités dans la forme du contour de la spore, mais il est difficile de conclure de cette seule forme à la nature de la différenciation au sein de la paroi. Si une troncature dans la région apicale correspond toujours à l'existence d'un pore germinatif, elle n'existe pas dans une minorité d'espèces porées, où elle est au contraire remplacée par une saillie en forme de papille; il ne saurait en être autrement chez les espèces, telles les *Lacrymaria* ou *Coprinus verrucispermus*, dont la piléomédulla est très bombée du côté externe, car celle-ci refoule les minces feuillets qui peuvent se trouver au-dessus, le myxosporium en particulier.

## 2. Le cal

Tel qu'il a été redéfini par R. Singer, le cal correspond à une différenciation sommitale caractérisée par un amincissement de la paroi et qui n'est jamais accompagnée par une troncature du profil; souvent au contraire, le sommet de la spore est plus ou moins bombé ou étiré en papille dans la région du cal.

Il s'agit d'une différenciation sommitale très répandue chez les *Galerina*, où nous l'avons particulièrement étudiée. L'électronique nous a montré (M. Besson-Antoine & R. Kühner, 1972a: fig. 8) que l'amincissement porte avant tout sur le sclérosporium; l'endosporium, présent dans toutes les espèces à cal étudiées par nous, peut ne pas être aminci au sommet comme le montrent nos clichés d'électronique, mais, d'après des observations en photonique, il n'est pas exclu qu'il soit lui aussi aminci au sommet dans plusieurs espèces.

Remarquons que R. Heim a été le premier à proposer le mot cal pour désigner une différenciation de la paroi à l'apex de certaines spores et que la définition qu'il en a donnée s'écarte de celle ultérieurement proposée par Singer. Pour Heim le cal correspond à une réfringence différente dans la membrane "accompagnant probablement une hétérogénéité dans la nature de la substance constituante, peut être l'existence d'un bouchon apical". Notre cliché relatif à *G. cedretorum* R. Maire montre qu'au niveau du cal il y a un amincissement de la paroi, conformément à la définition de Singer, mais il montre aussi que la couche qui en est l'objet – et qui correspond à notre sclérosporium – présente, dans la région amincie, une hétérogénéité dans la nature de la substance constituante, comme le supposait Heim; cette hétérogénéité

se manifeste encore par une plus grande sensibilité de la partie amincie du sclérosporium aux traitements alcalins; chez la plupart des *Galerina* dont la spore présente un cal, un traitement par KOH à 120° élimine cette partie, de sorte que l'extrémité de la papille endosporique affleure à la surface. Dans de tels cas les définitions fort différentes données du cal par Heim puis par Singer se complètent utilement, chacun de ces auteurs ne mentionnant qu'une des différenciations possibles de la paroi dans la région du cal. Mais il est clair que, si l'on conserve le mot cal, ce ne peut être que pour une différenciation présentant les caractères indiqués par Singer; en effet, aujourd'hui qu'on sait que le pore germinatif n'est pas une cavité vide, on ne voit pas en quoi le cal, tel qu'il a été défini par Heim, diffère du pore germinatif.

Même entre le cal sensu Singer et le pore la limite n'est pas facile à tracer, même en utilisant l'électronique. On pourra peut être s'aider de la remarque suivante, due à M. Besson-Antoine (1972): alors qu'en électronique on a souvent l'impression que la médulla porique passe progressivement à l'endosporium, ce qui a conduit certains auteurs à considérer que la médulla est un prolongement endosporique, la limite entre l'endosporium et la couche située immédiatement en dehors semble toujours nette chez les espèces à cal, même au niveau de ce dernier. Nous pensons néanmoins que, comme l'ont écrit Smith & Singer à la suite de leurs observations, toutes faites en photonique, il y a tous les intermédiaires entre le pore germinatif et le cal.

### 3. La papille pleine

Chez quelques *Cortinarius*, *Hebeloma* et *Alnicola* dont la spore présente une papille apicale, celle-ci est occupée par un bouchon hémisphérique ou campanulé provenant d'un brusque épaississement du sclérosporium au sommet (voir par ex. M. Besson-Antoine & R. Kühner 1972a: fig. 9); si cet épaississement peut, dans une certaine mesure, être comparé à la médulla des champignons à pore papilleux, on ne saurait parler de pore germinatif pour ces espèces car la pigmentation des couches externes de la paroi, si elle s'atténue en passant à la papille, le fait de façon très progressive, alors que chez les chromosporées à pore germinatif, qu'il soit tronqué ou papilleux, la pigmentation diminue ou cesse de façon très brusque lorsqu'on arrive à la région du pore, qui se présente lorsqu'il est examiné par sa face externe, comme un disque clair par rapport au reste de la spore et brutalement délimité.

## IV—LA PAROI SPORIQUE CHEZ LES AGARICALES À SPORES ROSES OU ROUGEÂTRES

### 1. Généralités

A première vue les deux grandes familles d'Agaricales à spores roses: Volvariacées et Rhodophyllacées, semblent ne pas avoir grand chose en commun. Les Volvariacées s'écartent des Rhodophyllacées par le stipe séparable du chapeau, les lames libres, les spores à contour régulièrement arrondi et lisse et la trame inversée de

leurs lames; cette structure de la trame des lames les éloigne d'ailleurs de toutes les autres familles d'Agaricales.

Aussi avons nous été fort surpris de constater que la spore des Rhodophyllacées est parfaitement comparable à celle des Volvariacées. Non seulement la paroi n'y offre aucune différenciation apicale frappante (pore ou cal par exemple), ce que l'on sait depuis longtemps, mais encore et surtout l'architecture de cette paroi est, à des détails près, la même dans ces deux familles et suffisamment originale pour qu'il ne soit pas facile d'en homologuer les divers feuillets à ceux des autres Agaricales.

En photonique, cette originalité se manifeste sur matériel traité par une lessive de KOH à 120° (30 minutes) et coloré ensuite par le rouge Congo ammoniacal. Pour une concentration convenable de la lessive potassique (souvent 2 à 3 %) la paroi se montre constituée par deux enveloppes brutalement distinctes, dont l'interne est seule congophile (M. Besson-Antoine & R. Kühner, 1972c et d).

Alors que l'enveloppe interne résiste à des lessives potassiques bien plus concentrées (entre 5 et 10 % par exemple), l'enveloppe externe non congophile est entièrement lysée par celles-ci (R. Kühner, 1948). Parmi les lessives de KOH qui laissent subsister l'enveloppe externe non congophile, les plus concentrées semblent décoller cette dernière de l'enveloppe interne congophile, et ceci parfois très largement; nous pensons que, au moins lorsque le décollement est léger, il ne s'agit pas d'un véritable décollement, mais d'une transformation de la couche interne de l'enveloppe non congophile, qui abaisse l'indice de réfraction de cette couche; cet abaissement est selon toute vraisemblance lié au gonflement alcalin qui, pour des concentrations plus fortes, conduirait à la lyse; la couche superficielle de l'enveloppe externe serait plus résistante aux traitements alcalins. Quoi qu'il en soit la séparation des deux enveloppes de la spore est causée par le gonflement de l'enveloppe externe, qui augmente considérablement de surface et d'épaisseur sous l'action de la potasse. Même lorsqu'il est très accusé ce gonflement alcalin est réversible; il disparait très vite en présence de solutions diluées d'acide acétique; on voit alors l'enveloppe externe se rapprocher de l'interne, puis se coller étroitement à elle et enfin diminuer d'épaisseur de façon telle que la paroi sporique parait simple. L'enveloppe externe des Rhodosporées se comporte en somme, vis à vis de la potasse et de l'acide acétique, comme le myxosporium de *Coprinus narcoticus*, lequel, selon M. Besson-Antoine & R. Kühner (1972b) se ratatine dans l'eau acétique après avoir subi un gonflement considérable par la potasse à l'autoclave.

Nous pensons que l'enveloppe externe des Rhodosporées est un myxosporium, non seulement pour cette raison, mais aussi parce qu'elle est facilement lysée par la potasse, et naturellement à cause de sa situation. Nous pensons que seule l'enveloppe interne congophile correspond à l'eusporium.

Apparemment une spore de Rhodophyllacée ne diffère d'une spore de Volvariacée que par la présence d'ornements portés par l'enveloppe congophile; ce sont ces ornements profonds, sur lesquels se moule l'enveloppe externe, qui, par leur forme et leur disposition, déterminent l'aspect de la surface de la spore, seul connu des systématiciens classiques: polyédrique chez les *Rhodophyllus*, à côtes méridiennes chez les *Clitopilus*, verruqueux chez les *Rhodocybe*.

## 2. Rhodosporées à spores ornées

Il s'agit des espèces appartenant à la famille des Rhodophyllacées, famille pour laquelle nous possédons actuellement le plus de documents.

Les photographies, en électronique, d'ultracoupes de spores, dont les premières sont dues, pour les *Clitopilus*, à J. Perreau-Bertrand (Pl. 5 fig. D) et pour les *Rhodophyllus* à H. Clémençon (fig. 8 à 10), ont confirmé ce que nous avait appris le photonique; en outre elles nous ont montré que l'enveloppe externe est très opaque aux électrons et généralement épaisse, alors que l'enveloppe interne est transparente et réduite à un mince feuillet.

Si nous n'avions disposé que de ces premières photographies en électronique pour interpréter l'architecture de la paroi des Rhodophyllacées, nous aurions sans doute considéré, avec J. Perreau-Bertrand et H. Clémençon, que le feuillet interne est l'endospore ou corium, tout en nous étonnant de voir un tel feuillet porter des ornements. Nous avons montré depuis (M. Besson-Antoine & R. Kühner, 1972d), d'abord en photonique, puis en électronique, que le feuillet qui porte les ornements, s'il est le plus interne de la paroi chez nombre d'espèces, ne l'est pas toujours. Chez plusieurs *Rhodophyllus* on trouve, sous la zone aux ornements profonds, un ou deux feuillets, parfois fort épais, qui, en électronique, présentent la structure hétérogène (Pl. 2 fig. 1) de ce que, dans d'autres familles, J. Perreau-Bertrand et H. Clémençon appellent respectivement épispore ou coriotunica, ces deux termes étant synonymes. Le feuillet qui porte les ornements profonds ne peut donc être un corium; nous avons proposé de l'appeler *pseudocorium*.

Il est fréquent que la matière des ornements profonds présente, en électronique, un aspect plus ou moins différent du pseudocorium. H. Clémençon, qui l'a souligné pour la première fois, en a conclu que les ornements appartiennent à une couche différente de son corium (c'est à dire de notre pseudocorium), couche qu'il nomme *épicorium*. Nous avons montré (M. Besson-Antoine & R. Kühner, 1972c et d) que ces différences d'aspect n'apparaissent que secondairement, et qu'à l'origine les ornements ne se présentent que comme des épaississements du pseudocorium; leur développement (1972c: Pl. 2) est fort curieux puisqu'avant de saillir essentiellement vers l'extérieur, ils saillent sur les deux faces du pseudocorium, se présentant alors comme des lentilles biconvexes et que, tout à fait au début, ils saillent essentiellement du côté interne, en direction du centre de la spore. Les ornements profonds des Rhodophyllacées se présentent donc comme des épaississements localisés du pseudocorium; Mme Perreau-Bertrand n'a pas interprété les ornements profonds des *Clitopilus*, mais il est bon de rappeler qu'elle a prétendu que, dans les familles autres que les Rhodophyllacées, les ornements (au moins dans leur partie fondamentale) se présentent comme des épaississements d'un feuillet continu, qu'elle appelle exospore. A la suite de nos observations, il ne parait plus possible de considérer l'épaisse enveloppe superficielle opaque, moulée sur la face externe des ornements profonds, comme correspondant à l'épispore, ce que J. Perreau-Bertrand a prétendu après nous, ou à la tunica des Agaricales d'autres familles comme semble le croire Clémençon. A la suite de ses premières recherches, M. Besson (1969b) a suggéré

qu'il pourrait s'agir d'une ectospore, simplement d'une épaisseur plutôt exceptionnelle. Il faut reconnaître que plusieurs photographies de la note citée plaidaient fortement en faveur d'une telle manière de voir, en particulier la fig. 1 Pl. 1, relative à *Rhodocybe truncata* (Schaeff. ex Fr.) Sing., où l'on voit les ornements profonds se former au sein d'une couche myxosporiale, comme dans les autres familles d'Agaricales.

Tout récemment M. Besson-Antoine & R. Kühner (1972d) ont cependant été amenés à une conception un peu différente, le premier de ces auteurs ayant réussi à mettre en évidence, chez quelques espèces, à la surface externe de l'épaisse couche sombre qui tapisse les ornements profonds, une fine pellicule particulièrement opaque, qui ne peut être que la véritable ectospore ou, si l'on préfère, le sporothécium (Pl. 2 fig. 1 et Pl. 3 fig. 4).

Les Rhodophyllacées différeraient donc des autres Agaricales à spores ornées par le fait que, chez elles, il y aurait une différenciation myxosporiale supplémentaire; au lieu d'être seulement à l'origine du sporothécium et de la couche au sein de laquelle se forment les ornements, le myxosporium différencierait une couche supplémentaire située entre la couche aux ornements et le sporothécium; cette couche très opaque vient doubler le sporothécium qu'elle renforce considérablement lorsqu'elle est très épaisse, comme c'est le cas habituel.

Par son opacité aux électrons et son épaisseur uniforme, elle fait penser à l'*épitunica* signalée plus haut chez les *Panaeolus* à spores lisses, mais au lieu de se différencier à la base du myxosporium comme dans ce dernier genre, elle se différencie dans sa partie supérieure, contre le sporothécium.

Apparemment cet ensemble myxosporial externe opaque devient de bonne heure rigide, car nous n'avons jamais trouvé, chez les *Rhodophyllus*, plusieurs spores englobées dans une enveloppe commune ou même simplement collées ensemble comme celà se produit (par accident) dans maintes espèces d'autres familles.

C'est sans doute la protection assurée par la partie externe du myxosporium des Rhodophyllacées qui a permis que, chez nombre d'entre elles, l'eusporium se réduise, au point de devenir parfois méconnaissable.

Il est sant doute raisonnable de ne considérer certaines des conclusions qui précèdent que comme des hypothèses de travail. Pour arriver à plus de certitude, il sera nécessaire, d'une part de suivre le développement de la paroi de leur spore depuis le moment ou celle-ci s'ébauche sur le stérigmate, et d'autre part d'étudier en parallèle la paroi sporique dans le groupe d'Agaricales apparemment le plus proche des Rhodophyllacées, la tribu des Lépistées, qui renferme, à côté d'espèces à sporée blanche, des espèces à sporée rose comme celle des Rhodophyllacées. L'une des photographies consacrées à *Lepista panaeola* par M. Besson (1970b: Pl. 1 fig. 1) montre clairement une différenciation de la matière des verrues de cette espèce, aboutissant à la formation d'un ornement profond coiffé par une couche épaisse, beaucoup plus opaque, qui correspond peut être à la couche opaque des Rhodophyllacées. Une comparaison avec la photographie de M. Besson relative à la Rhodophyllacée *Rhodocybe fallax* (Quél.) Sing. (1969b: Pl. 1 fig. 3) souligne bien l'intérêt d'une telle démarche.

### 3. Rhodosporées à spores lisses

*a. Volvariacées.*

A notre connaissance n'existe aucun document d'électronique concernant cette famille et ce sont seulement des recherches inédites en photonique sur les spores de *Pluteus cinereofuscus* J. E. Lange, *P. poliocnemis* Kühner, *Volvariella bombycina* (Schaeff. ex Fr.) Sing. et *V. speciosa* (Fr. ex Fr.) Sing., qui nous conduisent à l'idée que la seule différence importante entre la paroi des Volvariacées et celle des Rhodophyllacées est l'absence d'ornements sur l'enveloppe interne congophile.

Comme chez la plupart des Rhodophyllacées celle-ci parait réduite à un mince feuillet; cependant chez *P. cinereofuscus* nous avons trouvé de rares spores dont l'enveloppe congophile était un peu plus colorable que d'habitude et clairement constituée de trois minces lamelles très rapprochées, la moyenne moins réfringente que les deux qui l'enserrent, comme nous l'avions remarqué chez quelques Rhodophylles.

L'étude de matériel de *Volvariella speciosa*, traité par KOH à l'autoclave puis observé dans le rouge Congo ammoniacal, nous a fourni un argument que nous estimons décisif en faveur de l'idée selon laquelle l'enveloppe non congophile des rhodosporées est leur myxosporium: nous avons trouvé, incluses dans une épaisse masse de gelée commune non colorée, une fois deux, une fois quatre enveloppes congophiles, très écartées l'une de l'autre; l'acide acétique dilué, en contractant le mucilage de façon considérable, le rendait presque indiscernable et amenait au contact les diverses enveloppes congophiles.

Nous avons dit plus haut qu'il est vraisemblable que le myxosporium des Agaricales à spores roses est constitué de deux couches dont l'interne, plus sensible que l'externe aux lessives alcalines, y perd vite sa réfringence, faisant ressortir la couche externe qui apparait alors comme décollée de l'enveloppe congophile. Chez *Volvariella bombycina*, cette couche externe "décollée" montre elle même un feuillet interne plus réfringent que celui qui l'enveloppe. D'importantes différenciations peuvent donc survenir dans l'épaisseur du myxosporium des Agaricales rhodosporées.

*b. Macrocystidia cucumis (Pers. ex Fr.) Heim.*

R. Singer écrit que *Macrocystidia* est un genre assez isolé parmi tous les groupes d'Agarics. Il le range dans sa tribu des Marasmiées alors que Fries, suivi par nombre d'auteurs, plaçait *Agaricus cucumis* dans sa coupure *Naucoria*. C'est dans sa coupure *Nolanea*, qui fait aujourd'hui partie des Rhodophyllacées, qu'il rangeait par contre *Agaricus pisciodorus* Cesati qu'il croyait n'avoir jamais rencontré et que Quélet a synonymisé à *cucumis*. Nous pensons apporter aujourd'hui une solution définitive au problème de la position taxinomique du genre *Macrocystidia*. Observées dans le Congo ammoniacal après action de KOH à 2 ou 3 %, à l'autoclave, les spores de *M. cucumis* se présentent, en photonique, exactement comme des spores de *Pluteus*. Sur un cliché inédit d'électronique de M. Besson-Antoine (1972: pl. 13 fig. 5) la paroi sporique se montre formée de deux couches; l'interne très transparente, l'externe remarquablement opaque et épaisse (0,16$\mu$). Il est pour nous absolument évident que *Macrocystidia cucumis* est une Rhodophyllacée à pseudocorium lisse.

## V—L'APICULE ET LES RAPPORTS ENTRE LA PAROI DE LA SPORE ET CELLE DE LA BASIDE

### A—Généralités

L'apicule est la première partie de la spore à s'ébaucher; à son origine est l'apophyse de G. Malençon, ampoule plus ou moins globuleuse qui se forme à l'extrémité du stérigmate; le reste de la spore résulte du développement d'une gibbosité qui naît du côté de l'apophyse opposé à l'axe de la baside. Parce que l'apicule se développe peu par rapport à cette gibbosité, c'est paradoxalement lui qui, à maturité, se présente comme un appendice de la spore. La gibbosité apiculaire de la spore mûre comprend une paroi latérale qui n'est que la paroi de transition entre celle du reste de la spore et celle du stérigmate, et un dispositif obturateur, évidemment destiné à protéger le cytoplasme du milieu extérieur lorsque la spore se sera détachée du stérigmate.

Dans nombre d'espèces ce dispositif obturateur présente un bouchon très développé qui comble la gibbosité apiculaire sur toute sa longueur, comme le montre par exemple un cliché de M. Besson-Antoine (1972: Pl. 10 fig. 3 ou, ici même, Pl. 21 fig. 2) relatif à *Hebeloma radicosum*. Il est toujours facile de reconnaître l'existence d'un bouchon et de le distinguer de la paroi apiculaire, ceci même en microscopie photonique, au moins sur des spores ayant subi un traitement alcalin convenable. Bien des points de la structure fine de la région apiculaire ne peuvent cependant être abordés avec fruit qu'en électronique; il est étonnant que la structure de cette région ait si peu attiré l'attention des chercheurs; sans les résultats obtenus en électronique par M. Besson-Antoine, il nous aurait été impossible de rédiger les lignes qui suivent.

### B—Les feuillets qui constituent la paroi apiculaire

Tous les feuillets de la paroi du corps de la spore peuvent contribuer à former la paroi apiculaire; en règle générale lorsqu'un feuillet est épais sur le corps de la spore, il s'amincit de la base vers le sommet de l'apicule; l'amincissement du sclérosporium est souvent particulièrement frappant, comme on peut le voir par exemple, chez une Russule ou un *Melanoleuca* (M. Besson, 1970a: Pl. 1 fig. 1 et Pl. 2 fig. 1); lorsque le myxosporium est épais, il s'amincit de même dans la paroi apiculaire (Pl. 1 fig. 1), parfois même déjà dans la région périapiculaire, comme on peut le voir par exemple chez *Laccaria amethystea* (Bull. ex Mérat) Murrill (M. Besson, 1971: Pl. 2 fig. 1), ce qui explique que les ornements formés au sein du myxosporium soient plus bas, plus petits dans la région périapiculaire des *Laccaria* (M. Locquin, 1945) et, d'une façon presque générale, qu'il n'y ait pas d'ornements sur l'apicule.

Pour interpréter correctement certains feuillets de la paroi apiculaire, il peut être nécessaire de les suivre dans la paroi du corps principal de la spore. Par exemple dans l'épaisseur de la paroi apiculaire de *Russula maculata* Quél. (M. Besson, 1970a: Pl. 1

fig. 1) et de *Rhodotus palmatus* (M. Besson-Antoine, 1972: Pl. 13 fig. 2 ou, ici même, Pl. 22 fig. 4), on remarque facilement un mince feuillet qui tranche sur ceux qui l'enserrent par sa grande transparence aux électrons; or si l'on suit ce feuillet dans le corps de la spore, on s'aperçoit qu'il passe sous les ornements dans la première espèce alors qu'il se moule étroitement sur leur face externe dans la seconde; autrement dit c'est un médiostratum chez la Russule, un endosporothécium chez le *Rhodotus*. On comprend que s'il s'était agi de spores entièrement dépourvues d'ornements l'interprétation de ce feuillet transparent ne se serait pas imposée de façon aussi évidente. Cette difficulté a déjà été evoquée plus haut à propos des champignons à spores lisses autres que les Volvariacées.

Lorsqu'il y a un endosporium il se comporte souvent, au niveau de l'apicule, comme le sclérosporium, c'est à dire qu'il contribue, en s'amincissant beaucoup, à former la paroi de la gibbosité qu'est l'apicule. Nous connaissons cependant des cas où le feuillet de l'eusporium qui se trouve au contact du protoplasme tapisse la face interne du bouchon apiculaire; lorsqu'un feuillet se comporte ainsi nous disons qu'il est d'*origine secondaire*, par opposition aux feuillets qui forment la paroi de la gibbosité apiculaire. *Laccaria tortilis* (M. Besson, 1971: Pl. 1 fig. 1) fournit un exemple de feuillet interne secondaire particulièrement spectaculaire, même en photonique car, sur le frais, ce feuillet secondaire est seul à se colorer en pourpre par le Giemsa.

### C—L'OBTURATION DE L'APPENDICE APICULAIRE

Dans des Agaricales de genres variés le sclérosporium peut être suivi tout autour de l'extrémité de l'appendice apiculaire. A l'extrémité même il peut être beaucoup plus mince qu'ailleurs comme on le voit sur des clichés de M. Besson relatifs à un *Melanoleuca* (1970a: Pl. 3 fig. 1) ou à *Laccaria tortilis* (1971: Pl. 1 fig. 1); il peut au contraire y être plus épais comme l'a montré M. Besson-Antoine (1972), soit un peu plus épais, chez *Amanita vaginata* par exemple (Pl. 13 fig. 1 ou, ici même, Pl. 22 fig. 3), soit nettement plus, comme chez *Rhodotus palmatus* (Pl. 13, fig. 2 ou, ici même, Pl. 22 fig. 4).

On peut appeler *obturateur primaire*, ce prolongement de la paroi sclérosporiale de l'appendice apiculaire, autour de l'extrémité de celui-ci. Qu'il soit mince ou épais, cet obturateur est généralement concave du côté tourné vers le corps de la spore. Il semble que chez *Amanita vaginata* l'obturation de l'appendice apiculaire n'aille pas plus loin, que cet appendice reste donc creux (rempli de protoplasma) sur la plus grande partie de sa longueur.

Mais dans une foule d'Agaricales, après édification de l'obturateur primaire, la cavité de la gibbosité apiculaire se remplit par un matériel formant *bouchon*. Chez les *Rhodophyllus* on distingue facilement, en photonique, sur des spores ayant subi un traitement modéré par KOH à l'autoclave, le petit obturateur très réfringent du gros bouchon, qui l'est beaucoup moins.

En électronique la matière du bouchon apiculaire peut offrir le même aspect d'un bout à l'autre, mais il n'est pas rare qu'elle présente au contraire des différences

d'aspect qui permettent d'y distinguer plus ou moins nettement deux ou trois tronçons; c'est le cas, par exemple, chez *Hebeloma radicosum* (ici même Pl. 21 fig. 2).

Très souvent, sur une partie au moins de sa longueur, le bouchon est formé d'un matériel transparent, moucheté de flocons opaques, sa structure rappelant plus ou moins celle du bouchon qui obture le pore des Lépiotes de la section *Procerae*. Les photographies relatives à *Russula maculata* (M. Besson, 1970a: Pl. 1 fig. 1) et à *Laccaria tortilis* (M. Besson, 1971: Pl. 1 fig. 1) illustrent cette structure. Dans les images citées, on voit le matériel opaque prendre de plus en plus d'importance à l'approche du corps de la spore.

Mais il arrive aussi que la dernière partie du bouchon qui se forme ait une structure feuilletée, à feuillets concaves en direction du centre de la spore. Des figures relatives à *Melanoleuca grammopodia* (Bull. ex Fr.) Pat. (M. Besson, 1970a, Pl. 3 fig. 1) et à *Laccaria amethystea* (M. Besson, 1971: Pl. 2 fig. 1) montrent un bouchon à deux tronçons, dont le plus proche de la spore présente seul une structure feuilletée. Dans la seconde de ces espèces, les feuillets de la partie interne du bouchon se raccordent latéralement à ceux qui constituent la partie profonde de la paroi du corps de la spore.

Déjà en microscopie photonique, il est possible de distinguer plusieurs tronçons dans le bouchon apiculaire de certaines espèces, grâce notamment à des différences de réfringence ou d'affinité vis-à-vis du bleu coton.

### D—Les rapports entre les divers feuillets de la paroi sporique et ceux du corps de la baside

Il s'agit d'un problème délicat, qui ne peut guère être résolu qu'en électronique où il offre les difficultés techniques que l'on devine, ce qui explique le nombre très réduit d'espèces où il a été abordé à ce jour. Du point de vue théorique, c'est pourtant un problème très important aux yeux de plusieurs auteurs qui, admettant que l'ensemble des Basidiomycètes est dérivé d'ancêtres à asques, imaginent que la basidiospore est, comme l'ascospore, une spore interne; si la basidiospore se présente à première vue comme une spore externe, ce serait d'une part qu'elle ne se forme pas à l'intérieur du corps de la baside, mais dans l'extrémité d'un diverticule de celle-ci, diverticule dont la région inférieure est le stérigmate, et d'autre part que sa paroi s'édifie intimement soudée à la paroi du diverticule de la baside.

Admettant que la paroi de la baside comporte deux feuillets, Clémençon est conduit à penser que le sporothécium, qui, lui aussi peut comporter deux feuillets, représente le prolongement de la paroi de la baside autour de la spore. Une telle interprétation du sporothécium, certes séduisante par sa simplicité, rencontre cependant des difficultés d'ordres variés.

Tout d'abord, on connait des cas où un seul feuillet, le feuillet opaque, a pu être mis en évidence dans le sporothécium, et d'autres où même le feuillet opaque du sporothécium n'a pu être reconnu en toute certitude; on ne saurait évidemment l'affirmer sans avoir suivi le développement de la spore, s'il est vrai, comme le

prétend Clémençon, que dans plusieurs espèces le sporothécium peut s'évanouir à maturité.

Mais on peut aussi se demander si le feuillet opaque du sporothécium, l'ectospore de Heim, est un feuillet fondamental de la paroi sporique; il est possible qu'il ne représente qu'une différenciation survenue plus ou moins tardivement à la surface du myxosporium. Bien que celui-ci soit fort épais et gris clair sur la spore immature (excavation porique accusée mais encore occupée par le protoplasma) que M. Besson et R. Kühner figurent de *Panaeolus campanulatus* (1972a: Pl. 1 fig. 1), on ne voit aucune trace d'ectosporium à sa surface. Les images d'électronique que R. Hugueney a données du développement de la spore de *Coprinus cineratus*, espèce dont l'ectosporium opaque est anormalement épais à maturité, ne sont pas défavorables à cette manière de voir; en effet, sur les spores très jeunes la présence d'un ectosporium ne s'impose pas comme sur les spores mûres.

Est-il certain d'autre part, comme l'admet H. Clémençon, que les feuillets du sporothécium soient les seuls que la spore ait en commun avec la baside? Pour J. Perreau-Bertrand, se poursuivent de la spore à la baside: l'ectospore, c'est à dire la partie opaque du sporothécium, et en outre la couche sous-jacente transparente qu'elle appelle périspore. En somme pour ces deux auteurs ne se poursuivent de la spore à la baside que des feuillets appartenant à ce que nous appelons myxosporium.

Pourtant il ne parait guère douteux que, dans certaines espèces, la partie externe de l'eusporium, au moins la tunica, soit commune à la spore et au stérigmate; R. Hugueney l'a démontré récemment pour *Coprinus cineratus*, et Burge pensait déjà que, chez les Russulacées, son feuillet B de la paroi sporique, qui est la tunica à notre sens, peut être suivi de la spore à la baside.

### E—Le punctum lacrymans

On sait que A. H. R. Buller a montré que la projection de la basidiospore est précédée par l'émission d'une goutte liquide par la face de l'apicule qui regarde l'axe de la baside.

Buller a reconnu que cette émission se fait par un point étroit, mais que plus tard la goutte peut s'appliquer sur la partie inférieure du corps de la spore, naturellement sur la face où elle a été émise à l'origine; il est possible qu'elle influe alors sur la différenciation des couches superficielles de la paroi dans cette région, notamment qu'elle soit à l'origine de la plage lisse que l'on y observe dans maintes espèces à spores ornées.

R. Hugueney a montré récemment, qu'au niveau du point qui est le siège de l'excrétion d'eau, point qu'il appelle "*punctum lacrymans*", la structure fine de la paroi apiculaire telle que la révèle l'électronique peut être modifiée par rapport à ce qu'elle est ailleurs. Chez *Coprinus cineratus* par exemple, il a noté en ce point une interruption de la différenciation de la tunica.

Des différenciations de la paroi apiculaire dans la région du punctum lacrymans peuvent également se rencontrer chez des Champignons dont la paroi sporique est

mince et incolore. En réalisant une coloration nucléaire par la méthode de Giemsa sur du matériel frais, fixé au sublime acétiqué, de *Mycena subalpina* Höhn., nous avons remarqué l'existence d'un brusque épaississement hémisphérique de la paroi de l'apicule, du côté dorsal de la spore, c'est à dire en direction de l'axe de la baside; cet épaississement, frappant par la coloration pourpre intense à pourpre-noir qu'il prend, existe, non seulement sur les spores chues, mais également sur les spores en place sur le stérigmate, et déjà sur de jeunes spores dont les dimensions et la forme sont encore loin de ce qu'elles seront à maturité.

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## LÈGENDE DES PLANCHES 20 À 23

ABREVIATIONS: Ect, Ectosporium. — Ect S, Ectosporothecium. — End, Endosporium. — End S, Endosporothecium. — ET, Epitunica. — Md, Médulla. — Ms, Médiostratum. — Mx, Myxosporium. — PC, Pseudocorium. — Scl, Sclérosporium. — SM, SMx, Substance myxosporiale résiduelle. — T, Tunica.

### PLANCHE 20

1. *Lepiota procera*, sporée. — 2. *Amanita vaginata*, sporée. — 3. *Coprinus verrucispermus*. — 4. *Lepista panaeolus*, spore jeune. — 5. *Aspropaxillus giganteus*, sporée. — 6. *Gloeocystidiellum porosum*. Clichés M. Besson-Antoine (Thèse).

### PLANCHE 21

1. *Calocybe constricta*. — 2. *Hebeloma radicosum*, exsiccatum $NH_4OH$. — 3. *Fayodia bisphaerigera*. — 4. *Tubulicium clematidis*. Clichés M. Besson-Antoine (Thèse).

### PLANCHE 22

1. *Scytinostroma hemidichophyticum*. — 2. *Gloeocystidiellum furfuraceum*. — 3. *Amanita vaginata*, sporée, apicule. — 4. *Rhodotus palmatus*, apicule. Clichés M. Besson-Antoine (Thèse).

### PLANCHE 23

1. *Lepiota brebissonii*, HCl puis $NH_4OH$. — 2. *Lepiota procera*, sporée. — 3. *Macrocystidia cucumis*. Cliché's M. Besson-Antoine (Thèse).

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# ISOLATING MECHANISMS IN FUNGI—PREZYGOTIC, POSTZYGOTIC, AND AZYGOTIC[1]

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(With two Text-figures)

What then are the biological processes that influence fungal speciation? Three aspects of fungal biology discussed herein deserved to be reemphasized. First, the great majority of fungi are haploid organisms. Secondly, fungi have expended a considerable amount of genetic energy to control the formation and maintenance of specific heterokaryons. Thirdly, the fungi taken as a group are paradoxical; against a background of extravagant and varied sexual cycles, fungi have a tendency to restrict gene flow and recombination.

The prevalence of haploidy, the strict control of heterokaryosis, and an irregular but definite trend toward apomixis are attributes of fungal biology. These phenomena undoubtedly influence the operational details of fungal evolution and must be accommodated by any model which intends to explain the origin of fungal species.

Virtually nothing is known about rates of evolution in fungal populations. However, at least three patterns are now evident among fungi with regard to their potential for change in gene frequency through time. The first pattern is that exhibited by imperfect fungi. Evolution in these fungi would be dependent largely upon mutation and selection with, at best, some parasexual activity but generally impaired gene flow. The second pattern is typified by *Schizophyllum commune*. This pattern includes sexuality; gene flow is continuous and controlled through homogenic incompatibility. The third pattern is recognized in *Podospora anserina* as well as in several basidiomycetes, *Sistotrema brinkmannii*, *Mycocalia denudata*, and *Fomes pinicola*. These species combine opposite effects for recombination, and gene flow within the species is discontinuous. Evolution in species of the third pattern should occur in quantum jumps rather than as a continuum. Sewall Wright (1931, 1932) in considering rates of evolution among populations has suggested that most rapid evolution might progress through subpopulations partially isolated which only occasionally or indirectly exchange genetic material. We simply do not now have sufficient data from fungal populations to integrate the fungi into such evolutionary theory.

[1] Commentary and summary presented at the symposium on "Speciation Phenomena in Fungi" during the First International Mycological Congress, September 8, 1971 in Exeter, England.

Nature abhors categories. Of all categories, the one most difficult to reconcile with nature is the biological species. The fungal species is no exception, and in certain respects the fungi pose special problems for species delimitation. These problems are the subject of this symposium.

The most objective and widely accepted definition of the species is based on genetic homology. Simply defined, the species is an integral system for genetic recombination, and members of a given species are expected to share in a common gene pool.

It is apparent from what has been said here today that not all species of fungi conform with this definition. Gene flow within a fungal species may be discontinuous or even negligible. Moreover, related species of fungi may hybridize and thereby lose their specific identity. Sterility barriers *within* species and hybridization *between* species undermine the concept of the species as a well-integrated, reproductively isolated system for gene flow.

Nonconformity with the common-gene-pool concept of the species has long been recognized in nonfungal life-forms, principally in the higher plants (Stebbins, 1950), and is considered to be indicative evidence that speciation is the result of divergent and convergent evolution of existing populations through change in gene frequency. Clearly in fungi, as in other organisms, the population, not the species, is the unit of evolution. Populations that constitute a species embody change, and that change is brought about principally through three phenomena: mutation, selection, and recombination.

Mutation induction and selective pressures are largely extrinsic phenomena—influences of the environment. The characteristic intrinsic feature of a species is its potential for recombination of genetic material. In this regard, fungi display considerable diversity ranging from sexual dimorphism to apomixis. Recombination in most fungi is under strict genetic control through systems of incompatibility. Systems of incompatibility determine the breeding potential of a species in the absence of sexual dimorphism. Two functional types of incompatibility are now recognized in fungi, and these should not be confused, since one promotes outbreeding and the other promotes inbreeding. The first type is common-factor or homogenic incompatibility, commonly referred to as heterothallism (Blakeslee, 1904a, 1904b; Whitehouse, 1949a, 1949b). Homogenic incompatibility favors recombination through association of dissimilar alleles. The mating-type factors of bipolar and tetrapolar fungi are the elements of homogenic incompatibility. Homogenic incompatibility is analogous to sexuality only insofar as it confers self-sterility, cross-fertility upon individuals in a population. *Schizophyllum commune* demonstrates homogenic incompatibility at its best (Raper, 1966). This fungus with a two-factor, multiple-allelic system of incompatibility enjoys considerable potential for outbreeding. *Schizophyllum* fits well the concept of the species as an integral system for gene flow, since allopatric isolates of *S. commune* are panmictic, and incompatibility in that fungus is predictable on the basis of common mating-type factors. *Schizophyllum commune*, the most extensively studied of fungi, may not be typical of fungi with regard to their potential for recombination.

Some fungi are inbreeders and are not preoccupied with recombination. Ecological barriers and/or genetic factors operate in these fungi as isolating mechanisms to delimit gene flow. Although fungal populations have not been studied extensively in this regard, there is already sufficient evidence to indicate that isolating mechanisms act not only between species of fungi but *within* species of fungi as well.

This brings us to a second functional type of incompatibility now evident in fungi (Biggs, 1937; Burnett & Boulter, 1963; Esser, 1965, 1971; Grindle, 1963; Lemke, 1969; Mounce & Macrae, 1938). This type of incompatibility is heterogenic (Esser, 1965). Heterogenic incompatibility, in contrast with homogenic incompatibility restricts recombination when alleles differ. It therefore promotes inbreeding and homozygosity. Many of the sterility barriers recognized in species of fungi apparently have a genetic basis in heterogenic incompatibility. Heterogenic incompatibility may be superimposed on homogenic incompatibility as it is in *Podospora anserina* (Bernet, 1963; Bernet & *al.*, 1960; Rizet & Esser, 1953). As Bernet has pointed out, allelic differences at several loci are involved in producing partial or complete intersterility among isolates of *P. anserina*. Heterogenic incompatibility operates at different stages of the life cycle. It may influence heterokaryon formation or any of several sexual events leading to the formation of a zygote. Heterogenic incompatibility may function in the absence of homogenic incompatibility, as it does in certain homothallic and imperfect species of *Aspergillus* (Grindle, 1963; Jinks & *al.*, 1963; Caten, 1971).

Reduced potential for gene flow in fungi can be influenced by genetic factors other than those underlying heterogenic incompatibility. Homothallism in its various forms restricts recombination. Secondary or heterokaryotic homothallism promotes inbreeding in heterothallic fungi. Primary or homokaryotic homothallism is *de facto* loss of sexual competence, since no recombination is effected through meiosis from a homozygote. The formal absence of sexuality in the imperfect fungi represents considerable, if not complete loss of potential for recombination. Parasexuality in natural populations of these fungi doubtfully compensates for this loss (Caten, 1971).

Cytogenetic mechanisms, principally inversions and translocations, are known to control genetic recombination in higher plants and animals (for review see Stebbins, 1950; Ehrlich & Holm, 1965). Fungal populations are poorly understood in this regard. Since chromosomal abberations operate as underlying mechanisms for postzygotic isolation in other organisms, such mechanisms conceivably could also fractionate natural populations of fungal species.[2]

Prezygotic isolation, however, appears to be more characteristic of fungi and is

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[1] Recently, Perkins (1972) has shown that a translocation involving the mating-type locus of *Neurospora crassa* can lead to inviable progeny or to progeny inhibited for growth. The latter progeny are heterozygous for mating-type and contain duplications of the translocated region. The former progeny represent corresponding lethal deficiencies of the translocated region.

directed frequently toward the formation and maintenance of heterokaryons. Regulation of heterokaryosis provides fungi with a unique opportunity to experiment with genetic isolation, much as behavioral patterns in animals enforce species recognition and prevent gene wastage (Mayr, 1970). Heterogenic controls of heterokaryosis and of sexual events subsequent to heterokaryosis clearly operate not only *between* species but also *within* certain species of fungi. In *Podospora anserina* such controls are polygenic. It is reasonable to assume that incompatibility *between* species of fungi is also heterogenic and determined through numerous genetic loci. Fungi, relative to higher plants, have a limited potential for interspecific hybridization. As a rule, restrictions to heterokaryon formation between fungal species are stringent. Confirmed examples of interspecific hybridization in the fungi, although indeed rare, are available for all major taxonomic groups of the true fungi. Undoubted instances of such interactions have been reported in phycomycetes, principally *Allomyces* (Emerson & Wilson, 1954); in ascomycetes, both in yeasts (Winge & Roberts, 1949) and filamentous genera, *Neurospora* (Dodge, 1927; Howe & Haysman, 1966) and *Cochliobolus* (Nelson, 1963); and finally in basidiomycetes, notably in smuts (Holton, 1931; Holton & Fischer, 1941; Holton & Kendric, 1956) and recently in *Sistotrema* of the homobasidiomycetes (Lemke, 1966, 1969).

Interspecific hybridization, when it does occur in fungi, does not occur with impunity. Hybrid progeny show reduced viability, an indication that postzygotic isolation may operate as well in fungi to maintain separate species.

The resupinate basidiomycete *Sistotrema brinkmannii* embodies several of the speciation phenomena discussed in this symposium. Biggs (1937) recognized six intersterile groups among fourteen isolates of this fungus. Two groups were bipolar, three groups were tetrapolar, and the remaining group was homothallic. All six groups were sympatric and morphologically similar on the basis of hymenial structures. Biggs in 1937 suggested that *S. brinkmannii* represented a minimum of three cryptic species, a homothallic species, a bipolar species, and a tetrapolar species; and that sterility barriers were present in the two heterothallic species. Between 1963–1966 I reinvestigated this system and essentially confirmed Biggs' earlier observations (Lemke, 1966, 1969). Sterility barriers for heterokaryon formation exist in all three component species, the homothallic as well as both heterothallic species. The homothallic species exhibits primary or homokaryotic homothallism, and homokaryons are phenotypically dikaryotic with clamp connections. Dikaryosis in heterothallic species is heterokaryotic and controlled through multiple-allelic incompatibility.

Homothallic strains were paired with heterothallic strains, and genetic evidence for heterokaryosis (allothallism) was obtained in one instance (Fig. 1). This nutritionally forced heterokaryon between a homothallic (I) strain and bipolar (II) strain proved to be dikaryotic in phenotype and was brought to sporulation after eleven weeks' incubation. From the specific cross a sample of 109 germinating basidiospores was isolated. From this sample only eight mycelia developed, and an analysis of these sparse progeny revealed a number of interesting points: (a) seven of the eight progeny were recombinant, (b) only one of eight progeny was homo-

**CROSS**

I *inos* X II A1 *meth*

**PROGENY**

4 II A1 *inos meth*
II A3 *inos meth*
II A1 *meth* (parental)
II A1 *inos*
I *meth*

[a] I = homothallic homokaryon; II = bipolar homokaryon; *inos* = *inositol*-less; *meth* = methionine-less (for details see Lemke, 1969).

Fig. 1. Hybridization in *Sistotrema brinkmannii*[a]

thallic (phenotypically dikaryotic) and this strain was recombinant for both nutritional markers, it sporulated and appeared normal in all respects, (c) all seven bipolar (nondikaryotic) progeny were compatible with a nonparental bipolar strain of *A*2 mating-type, (d) only six of these bipolar progeny were incompatible with the parental bipolar strain, *A*1, (e) the aberrant strain was compatible with *both the parental*, *A*1, *and nonparental*, *A*2, *strains*. This atypical strain, designated *A*3, apparently obtained a new mating-type specificity through recombination with its homothallic parent. This result is subject to further testing but provides evidence for latent genetic structure for incompatibility in the homothallic strain.

In higher basidiomycetes the homothallic and heterothallic conditions may not be phylogenetically as distinct as they outwardly appear to be. Raper and coworkers (1965) and Parag (1962) have demonstrated that the *A* and *B* incompatibility factors in the tetrapolar *Schizophyllum commune* are subject to mutational impairment. The homokaryon of *Schizophyllum* carrying mutations for both factors, *A mut B mut*, is phenotypically dikaryotic and fertile (Koltin, 1970). This doubly mutant homokaryon provides experimental evidence for derivation of a homothallic condition from a heterothallic one. The idea that homothallism evolved from heterothallism in higher basidiomycetes through specific mutations is at least mechanistically feasible.

The homothallic (homodikaryotic) species of *Sistotrema brinkmannii* has been investigated further (Lemke, 1966). Mutations that lead to self-sterility in homokaryons were obtained readily and these often disrupted dikaryosis. Four distinct phenotypes were observed among self-sterile homokaryons. Hyphae were either (a) simple-septate, (b) irregularly clamped with scattered pseudoclamp-connections, (c) regularly clamped and dikaryotic or (d) dikaryotic with aborted or immature basidia. Forty of the self-sterile mutations were analyzed through complementation

analysis. In this analysis for cross-fertility, only one of the forty mutations proved to be dominant, and all crosses involving it exhibited heterokaryon incompatibility. Otherwise, the mutations to self-sterility were recessive and crosses resulted in normal dikaryosis and sporulation in practically all cases. Six of the self-sterility mutations were genetically mapped and are distributed on three linkage groups.

These results with a homothallic strain of *Sistotrema* are comparable to those from studies conducted with homothallic ascomycetes by other investigators (El Ani & Olive, 1962; Olive 1958; Wheeler, 1954). Studies with both groups of homothallic fungi indicate that sexual progression in a homothallic homokaryon comprises a large number of distinct stages subject to mutational impairment. In *Sistotrema* the loci for forty such mutations are scattered and their number, although uncertain, is a minimum of six and a maximum of thirty-six, probably closer to the latter number. It should be emphasized that none of the mutations to self-sterility in *Sistotrema* formed a pattern of heterothallism comparable to bipolarity or tetrapolarity of higher basidiomycetes. These mutations rather constitute a *separate* order of phenomena leading to self-sterility-cross-fertility. They are unrelated to multiple-allelic heterothallism and most likely represent mutations that modify any of the many structural genes that encode for dikaryosis and sporulation in a basidiomycete.

The relatively simple biallelic form of heterothallism present in the ascomycetes may have been derived from homothallic ancestry through complementary mutations to self-sterility. This hypothesis has been proposed independently by Olive (1958) and Wheeler (1954) and is supported principally by studies with *Sordaria fimicola* (El Ani & Olive, 1962). In that homothallic fungus, two very closely linked mutations to selfsterility have been obtained which exhibit complementation for crossfertility. Two complementary, nonrecombinable mutations for self-sterility would, in essence, constitute the biallelism characteristic of bipolarity in ascomycetes. The suggestion that heterothallism in ascomycetes evolved repeatedly from homothallic forms through intragenic self-sterility mutations is at least plausible.

Isolation among fungi can be brought about by ecological factors-microecological as well as macroecological (Kukkonen, 1971). The physiological races of rust fungi demonstrate intraspecific isolation imposed through host specialization (Stakman & Harrar, 1957). Host and parasite are genetically balanced with respect to resistance and virulence. This balance is restrictive for outbreeding and maintains the physiological race, (Flor, 1956; Person, 1966). Although host-parasite associations are not, strictly speaking, heterokaryotic, they do involve a highly specialized form of genetic "complementation".

Ecological barriers presumably operate but are not always apparent in saprobic species. Intersterile races have been recognized among North American isolates of *Fomes pinicola*, a wood-rotting basidiomycete. Isolates from the same tree may belong to separate races (Mounce & Macrae, 1938). An extreme case for the presence of a sterility barrier within a single ecotype of a given species involves *Mycocalia denudata*, a bipolar gasteromycete (Burnett & Boulter, 1963). Two genetically isolated races of this fungus were obtained from a single fructification. In this instance, the one

apparent fructification encompassed two confluent but reproductively isolated basidiocarps. *Mycocalia denudata* illustrates well a problem inherent in the study of fungal populations. A fungus in nature may represent a genetic mosaic. The intermingling of genetically distinct heterokaryons complicates resolution of fungal populations into individual phenotypes. Any statistical analysis of gene frequencies within fungal populations must take into consideration.

Little has been said during this symposium about a rather large group of fungi, the imperfect or azygotic fungi, and of their potential for speciation. The deuteromycetes are considered to be the derived or relic species of perfect ancestors, and there is ample taxonomic evidence to support this conclusion. The imperfect fungi have yet retained specific identity in the formal absence of sexuality. The large number of imperfect species and their diversity provide convincing testimony for successful exploitation of prezygotic, or more correctly azygotic, isolation by fungi to maintain the integrity of species.

Parasexual or somatic recombination was discovered twenty years ago in *Aspergillus nidulans* (Pontecorvo & *al.*, 1953) and has been recognized experimentally in several fungi. Parasexuality offers a recourse for some recombination in the absence of meiosis, and, in view of this, the parasexual process should have special significance among populations of imperfect fungi. This, however, does not appear to be the case in *Aspergillus* (Caten, 1971; Grindle, 1963; Jinks & *al.*, 1966). Conspecific isolates of *Aspergillus* have been examined in considerable detail for competence to form heterokaryons. Heterokaryon incompatibility has proven to be rampant among wild-type isolates of a given species. For example, Caten (1971) reported that among 126 combinations involving 21 isolates of *A. versicolor* only three combinations or about 2 percent of the sample formed heterokaryons. Heterokaryon incompatibility effectively precludes parasexual recombination. Thus, parasexuality may simply be an incidental derangement of mitosis with no real significance for genetic recombination in natural populations.

The trend to restrict recombination is not exclusively that of imperfect fungi. Many fungi with known perfect states are essentially asexual species in nature. The incidence of sexual reproduction in the Mucorales is recognized to be low because of the poor frequency for germination of zygotes and the common occurrence within the order of sexually neutral strains (Blakeslee & *al.*, 1927). Even in higher fungi, sex is often vestigial. Witness such species as *Emericella* (*Aspergillus*) *nidulans*, *Neurospora* (*Monilia*) *sitophila*, or *Thanatephorus cucumeris* (= *Rhizoctonia solani*). Although these fungi exhibit metagenesis, they are for all intents and purposes deuteromycetes.

The following figure (Fig. 2) is an attempt to provide a synoptic outline of speciation phenomena in fungi. Three basic phenomena underlie speciation in fungi, as in other biological systems. These are mutation, selection, and recombination. Although the induction of mutations and the pressures of selection are acknowledged as significant factors in fungal speciation, these phenomena have not been discussed extensively here today. This symposium has been concerned rather with the competence of fungal populations to exchange genetic material.

## SPECIATION PHENOMENA IN FUNGI

**mutation** **recombination** **selection**

decreased gene flow
divergence

*HETEROGENIC INCOMPATIBILITY*
- *prezygotic*
- *zygotic*
- *postzygotic*

*HOMOTHALLISM*
- *heterokaryotic*
- *homokaryotic*

*ECOLOGICAL BARRIERS*
- *microecological*
- *macroecological*
- *host specialization*
- *geographical isolation*

*LOSS OF SEXUALITY (apomixis)*

increased gene flow
convergence

*HOMOGENIC INCOMPATIBILITY (heterothallism)*
- *bipolarity*
- *tetrapolarity*

*MORPHOLOGICAL DIFFERENTIATION*
- *(sexual dimorphism)*

*HYBRIDIZATION*
- *interspecific*
- *introgressive*
- *allothallism*

*PANMIXIS*

*PARASEXUALITY*

Fig. 2.

It has been pointed out that fungal species vary considerably in this regard. Certain fungi are inbreeders and limit gene flow through any of several mechanisms—i.e., heterogenic incompatibility, homothallism, apomixis, or restrictive ecological adaptations. On the other side of this ledger are fungi that typically outbreed and recombine efficiently through homogenic incompatibility and panmixis. A few fungal species exhibit morphological differentiation *as per* sexual dimorphism, and even fewer fungal species are known to converge through hybridization. The best documented case of interspecific hybridization in fungi involves formation of the natural hybrid, *Allomyces javanicus*, in a cross between related species of different ploidy (Emerson & Wilson, 1954). Among viable hybrids from the cross were forms intermediate between the two parents, *A. arbuscula* x *A. macrogynus*, and karyological data confirmed the hybrid nature of these progeny.

In another study of hybridization, Nelson (1963, 1964) crossed sixteen species of *Cochliobolus* (*Helminthosporium*) in all combinations. The majority of crosses were either completely infertile or produced only immature or sterile asci. However, thirteen out of 120 crosses yielded progeny, but the viability of ascospores was, in all instances, low. A few of the surviving hybrid progeny were subsequently back-

crossed or outcrossed, and in some instances, second generation progeny from these crosses exhibited increased viability (Nelson, 1964). Improved viability of hybrid progeny through backcrossing or outcrossing has been observed in higher plants and is known as introgressive hybridization (Stebbins, 1950).

Some fungi are clearly paradoxical with regard to their potential for gene flow, as populations often combine genetic systems that have opposite effects on recombination. Secondary or heterokaryotic homothallism is often superimposed on homogenic incompatibility. In the bipolar *Mycocalia denudata* secondary homothallism is determined by a dominant allele (*Pd*) for precocious mitotic division of the four meiotic products in the basidium (Burnett & Boulter, 1963). The resultant eight nuclei are distributed at random into four basidiospores. Thus, 50 percent of spores are heterokaryotic with respect to mating-type factors. In the absence of the dominant allele for precocious division (*pd*), basidia of *M. dentudata* regularly contain four nuclei and basidiospores are uninucleate upon their inception. Basidiospores at maturity are binucleate but homokaryotic. In *Coprinus bisporus* secondary homothallism is brought about in yet another way—by reduction of spore number per basidium. The selective pressures for secondary homothallism in this species may be related to genetic restriction upon hyphal anastomosis and nuclear migration (Kemp, 1971).

As mentioned earlier, heterogenic incompatibility and homogenic incompatibility can coexist in the same species. *Podospora anserina* demonstrates this paradoxical association, and gene flow in this species is further complicated by secondary homothallism.

In view of the diversity among fungi for the control of recombination, it is indeed difficult to generalize as to the significance of gene flow in fungal speciation. Much has been said in the past about the importance of sexuality and of recombination in fungal evolution (Kniep, 1928; Hartman, 1943; Whitehouse, 1949a, 1949b; Raper, 1966), but there has been relatively little discussion concerning selective pressures for asexuality and for nonrecombination in fungi. Sex and recombination are clearly dispensable commodities in a great many fungi, and the selective advantage for their dispensation is not now apparent.

In the absence of recombination, speciation should be brought about principally through the interplay of mutation and selection. Fungi are predominantly haploid organisms, and mutant genotypes in haploid populations can be conserved or eliminated directly through selection. Thus, fungi, relative to higher diploid organisms, should be more readily susceptible to the affects of mutation and selection (Raper, 1968).

Forty years ago, H. J. Muller (1932) suggested that there was no basic biological reason why evolution, especially in haploid forms, could not go on indefinitely without sexuality. In his opinion, "Sex is not an absolute necessity, it is a luxury. It is necessary only in a relativistic sense, for sexless beings, although often at a temporary advantage, cannot keep up the pace of evolution set by sexual beings. In an evolutionary race between competitive species, the sexless must eventually

lose out." Stebbins (1950) extends this dialectic with two further generalizations. First, "in rapidly reproducing organisms the genetic system that operates is usually one which favors fitness at the expense of flexibility." Secondly, "that genetic system most strongly promoting immediate fitness at the expense of flexibility is one in which sex is absent." Organisms committed to immediate fitness are prone to compromise recombination for the safety of numbers and resort to proliferous asexual multiplication.

Spores and vegetative propagules of several types are formed by fungi in great profusion. These cells represent a vast collection of haploid genotypes which, subject to mutation and selection, could be channelled into a wide variety of specialized ecological situations. Divergent speciation could thus occur in haploid organisms without recombination. However, species generated in this fashion would probably be highly specialized, isolated entities, filling extremely narrow ecological niches. The physiological races of parasitic fungi and the heterogenic races of imperfect and perfect fungi conceivably have arisen through such divergence and may represent incipient species.

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# CHAMPIGNONS HYPOGÉS DU NORD DE L'AFRIQUE—I

## Ascomycètes

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Compte tenu de l'influence du climat sur la composition de la Flore des Champignons souterrains (Fungi Hypogaei), la présente étude s'attache à une quinzaine d'Hypogés ascosporés, recueillis dans le Nord de l'Afrique et répartis dans les genres: *Hydnocystis*, *Geopora*, *Balsamia*, *Labyrinthomyces*, *Tuber*, *Delastria*, *Terfezia* et *Tirmania*. Deux d'entr'eux: *Labyrinthomyces donkii* Malçn. et *Terfezia eremita* Malçn. sont décrits comme nouveaux, ainsi qu'une variété: *Tuber borchii* var. *sphaerosperma* Malçn., en même temps que la diagnose du genre *Labyrinthomyces* Boedijn est assouplie. Le *Terfezia pinoyi* Maire est versé au genre *Tirmania* et son ornementation sporale précisée.

Tout comme il en est pour les Agarics terricoles, le climat de l'Afrique septentrionale impose une sévère contrainte aux formes hypogées qui s'aventurent dans son domaine. Ses étés brûlants, les fortes températures au sol qui s'ensuivent, sa sécheresse méditerranéenne de quatre à six mois consécutifs, frappent leur mycélium des mêmes destructions périodiques et lui posent les mêmes problèmes de survie, résolus d'ailleurs de la même manière par des refuges mycorrhiziens, combinés à une active reconstruction automnale ou printanière. Moyennant quoi, ils existent.

Cependant, si l'on peut admettre que ce schéma d'adaptation suffit pour les Agarics terricoles où l'évolution relativement fugitive du carpophore écarte celui-ci du conflit climatique dont à peu près toute la charge est laissée au mycélium[1], il n'en va plus tout à fait de même avec les Hypogés. Qu'ils soient ascomycètes ou basidiosporés, le carpophore s'élabore chez eux lentement, par constructions tissulaires accumulées, sans connaître les déhiscences et les épanouissements rapides d'un primordium, qui sont la règle chez la plupart des Agarics. Sous l'abri bien illusoire du peu de terre qui le recouvre, le fruit en formation demeure alors de longues semaines – parfois davantage – à la merci des aléas du milieu environnant auxquels il ne peut en aucune manière échapper. A l'épreuve initiale commune du mycélium s'ajoute donc, pour les Hypogés, une sélection du second degré au niveau du fruit, où s'éliminent à leur tour les espèces trop délicates sous forme embryonnaire ou tout au moins juvénile.

Ce double barrage ferme l'Afrique du Nord à de nombreuses espèces de l'Europe tempérée, tout en permettant, en retour, l'implantation de formes xérothermophiles qui modifient sensiblement la physionomie d'ensemble de ce monde mycologique

[1] Cfr. Malençon & Bertault, 1970: 9–16.

souterrain. Et celà d'une façon plus apparente encore que chez les Agarics où n'intervient guère que la sélection mycélienne et chez lesquels les formes de remplacement paraissent en définitive comparativement moins nombreuses. Pourtant, aussi particulière puisse-t-elle sembler, la Flore des champignons hypogés nord-africains reste étroitement liée à celle du continent européen. Si l'on prend comme point de départ son homologue des régions nord-occidentales d'Europe, elle résulte d'une lente transformation de celle-ci sous l'influence de la latitude, transformation dont les premiers indices se décèlent en France à hauteur de l'embouchure de la Loire, vers le 47° parallèle Nord, et qui se multiplient à mesure que l'on descend vers les rivages méditerranéens. Les petites Truffes blanches du type *puberulum*, ou l'*Hydnobolites cerebriformis*, par exemple, se raréfient puis disparaissent, de même certains *Genea* (*G. hispidula*) ou *Pachyphloeus* (*P. citrinus*), mais les plus touchés restent encore les *Elaphomyces*—d'abord les roux puis les noirs—qui atteignent bien la mer mais dont aucun ne la franchit, au point que nul représentant de ce genre n'a été jusqu'à-présent observé en Afrique du Nord[2]. A mesure que la latitude s'abaisse et que les défections s'accumulent, l'arrivée de formes xérothermophiles comble les vides en modifiant à proportion la physionomie primitive de cette Flore nordique, qui devient bientôt méditerranéenne, puis africaine. Elle acquiert alors, au cours de ce trajet, son plein épanouissement et sa plus grande diversité dans le Midi de la France (Périgord, Languedoc, Provence) et l'Italie du Nord (Piémont, Ligurie, Lombardie, Toscane) avec la multiplicité des Truffes noires et l'éclosion de genres nouveaux: *Delastria*, *Delastropsis*, *Genabea*, *Hydnocystis*, *Terfezia*, etc. . . . De là, elle longe avec plus ou moins de succès les côtes orientales de l'Espagne et celles d'une bonne partie du Portugal, descend en Italie péninsulaire, en Sicile, et parvient enfin en Afrique du Nord, appauvrie en Truffes noires—et même d'une façon plus générale en *Tuber* quels qu'ils soient—dépossédée semble-t-il de quelques genres (*Genabea*, *Picoa*), mais sensiblement plus généreuse en *Terfezia* qui trouvent là leur véritable territoire et forment l'essentiel de la production hydnologique de cette partie méridionale de la ceinture mésogéenne. Plus bas, vers le Sahara, tout ceci disparaît, sauf pourtant quelques *Terfezia* ou *Tirmania* qui, loin dans le Sud, peuvent se maintenir auprès des points de végétation, quand il y en a, et fructifier de temps à autre à la faveur des pluies qui s'abattent parfois sur ces contrées singulièrement déshéritées[3].

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[2] En mars 1931, nous avons observé l'*Elaphomyces anthracinus* dans le Sud du Portugal (Algarve). C'est, pensons-nous, le pointage le plus méridional du genre dans le domaine méditerranéen.

[3] Dans les régions très écartées du Sahara central, une végétation ligneuse au système radiculaire dimorphe particulièrement adapté (cfr. Th. Monod: *Méharées*) peut subsister çà et là dans les dépressions ou les lits d'oueds temporaires, grâce au ruissellement souterrain d'un *underflow* permanent. Quelques Gastéromycètes (*Battarraea*, *Dictyocephalus*) ou Hypogés (*Terfezia*, *Tirmania*) se maintiennent parfois là, en profondeur, à proximité des ces racines ou en association avec certaines d'entr'elles (*Tamarix*, *Plantago*, *Helianthemum*) sous une forme végétative contractée, et sans presque jamais fructifier. Sauf quand intervient l'apport supplémen-

En bref, et forcément schématisée, telle est donc la situation d'ensemble des champignons hypogés dans les régions du Nord de l'Afrique. Ceci dit, il faut bien constater qu'ils y sont assez peu nombreux et—mis à-part les *Terfezia* recherchés pour des fins alimentaires—reconnaître en même temps que nos connaissances à leur égard résultent beaucoup plus de découvertes fortuites que d'observations poursuivies de façon rationnelle. Nous avons alors tenté, surtout au Maroc, de pallier cette carence dans la mesure de nos possibilités, et ceci va nous permettre, dans les lignes qui vont suivre, de donner une première liste des formes ascosporées que nous avons eues entre les mains, tant à la suite de son prospections personnelles que grâce aux envois d'obligeants collecteurs, en particulier MMrs. R. Bertault, Ch. Chabrolin, Th. Monod, qui voudront bien trouver ici l'expression de notre très vive et amicale gratitude.

## HYDNOCYSTIS Tulasne, 1845

*Hydnocystis clausa* (Tul.) Ceruti, 1960.
*Genea clausa* Tul., 1844. — *Geopora clausa* (Tul.) Burdsall, 1968.
*Hydnocystis arenaria* Tul., 1851.
*Hydnocystis beccarii* Mattirolo, 1900.

Espèce circum-méditerranéenne observée de temps à autre, entre novembre et mars, dans les maquis arborés et les forêts claires de la côte marocaine, sous les chênes-lièges et les pins (*Pinus halepensis*, *Pinus pinea*). Nous l'avons aussi recueillie dans le Sud du Portugal (Serra de Monchique), en mars 1931, dans un maquis dénudé.

Péridium (excipulum) parenchymateux à surface brunie et craquelée en fines verrues pyramidales surbaissées, au sommet desquelles s'attachent de longs poils bruns épars, flexueux et septés, larges de 12–14$\mu$, à parois épaissies et base généralement renflée. Vers l'intérieur la structure fait place à un tissu d'éléments allantoïdes

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taire d'une pluie occasionnelle *et suffisante*; ce qui en fait en définitive des champignons très rares mais qui, néanmoins, *vivent* là-bas.

Au reste, si le Sahara est souvent muet, est-il beaucoup moins mort qu'on l'imagine. Au cours de nos randonnées à travers le Tidikelt et le Tademaït, il nous est arrivé de parcourir durant des heures un paysage en apparence intégralement minéral, formé d'un "reg" caillouteux parfaitement plan et non moins parfaitement azoïque, sans végétation, sans oiseaux, sans insectes, avant de nous trouver soudain en présence d'un humble brin d'herbe, bien vert, innocemment germé – tout seul – au milieu de la pierraille. Quelques kilomètres plus loin, on en rencontrait un second, et guère plus à de larges distances à la ronde. Comme il s'agissait de germinations et non de reprises d'activité d'une Graminée vivace, l'underflow ne pouvait être invoqué pour justifier le phénomène. La seule explication était qu'un orage très local avait réveillé ici la dormance hétérochronique de quelques graines disséminées dans la région, révèlant par là leur présence et en même temps tout l'illusoire de la "mort" du désert, qu'une simple pluie suffisait à démentir.

La découverte d'un *Podaxon* on d'un *Phellorinia* est parfois tout aussi démonstrative.

hyalins, d'abord confus puis couché-péricline, qui engendre un hyménium monostrate palissadique tapissant l'unique et ample cavité du fruit.

Thèques octospores, cylindracées, non amyloïdes et dépourvues généralement d'opercule apparent: 225–280 × 19–21$\mu$. Spores ovoïdes, hyalines, lisses, non amyloïdes, à gros globule oléagineux central accompagné de nombreuses gouttelettes beaucoup plus petites: 22–25 × (16–)17,5–19$\mu$ rarement 30 × 20$\mu$ et, dans ce cas, avec deux gros globules internes.

Paraphyses nombreuses simples ou seulement fourchues vers la base, grêles (3$\mu$ crass.), égales on à peine élargies au sommet, hautes d'environ 350 à 400$\mu$, dépassant par conséquent les thèques d'à peu près la moitié de leur hauteur et formant au-dessus d'elles un fin velouté blanc qui s'étend sur l'ensemble de l'hyménium.

H. H. Burdsall Jr. (1968: 509) indique chez cette espèce des thèques operculées. La présence de cet appareil de déhiscence est ici tout à fait vraisemblable mais nous n'avons jamais eu l'occasion de l'observer sur le matériel frais dont nous avons disposé. Ceci semble indiquer qu'il est davantage un témoin phylétique qu'un dispositif fonctionnel efficace et que la libération des spores s'effectue plus habituellement par destruction de la paroi des thèques.

## GEOPORA Harkness, 1885

*Geopora cooperi* Harkness, 1885.

*Pseudohydnotria harknessii* E. Fischer, 1897. — *Geopora harknessii* (E. Fischer) E. Fischer, 1908.

*Geopora magnifica* Gilkey, 1916.

Une dizaine d'exemplaires sous *Pinus laricio* au sommet du versant Sud du Jbel Tisuka, dans la chaîne calcaire du Rif (Maroc, alt. 2000 m env.), le 19 novembre 1957. Première et unique récolte de cette espèce sur le continent africain, d'ailleurs entièrement conforme aux spécimens d'Europe et d'Amérique du Nord.

Thèques cylindracées ou étroitement claviformes, octospores, non amyloïdes: 165–200 × 22–25$\mu$, dont certaines peuvent s'ouvrir par un opercule sommital parfaitement net. Spores unisériées, hyalines, lisses, ellipsoïdes, à deux gros globules oléagineux internes accompagnés de plus petits: 23,5–28 × 13,5–15,5$\mu$, le plus souvent 24–25 × 14–15$\mu$. Nombreuses paraphyses simples, septées, larges de 3,5–6,5$\mu$ à sommet légèrement élargi (6–11$\mu$), aussi hautes que les thèques ou les dépassant à peine.

H. H. Burdsall Jr. (1968: 513 et 518) donne à la forme longisporée typique le nom de *Geopora cooperi* Hark. f. *cooperi*, et crée une f. *gilkeyae* pour des spécimens à spores globuleuses ou subglobuleuses de (19–)20–25(–28) × (15–)16–21(–24) $\mu$ où le rapport longueur/largeur tombe à 1,25, contre 1,5–1,8 chez le type.

## BALSAMIA Vittadini, 1831

*Balsamia platyspora* Berkeley, 1844.

Un unique spécimen sous les *Quercus lusitanica*, à proximité de cèdres, dans le haut de la forêt d'Azrou (Moyen Atlas, alt, 1650 m), le 6 mai 1941.

## LABYRINTHOMYCES Boedijn, 1939

**Labyrinthomyces donkii** Malençon, *n. sp.*—Fig. 1

Entièrement hypogé mais enfoui à quelques centimètres seulement de profondeur. Typiquement sous *Eucalyptus* purs (*E. camaldulensis*, *E. gomphocephala*, *E. rostrata*, etc.); par exception, et de façon plutôt accidentelle, sous *Acacia cyanophylla* et *Olea europaea*. Répandu et parfois abondant dans toute l'étendue de la Meseta marocaine (Tanger, Rabat, Casablanca, El Jadida, Settat, Safi, Essaouira, Skhour des Rehamna, etc.); mûrit en avril mais commence à se former dès le mois de janvier.

Tuberculis carnosis ac lentis, globosis vel pulvinatis, subregularibus, 10–30 × 10–20 mm, basi adhaerentibus; totis clausis, neque gelatis, neque diffluentibus, sed diffractis ac maturis sponte sua desaggre. Peridio simplici, albo vel cremeo, levi, glabro, impolito, adnato, prosenchymatoso-periclini, 80–100 $\mu$ crasso. Gleba albida, sicca, e basi ramoso-venosa; loculis angustis elongatis, modice sinuosis, parte cava reducta ac clausa, hymenio rufo vel fulvo, trama filamentosa subregulari. Thecis fusiformibus vel claviformibus, 2–3 sporis, 250–300 × 47–55$\mu$; paraphysibus multis, simplicibus, septatis, summis haud incrassatis tam altis quam thecis. Sporis haud amyloideis, maturis ochraceis, globosis (34–)40–47$\mu$, guttulis oleaginosis confertis, grandibus verrucis hemisphaericis extrinsecus tuberculatis. Odore fungo debili, interdum leviter sicut apud *Tubera*; sapore miti; verisimiliter edibilis.

Hab. — Sub *Eucalypto* sp. sp., raro sub *Acacia cyanophylla* et *Olea europaea*, vere vulgatissimus in tota Meseta maroccana.

TYPUS: No 2938, Herb. MAROC G. Malençon, Inst. Bot. Monspeliensis.

Fructifications charnues-élastiques, globuleuses ou pulvinées, quelquefois un peu bossuées ou allongées mais d'ordinaire peu déformées: 10–30 × 10–20 mm, le plus souvent 15–19 × 14 mm, à petite base de fixation légèrement proéminente et plissée, parfois peu distincte; glabres, mates, d'apparence feutrée, blanches ou crème et lisses sur le frais, rousses et fripées en herbier; de structure sèche et longtemps closes mais s'éclatant et se fragmentant spontanément et de façon irrégulière à complète maturité, sans intervention de gélification ou de diffluence.

Odeur fongique légère, banale, à laquelle peut se superposer un faible parfum de Truffe (*Tuber melanosporum*) et un relent acétylénique; saveur douce. Serait comestible.

Péridium adné, épais de 80-100$\mu$, construit en prosenchyme péricline dense, aux parois coalescentes faiblement jaunies, passant vers l'intérieur à une structure moins compacte, plus visiblement filamenteuse, couchée et hyaline, qui se raccorde à la gleba. Gleba blanche ou blanchâtre, sèche, parcourue de veines peu serrées, soyeuses chez la plante ressuyée et aqueuses quand elle est imbue, s'élevant de la base du fruit. Logettes closes, indépendantes, modérément sinueuses, disposées sans ordre apparent ou parfois subrayonnantes, à cavité manifeste mais le plus souvent très étroite et tapissée par un hyménium roux ou fauve (à maturité!); trame de filaments larges de 5–8$\mu$, aux parois minces et fragiles, organisés en médiostrate à peu près régulier bordé d'une zone plus confuse et subvésiculeuse sous l'hyménium.

Hyménium blanc hyalin dans la jeunesse, devenant à maturité roux ou fauve par les spores, palissadique et monostrate. Thèques 2–3-spores, fusoïdes ou claviformes, souvent arquées, à base grêle pédonculée, à membrane non amyloïde épaisse de 1,5$\mu$ mais amincie à l'extrême sommet: 250–300 × 47–55$\mu$. Paraphyses abondantes et denses, droites, non ou à peine épaissies à leur extrémité, groupées en épais fascicules qui s'interposent entre les thèques, hyalines, septées, simples mais souvent

anastomosées, larges de 3–5$\mu$, hautes de 250$\mu$ et davantage, atteignant par conséquent le sommet des thèques ou pouvant même le dépasser.

Spores longtemps hyalines puis ocre clair à maturité complète, avec une membrane de 8$\mu$ d'épaisseur; sphériques, volumineuses: (34–)40–47$\mu$ diam., le plus souvent bourrées de globules oléagineux, et entièrement couvertes de grosses verrues arrondies serrées les unes contre les autres.

A premier examen, et chez les éléments subadultes, l'enveloppe de ces spores paraît simplement formée d'une épispore d'environ 3 $\mu$ recouverte d'une grosse périspore homogène épaisse de 7 $\mu$[4]. Après une heure ou deux de contact, l'ammoniaque ($NH_3$) y provoque cependant des gonflements et des clivages. L'épispore se dédouble en deux couches concentriques d'épaisseur inégale, la plus forte demeure au contact immédiat du contenu sporal et représente semble-t-il l'épispore vraie, bien qu'on puisse à l'occasion la voir se dédoubler à son tour et mettre en évidence une mince endospore ordinairement indécelable. A l'opposé, la couche superficielle, plus ténue, se détache de la précédente et se distend sous l'effet du réactif. Elle entraîne alors dans son extension la grosse coque périsporique à laquelle elle adhère et dont elle est en réalité le support. C'est l'*assise sous-périsporique* de la terminologique de Mme. M. Le Gal (1947: 82), autrement dit la membrane de base de tout l'ensemble périsporique. Autour d'elle s'étend l'épaisse couche molle et hyaline de la "*coque interpérisporique*" gonflée par le réactif avec, en extrême périphérie, un mince "*feuillet périsporique*" tenace qui retient et limite tout l'ensemble. En tout cinq téguments superposés.

D'autre part, et sans qu'il soit besoin cette fois de recourir à des procédés artificiels, l'examen direct dans l'eau pure permet de constater, un peu avant la maturité complète de la spore, quand son contour est encore lisse, que la coque interpérisporique est traversée dans toute son épaisseur par d'innombrables baguettes radiantes, incolores comme elle mais moins réfringentes, appuyées sur l'assise sous-périsporique, et rayonnant jusqu'au feuillet périsporique qu'elles atteignent mais ne dépassent pas. A ce stade, la spore paraît alors densément hérissée de fins aiguillons *inclus* dont la position intratégumentaire laisse parfaitement lisse le profil général. Puis le feuillet périsporique se rompt sous l'effet de la contraction de la périspore qui se craquèle en blocs tronc-coniques dressés, assez réguliers, ébauchant les verrues tuberculeuses de l'organe mûr, et dans lesquels on distingue encore quelque temps les aiguillons inclus, jusqu'à ce que la contraction et la coloration finales les oblitèrent peu à peu.

Nous dédions à la mémoire du très regretté Dr. M. A. DONK cette remarquable espèce dont la première récolte a été effectuée au Maroc par Mr. le Dr. J. Fontvieille, au Skhour des Rehamna[5], où elle croissait en multitude dans un petit bois d'*Eucalyptus*. Par ses traits généraux, en particulier par ses spores, elle entre de toute évidence dans le genre *Labyrinthomyces* Boedijn (1939: 238–240), tout en étant bien

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[4] Ce total de 10$\mu$ se réduira à 8$\mu$ chez la spore mûre, quand l'enveloppe se sera indurée, colorée et quelque peu contractée.

[5] Approximativement à mi-chemin entre Casablanca et Marrakech.

distincte du *L. steenisii* Boed. (Fig. 2) seul représentant jusqu'ici de ce genre d'Hypogé d'Extrême-Orient.

Décrit en 1939 par le Dr. Boedijn (l.c.), le *Labyrinthomyces steenisii* a été en effet découvert initialement à Java au milieu de cultures ("between fields planted with tobacco and cabbage"), puis revu quelques années plus tard (1953) en Australie, près de Sydney, par N. M. White[6], cette fois en terres vierges et sous le couvert d'*Eucalyptus* (*E. pilularis* et *E. saligna*). En tout deux récoltes, la seconde limitée à un seul exemplaire, qui constituent croyons-nous tout le matériel que l'on possède de cet intéressant champignon.

Grâce à l'amabilité des Miss H. M. Gilkey, récemment disparue, il nous a été possible de disposer d'un fragment de l'échantillon australien, chez lequel nous avons retrouvé tous les caractères de la récolte de Java mentionnés dans l'excellente description de Boedijn. Selon ce que nous avons constaté l'espèce possède un cortex d'un brun foncé, épais de 600 à 700 $\mu$, prosenchymateux-confus quoique d'orientation générale péricline. Il entoure une gleba aux logettes peu nombreuses et modérément sinuées, à cavité très étroite tapissée d'un hyménium de thèques octospores, cylindracées à base atténuée, mesurant 380–420 × 30–35 $\mu$, à membrane épaisse jusqu'à 2 $\mu$ mais amincie à 0,75 $\mu$ au sommet. Paraphyses nombreuses, hyalines, rigides, simples, septées, larges d'environ 3 $\mu$, à peine épaissies au sommet et *remarquablement courtes* puisqu'elles ne mesurent que 170 à 200 $\mu$ de haut, soit tout au plus la moitié de la hauteur des thèques. Spores encore hyalines dans le spécimen examiné, sphériques: 20–22 $\mu$ diam., remplies de gouttelettes oléagineuses et couvertes de grosses verrues arrondies, tantôt très serrées comme les représente Boedijn (1939: fig. 2), tantôt au contraire clairsemées[7].

En regard, le *Labyrinthomyces donkii* apparaît, comme on l'a vu, avec un cortex mince de couleur claire, des thèques 2–3-spores, fusoïdes et relativement petites, des spores par contre beaucoup plus volumineuses, et des paraphyses atteignant aisément la hauteur des thèques. Ce qui justifie amplement la création d'une épithète spécifique particulière.

Quant au genre *Labyrinthomyces* lui-même, les enseignements apportés par l'analyse du *L. donkii* rendent nécessaire d'en assouplir légèrement la diagnose, qui fait état de thèques cylindracées octospores et de paraphyses "brevissimis" uniquement propres au *L. steenisii*. On le définira donc désormais de la façon suivante:

### LABYRINTHOMYCES Boedijn emend.

Carpophoris hypogaeis, globosis, pulvinatis vel oblongis, carnosis, peridio adnato. Gleba e loculis angustis, modice gyroso-labyrinthiformibus, extus non apertis. Thecis elongatis,

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[6] cfr. *In* Trans. Br. mycol. Soc. **39**: 341–342. 1956.

[7] Nos dimensions concordent de façon satisfaisante avec celles fournies par Boedijn dans son texte, mais les grossissements indiqués sur sa fig. 2 sont erronés. Au lieu de "asci and paraphyses × 150; spores × 675" il convient de lire respectivement: × 300 et × 1350. Sinon ces éléments ressortent deux fois plus gros qu'ils ne sont en réalité !

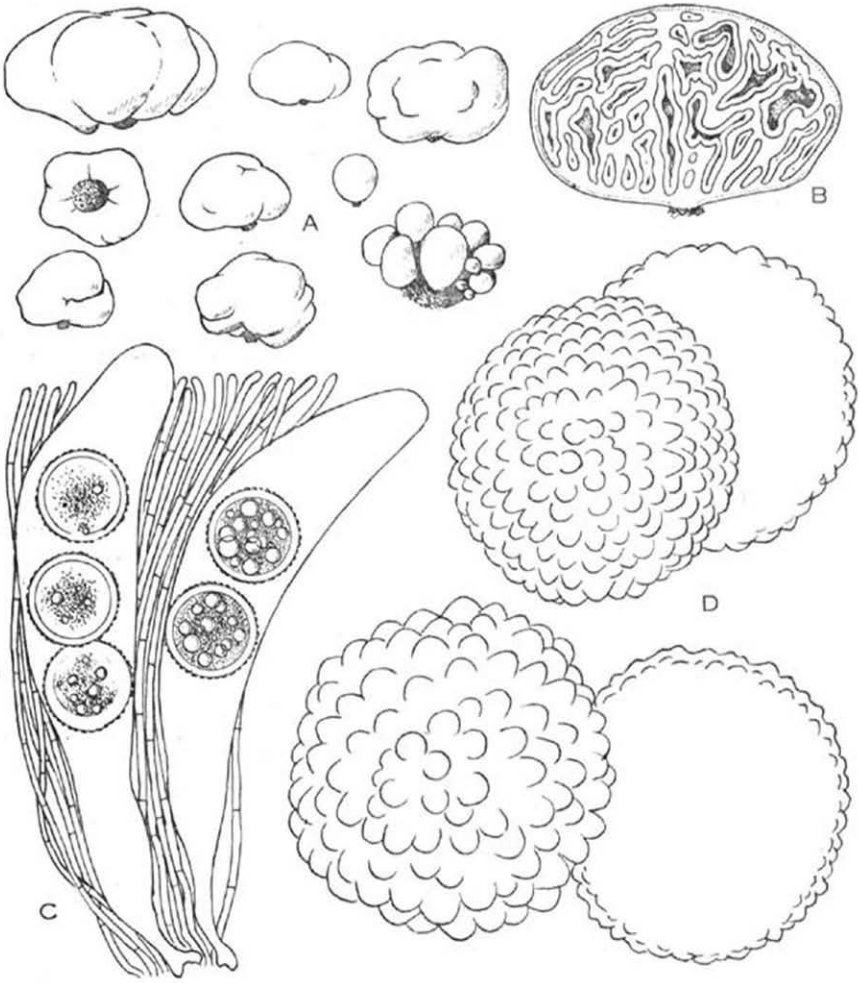


Fig. 1. *Labyrinthomyces donkii* Malçn. — A. Fructifications isolées ou groupées (× 1). — B. Coupe verticale d'un spécimen adulte (× 2). — C. Thèques et paraphyses (× 300). — D. Quatre spores, dont deux en relief et deux en silhouettes (× 1000).

cylindraceis vel fusiformibus, 2–8 sporis. Sporis 1-seriatis, hyalinis, dein tarde coloratis, tuberculatis. Paraphysibus multis, simplicibus, septatis, brevissimis, vel thecis aequalibus. Typus: *L. steenisii* Boedijn, 1939.

Ainsi précisé, ce genre vient semble-t-il se placer au voisinage de *Choiromyces* Vitt. et surtout de *Hydnotria* Berk. où les fructifications sont évidemment plus tourmentées, les logettes plus amples et parfois ouvertes vers l'extérieur, et la texture plus tenace, mais en fait d'organisation fondamentale très similaire. Avec, par surcroît chez *H. tulasnei* Berk. & Br., des spores sphériques entourées d'une forte périspore, qui ne se fragmente pas en verrues et se contracte simplement de façon irrégulière, mais dans l'épaisseur de laquelle on distingue longtemps, comme chez le *L. donkii*, une striation radiante de fines colonnettes plus mates qui s'oblitèrent seulement à maturité[8].

Dès le début de sa découverte, le *L. donkii* s'est montré étroitement lié aux *Eucalyptus*, et la constance de cette association s'est confirmée au cours des nombreuses recherches effectuées par nous dans les années qui ont suivi. En particulier, au printemps de 1960 et de 1961 où, pour connaître sa répartition au Maroc nous avons visité de façon méthodique un grand nombre de plantations disséminées dans les régions les plus variées de la Meseta, nous l'avons rencontré partout — clairsemé ou abondant —, mais inévitablement présent chaque fois qu'il s'agissait d' *Eucalyptus*. Par contre, les formations arbustives artificielles ou naturelles (plantations d'*Acacia* ou de *Pinus*, callitraies, subéraies, maquis divers) visitées de la même manière et aux mêmes époques, ne nous ont jamais rien fourni. A l'exception toutefois de deux maigres récoltes sous *Acacia cyanophylla* à El Jadida et Essaouira, plus une troisième sous un bouquet d'oliviers près de Tanger (Cherf-el-Akab), qui sont venues rompre cette uniformité. Mais, comme l'*Eucalyptus* est partout répandu au Maroc, notamment dans ces localités, et qu'à El Jadida ses plantations longent celles de l'*Acacia cyanophylla* où nous avons effectué une de nos récoltes aberrantes, il est permis de croire que ces exceptions stationnelles ont été le fait d'accommodats fortuits par voisinage, ou même peut-être de simples apparences. De toute manière elles ne peuvent suffire à contredire l'extrême et évidente affinité du *L. donkii* pour les *Eucalyptus* dont il est vraisemblablement un symbionte. Aussi, malgré sa découverte au Maroc où il arrive à pulluler en certaines stations, doit-on voir en lui un champignon originaire des mêmes régions que ses hôtes, c'est à dire d'Extrême-Orient. Il en a été sans doute transporté avec eux et s'est particulièrement bien acclimaté au milieu méditerranéen, comme l'ont fait l'*Urnula platensis* Speg., le *Lyophyllum buxeum* R. Maire, et le *Naucoria rheophylla* Bert. & Malçn. alors que le *L. steenisii*, aux exigences sans doute différentes, ne l'a pas suivi.

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[8] La comparaison discriminatoire de H. H. Burdsall Jr. (1968: 523) entre *Hydnocystis singeri* Gilkey et *Labyrinthomyces steenisii* Boedijn, apparaît sans objet et repose sur une conception toute théorique et artificielle du genre de Boedijn.

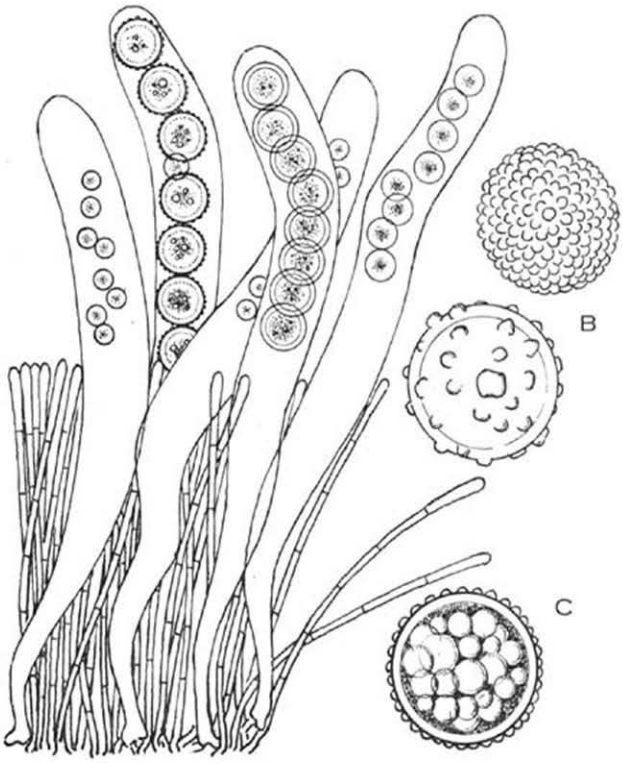


Fig. 2. *Labyrinthomyces steenisii* Boedijn — A. Thèques et paraphyses (× 300). — B. Deux spores (× 1000). — C. Une spore en coupe optique (× 1000).

## TUBER Micheli ex Hooker, 1821

*Tuber asa* Tulasne, 1851.
*Tuber lacunosum* Mattirolo, 1900.
*Terfezia gennadii* Chatin, 1896. — *Tuber gennadii* (Chat.) Patouillard, 1903.

Assez commun au premier printemps (mars-avril) au Maroc; récolté par nous près de Rabat, en forêt de Mamora (*Quercus suber*), et observé de temps à autre sur les marchés locaux, en mélange avec les Terfès qu'on y apporte.

Fructifications de taille modeste, dépassant rarement celle d'une noix, grossièrement arrondies à base un peu déprimée; fermes, dures, cornées à sec, extérieurement mates, pubérulentes ou cotonneuses-feutrées, blanches sur le frais et encore jeunes mais se salissant de jaunâtre avec l'âge et finalement ocracé terne. Gleba marbrée de blanc jaunâtre sale, d'ocracé puis de gris violacé, parcourue de veines

aérifères plus claires, nombreuses, compliquées, rayonnant de façon plus ou moins nette à partir de la base vers la périphérie et s'ouvrant çà et là sur l'extérieur; compacte sur le frais, exceptionnellement çà et là lacuneuse (*T. lacunosum* Matt.), rétractée en sèchant et parfois même ouverte en fissures au niveau des veines. Odeur caséeuse ou de levûre de bière.

Thèques largement claviformes ou subpiriformes à 1–4-spores: 130–170 × 60–65$\mu$, entourées de paraphyses claviformes dressées, septées, plus courtes qu'elles (80–90$\mu$). Spores brun clair translucide à maturité, typiquement ellipsoïdes-limoniformes à deux mucrons polaires (ophtalmiformes), mais aussi souvent mêlées d'éléments sphériques dans le même échantillon, ornées d'un réseau d'alvéoles penta- ou hexagonaux larges de 7–12$\mu$ (5 à 7 alvéoles par demi-spore), mesurant 50–55 × 43–50$\mu$ (réseau compris) pour les éléments ophtalmiformes, et 33–44$\mu$ pour ceux de contour circulaire.

TUBER BORCHII Vitt. var. **sphaerosperma** Malençon, *n. var.*

Peu enfoui ou partiellement émergent et pas très rare vers avril-mai, en sols sableux, dans les plantations de *Pinus halepensis* et *Pinus pinea* du littoral atlantique marocain (Témara, Rabat, Larache).

A typo differt sporidiis perfecte et constanter sphaericis. Hab. — In pinetis sabulosis Mauritaniae; vere.

TYPUS: No. 437, Herb. MAROC G. Malençon, Inst. Bot. Monspeliensis.

Fructifications de 30-55 mm diam., fermes, globuleuses, ellipsoïdes ou difformes, rarement régulières, en général bossuées, tuberculées ou sillonnées, fortement crevassées avec l'âge et d'ordinaire sans base décelable; blanches et brièvement pubérulentes dans la jeunesse, vite glabres, mates et envahies d'ocre rosé, à la fin d'une teinte alutacé terne uniforme. Odeur faible, non caractéristique, au moins chez les spécimens jeunes.

Péridium lisse, adné, mal défini, épais de 350 à 400$\mu$, parenchymateux dans sa région corticale sur une épaisseur de 90–110$\mu$ où il montre des éléments arrondis ou ovalaires larges de 7–12$\mu$, à membrane cyanophile renforcée jusqu'à près de 1$\mu$, et accolés sans excès. La structure passe ensuite, en profondeur, à un prosenchyme confus, cohérent, d'hyphes larges de 5–7$\mu$, à parois minces, qui se poursuit sans changement jusqu'au contact de la gleba et duquel se dégagent, sans autre modification qu'une disposition un peu plus étirée, les veines dont celle-ci est traversée.

Gleba ferme, compacte, blanche puis marbrée de jaunâtre, de gris clair ocré, de brunâtre plus ou moins foncé, parcourue d'un réseau de veines plus pâles nées, comme dit plus haut, du péridium. De part et d'autre de ces veines s'établit un hyménium de thèques et de paraphyses, net et régulier dans les formes jeunes, mais insensiblement dégradé et chaotique avec l'âge.

Thèques 1–3 spores, subglobuleuses ou brièvement piriformes, de 75 × 60$\mu$ et davantage, naissant dès la base de l'hyménium et même parfois en partie incluses dans la trame, puis dégagées et superposées sans ordre. Entr'elles s'élèvent de nombreuses paraphyses grêles, ramuleuses, septées, qui les enveloppent de tous côtés, finissent par les dépasser et forment au-dessus d'elles, avec leurs extrémités peu renflées et fastigiées, un gazon palissadique régulier qui tapisse l'étroite cavité des veines. De ce stade, et de plus en plus nombreuses à mesure que la plante avance en âge, ces extrémités prolifèrent en longs poils flexueux irréguliers, cloisonnés, bientôt enchevêtrés en tissu aérifère cotonneux.

Spores d'un jaune-brun translucide s. l., *parfaitement et constamment sphériques* (!),

ornées d'un réseau d'alvéoles 5–6-gones hauts de 3,5–5$\mu$ et larges de 5–7$\mu$ (exceptionnellement 7–10$\mu$). Selon qu'elles sont issues de thèques 3–2- ou 1-spores, elles mesurent 26–38$\mu$ diam. sans l'ornementation, et de 32 à 48$\mu$ réseau compris.

A la suite d'une identification trop rapide et qui n'avait pas été remise en cause, nous avons longtemps considéré cette espèce comme étant le *Delastreopsis oligosperma* Matt. et l'avons signalée sous ce nom, alors que son organisation hyménienne témoigne qu'il s'agit bien d'une truffe. Elle ne peut alors être rapportée qu'au *Tuber borchii* Vitt., espèce précisément printanière comme elle dont elle réunit par ailleurs tous les autres caractères, hormis ses spores invariablement sphériques. En nous basant sur cette constante nous créons donc pour elle une désignation variétale particulière; et nous le faisons d'autant plus volontiers que le *T. borchii* ellipsosporé typique n'a jamais été rencontré en Afrique du Nord, alors qu'on le trouve en Europe jusqu'à la latitude de l'Angleterre[9]. Il se pourrait donc que la sphéricité sporale soit ici l'extériorisation morphologique d'un jordanisme méridional accommodé à des conditions climatiques trop sévères pour le type Européen.

*Tuber excavatum* Vittadini, 1831.

Dans le courant du mois d'avril, c'est à dire vers la fin de la saison humide, on récolte de temps à autre au Maroc, dans la région d'Azrou (Moyen Atlas, alt. 1550 m), quelques spécimens à peine ébauchés de cette espèce, qui selon toute vraisemblance ne parviendront pas à achever leur cycle évolutif. En fatt il semble bien que le *T. excavatum* ne parvient à sporuler qu'au cours d'années où les pluies de printemps se prolongent au-delà des limites habituelles, et qu'il se maintient le plus souvent sous sa forme uniquement mycélienne.

*Tuber rufum* Pico ex Fr., 1823.

De temps à autre, au Maroc, dans le Moyen Atlas (Dayete Ahoua, Jbel Hebbri, Azrou) jusqu'à 2000 m d'altidude, de juin à novembre, sous *Quercus ilex*. Non signalé jusqu'à ce jour en Afrique du Nord.

*Tuber uncinatum* Chatin, 1887

Une récolte fortuite dans des terres retournées et fouillées par les sangliers, en Forêt de Jaâba, près Ifrane (Maroc: Moyen Atlas, alt. 1600 m.), en novembre 1960.

DELASTRIA Tulasne, 1843

*Delastria rosea* Tulasne, 1843.—*Terfezia rosea* (Tul.) Torrend, 1907.

De temps à autre au Maroc (Rabat, Larache) entre décembre et mars, semi-épigé ou peu enfoui dans les pinèdes arénacées à *Pinus halepensis* et *Pinus pinea*. Peu commun et non encore signalé en Afrique du Nord.

[9] Mattirolo (1928) a signalé que le *Tuber borchii* (ellipsosporé) est l'espèce la plus commune des pinèdes de Toscane d'où elle fait l'objet d'un commerce d'exportation.

Fructifications subglobuleuses ou brièvement turbinées de 20 à 35 mm de diamètre, bossuées de protubérances arrondies irrégulières laissant deviner la constitution nodulaire de la gleba, sans base bien distincte ou atténuées en court et grossier pédicule de fixation agglutinant le sable, fragiles, extérieurement cotonneuses et d'un blanc éclatant en pleine fraîcheur, mais vite fanées, feutrées et ternies de jaunâtre sale par la dessication ou les manipulations. Péridium inexistant, totalement indifférencié en dehors d'un simple affaissement feutré, superficiel et mécanique, de l'enveloppe cotonneuse générale du fruit. Gleba tendre, charnue, dépourvue de logettes, formée d'un agrégat de gros nodules fructifères compacts, pulpeux, rose tendre, rose lilacin, rose saumoné, rose brun, noyés dans un byssus commun issu de la périphérie, qui les sépare les uns des autres par de larges travées blanches dont les ramifications les pénètrent et les découpent en masses arrondies de plus en plus petites.

Sans doute comestible car rencontré parfois sur les marchés, mélangé aux Terfès qu'on on y vend. Odeur et saveur nulles.

Thèques inordinées, 2-3-spores, claviformes ou piriformes sessiles, souvent arquées: 150–200 × 60–70$\mu$. Spores sphériques à gros globule oléagineux central, hyalines ou à la fin jaunâtres, ornées d'un beau réseau typiquement alvéolaire mais passant aisément à l'échinulation par abaissement progressif puis disparition des parois des alvéoles; il s'ensuit le plus souvent une ornementation intermédiaire dite "alvéolée-muriquée" qui a pu passer pour typique du genre, où les noeuds du réseau ressortent en courts aiguillons obtus au-dessus des alvéoles. Ces spores mesurent 27–29$\mu$ diam., plus l'ornementation elle-même haute de 4 à 6$\mu$, ce qui donne en définitive un diamètre total de 38 à 40$\mu$ dans la plupart des cas.

### TERFEZIA Tulasne, 1851

*Terfezia Claveryi* Chatin, 1891.

Espèce répandue dans tout le Bassin méditerranéen et le Proche-Orient, mais dont la fréquence s'accroît d'Ouest en Est. Croissant en association avec des Hélianthèmes ligneux, et relativement thermophile, elle apparaît en Afrique du Nord au voisinage des régions prédésertiques du Sahara septentrional et, plus à l'Est, descend selon Mattirolo (1914) jusqu'en Tripolitaine. Elle est rare au Maroc où ses stations, limitées aux régions du Sud, s'échelonnent au long du 32° parallèle Nord, près des centres de Ksar-es-Souk, Bou-Bernous, Bou-Denib et Figuig, dont les marchés l'offrent sous le nom de "Terfès rouge du Tafilalelt". Nous l'avons aussi reçue d'Algérie (Oasis de Laghouat, leg. Dr. Arnaud), des environs de Tunis (M. Chabrolin), et Miss Gilkey nous en a communiqué des spécimens provenant d'Irak, d'Iran, et du Koweit.

Thèques octospores subsessiles, ellispoïdes ou largement piriformes: 86–100 × 65–85$\mu$. Spores hyalines, sphériques: 16–20–23$\mu$ diam., ornées d'un beau réseau superficiel bas et serré qui, chez certains sujets, peut se dérègler et passer à la simple verrucosité par renforcement des noeuds et effacement progressif des mailles.

**Terfezia eremita** Malençon, *n. sp.*—Fig. 3.

Dans le sable des dunes de l'Ouarane (Mauritanie, 21° lat. N, à 750 km au Sud de Tindouf) leg. Pr. Th. Monod, N° 11314, le 22 janvier 1955.

Carpophoris hypogaeis, dein emergentibus, obpiriformibus, subpedunculatis: 25 × 22–25 mm. Peridio 1 mm crasso, coriaceo, glabro, levi vel leviter venuloso, ex alcoholate umbrino. Gleba compacta, ex alcoholate fusca, venis pallidioribus marmorata, areas rotundas fertiles limitantibus. Thecis inordinatis, 8-sporis, ovatis vel piriformibus: 65–70 × 50–55$\mu$ (raro 80–85 × 60$\mu$). Sporis late ellipsoideis, tunica 1$\mu$ crassa, s. l. pallide luteis rotundatis vel conicis plus minusve stipatis sparsis: 12,3–14,7 × 11,5–13$\mu$ (sine verrucis).

Hab.—In arenis dunensibus Ouaranae (Mauretania), Pr. Th. Monod leg. No 11314, 22.01.1955.

TYPUS in Herb. GÉNÉRAL G. Malençon, Inst. Bot. Monspeliensis.

Fructifications hypogées ou émergeant à ras du sol, obpiriformes, la base atténuée sessile ou brièvement pédonculée, le sommet aplani, craquelé par son exposition à l'air: 25 × 22–25 mm. Péridium d'environ 1 mm d'épaisseur, coriace, à section brune, extérieurement glabre, lisse ou faiblement veinulé, brun d'ombre *ex alcohol*, un peu plus olivâtre sur exsiccata. Gleba compacte, bistrée (*ex alcohol*), parcourue de veines plus pâles délimitant des nodules globuleux, eux-mêmes intérieurement veinulés; la base stérile très brève, homogène et charnue.

Hyphes ascogènes larges de 6–8$\mu$, confuses, rameuses, septées, portant des groupes de thèques octospores, ovoïdes ou piriformes non organisées en hyménium, mesurant 65–70 × 50–55$\mu$, plus rarement 80–85 × 60$\mu$. Spores groupées par huit dans chaque thèque ou en nombre plus réduit par avortement d'une ou plusieurs d'entr'elles, mais parfois aussi en surnombre, jusqu'à 12–14; largement ellipsoïdes, à membrane épaisse de 1$\mu$ parsemée de verrues obtuses ou coniques hautes de 0.4–1$\mu$, denses ou clairsemées et d'autant plus robustes qu'elles sont peu nombreuses: 12,3–14,7 × 11,5–13$\mu$ (sans les verrues).

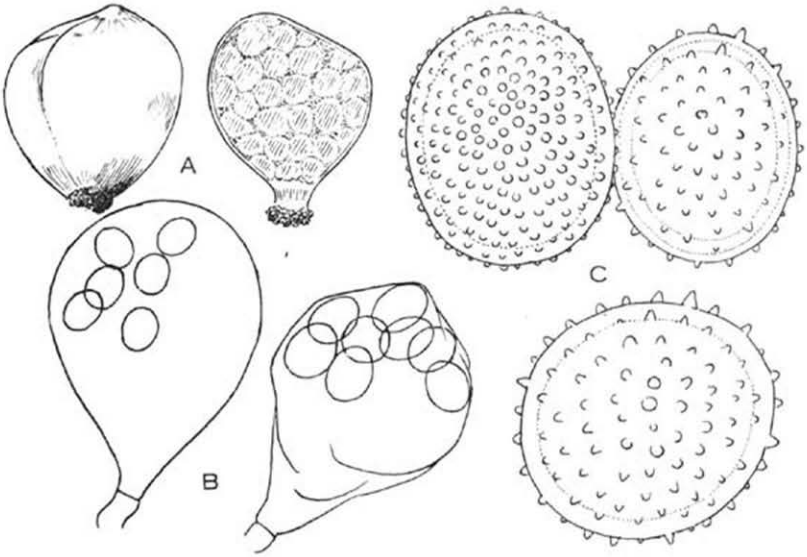


Fig. 3. *Terfezia eremita* Malçn. — A. Deux spécimens en grandeur naturelle, dont l'un coupé verticalement — B. Thèques (× 600). — C. Spores (× 2600).

Cette espèce ne répond à aucune forme décrite. Tout au plus peut-on la situer au voisinage du *Terfezia leptoderma* Tul. (incl. *T. fanfani* Matt.), dont elle reste néanmoins distincte par ses spores moins volumineuses, ellipsoïdes, et ornées de verrues beaucoup plus basses[10].

*Terfezia leonis* Tulasne, 1851.

C'est à beaucoup près le Terfès le plus commun de la zone côtière sableuse du Bassin méditerranéen occidental, où il fournit l'essentiel de la consommation locale de ce type de champignons. Il s'étend même jusqu'au Portugal où Mattirolo (1904) l'a depuis longtemps signalé en Alemtejo et en Estremadure, et où nous-même l'avons observé dans la province méridionale d'Algarve. Cependant nous le connaissons surtout, vivant en symbiose avec les petits Hélianthèmes annuels du type *H. guttatum*, des pâturages sablonneux et des forêts claires de la Meseta marocaine, entre Rabat et Tanger, où il fait au printemps l'objet d'une active recherche pour la vente sur les marchés.

Tubercules de (3)–5–7 cm de diamètre, subglobuleux, cordiformes, bossués, terminés en courte base proéminente ensablée, a péridium lisse, mat, alutacé terreux, passant avec l'âge au brun-roux plus ou moins obscur. Gleba pulpeuse, blanchâtre puis marbrée de rose ocré, finalement vineuse ou brunâtre. Tous ces caractères extérieurs n'étant d'ailleurs guère décisifs à l'égard du *T. claveryi* qui peut revêtir une apparence très similaire.

En fait le *T. leonis* est surtout caractérisé par ses spores sphériques à grosses verrues cylindracées *tronquées au sommet* (celles du *T. boudieri* sont plus petites et arrondies), mesurant de 19 à 23$\mu$ diam. sans les verrues, ou 27–31$\mu$ verrues comprises. Il s'agit d'ailleurs, en ce qui concerne ces verrues, non pas de formations élaborées, mais des craquelures prismatiques d'une épaisse coque périsporique primitivement continue, chaque prisme emportant et conservant à son sommet le fragment de feuillet périsporique qui le recouvrait et lui donne à maturité cet aspect tronqué caractéristique. L'ébullition en acide lactique additionné de Bleu coton colore la masse des verrues en bleu obscur et fait apparaître à leur sommet une petite ampoule presque incolore et vide, qui n'est autre que le fragment de feuillet périsporique en question, apprimé à l'origine, décollé et dilaté sous l'effet du traitement.

L'examen d'un certain nombre de lots nous a montré que la forme, la taille et la densité de répartition de ces verrues sporales variaient dans des proportions souvent notables selon les spécimens et les récoltes. C'est ce qui a conduit naguère à des découpages spécifiques ou infraspécifiques dont la valeur apparaît aujourd'hui discutable. Dans cet ordre d'idées nous pensons que les var. *typica* Maire, *goffartii* (Chatin) Maire, *heterospora* Chatin, *mellerionis* Chatin, admises et citées au Maroc par R. Maire & R. G. Werner (Fungi maroccani N° 77, 1937: 17) ne doivent être

[10] Après comparaison de nos spécimens avec le type du *T. fanfani* Matt., le Dr. J. M. Trappe (Corvallis) nous a confirmé ces différences. Nous le remercions vivement ici de son obligeance.

retenues qu'avec prudence, tant qu'une revision du matériel nord-africain de ces auteurs, s'il existe encore, n'aura pas été effectuée[11].

## TIRMANIA Chatin, 1891

*Tirmania nivea* (Desf. ex Fr.) Trappe, 1971.

*Tuber niveum* Desf. ex Fr., 1823.
*Terfezia ovalispora* Patouillard, 1890. — *Tirmania ovalispora* (Pat.) Pat., 1892.
*Tirmania africana* Chatin, 1892. — *Terfezia africana* (Chat.) Maire, 1916.
*Tirmania camboni* Chatin, 1892.

Un lot de ce *Tirmania* nous a été apporté en avril 1952[12] de la Hamada de la Daoura (Sud marocain, 29° lat. N) par M. Reymond, entomologiste à l'Institut scientifique chérifien.

Selon ce que nous a exposé ce collecteur et que nous ont confirmé les sahariens de la région, le champignon croît complètement épigé et, lors des années favorables où il a plu suffisamment, se montre en colonies parfois nombreuses disséminées sur de larges surfaces.

De l'extérieur, il évoque assez bien un *Bovista gigantea* de moyenne grosseur avec ses fructifications sphériques ou pulvinées de 10 à 25 centimètres de diamètre, d'un beau blanc lacté ou à peine jaunies par l'âge, nues, mates et lisses, fermes-élastiques mais légères eu égard à leur volume, et que fixe au sol une attache basilaire rétrécie. Le péridium n'y atteint pas 1 mm d'épaisseur. Entièrement adné, peu manifeste à la coupe, il limite une immense gleba d'apparence homogène, charnue-spongieuse, blanche ou jaunâtre elle aussi, dépourvue de base stérile distincte et ne montrant que quelques veines ramuleuses subconcolores, peu perceptibles. De structure assez fruste, ce même péridium se ramène à une simple enveloppe péricline épaisse de 500 à 600$\mu$ composée de grosses hyphes cohérentes larges de (5–)10–18$\mu$. En profondeur ces hyphes tombent à 7–10$\mu$ diam., leur cohésion s'altère et l'enveloppe se dissocie en cordonnets partiellement indépendants, vite infléchis, ramifiés et entrecroisés vers l'intérieur du fruit en un réseau assez lâche, entre les mailles duquel apparaissent alors les thèques. Si bien que le péridium apparaît en définitive comme l'extrême surface stérilisée et comprimée du tissu ascogène, et non comme une formation anatomiquement et organiquement autonome.

Thèques octospores, claviformes, ovoïdes ou piriformes à base courte: 80–90 × 35–48$\mu$, *à paroi amyloïde en bleu indigo clair* dans le liquide de Melzer. Spores hyalines, lisses ou sublisses, ellipsoïdes à membrane peu épaissie: 18–20 × 12,5–14,5$\mu$.

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[11] Le Dr. J. M. Trappe qui a examiné les types des *Terfezia* et *Tirmania* a bien voulu nous préciser (*in litt.* 25.03.1968) que le *Terfezia goffartii* était synonyme de *T. olbiensis* Tul., et le *Terfezia deflersii* Chat., cité également au Maroc par R. Maire & R. G. Werner (l. c.), synonyme de *T. boudieri*.

[12] La mention de Chatin (1892: 80, infra) selon laquelle il s'agit, d'après ses collecteurs d'une espèce automnale "se récoltant en octobre", contrairement aux Terfez habituels, ne s'accorde pas avec nos informations. La récolte de M. Reymond en avril 1952, celle antérieure du Dr. Foley en avril 1913 près de Figuig (cf. R. Maire, 1916), et les renseignements que nous avons recueillis au Tafilalelt, établissent que le *T. nivea* (= *ovalispora*) est une plante normalement printanière, liée aux pluies de cette saison. Elle peut toutefois se conserver longtemps sur place à peu près intacte, ce qui explique – ou peut expliquer – certaines récoltes plus tardives.

**Tirmania pinoyi** (Maire) Malençon, *comb. nov.*—Fig. 4.

*Terfezia pinoyi* Maire, 1906: 332 (basionyme).

Nous n'avons vu cette espèce qu'une seule fois, en avril 1939, vendue comme "Terfez blanc du Tafilalelt" sur le marché de Ksar-es-Souk (Sud marocain) où elle avait été apportée des environs de Bou-Bernous, situé plus à l'Est.

Tubercules subglobuleux ou ovalaires atteignant 8 cm de diamètre, charnus, glabres, blanchâtres puis jaunissant ou nuancés de fauve sale avec l'âge ou par altération, paraissant uniquement formés d'une large chair caséeuse un peu rosée, homogène, marbrée de quelques veinules concolores ascendantes et peu visibles. Péridium mal défini, à peine différencié, réduit à un feutrage stérile de la périphérie de la gleba. En coupe radiale il montre une mince zone prosenchymateuse péricline peu tenace, trouée çà et là de grandes lacunes ellipsoïdes, également couchées, qui représentent autant de thèques stériles, étirées et comprimées, vides ou presque vides, enrobées dans le tissu qui les enserre. Mais, dès que l'on s'écarte si peu que ce soit de la périphérie, on les voit devenir plus obèses, se redresser, s'orienter dans différents sens, commencer à former de place en place des ébauches de spores, pendant que le feutrage mycélien relâche son étreinte et se résoud en hyphes ascogènes rampantes et ramifiées. On passe ainsi très vite à la gleba fonctionnelle, qui est une énorme masse uniforme de thèques et de filaments enchevêtrés, au milieu de laquelle il est difficile de découvrir une organisation définie.

Thèques piriformes à bref pédoncule: 90–100 × 50$\mu$, octospores, *à membrane bleuissant par l'iode* (Melzer), surtout quand elles sont flétries. Spores sphériques: 15–19$\mu$ diam., ou brièvement ellipsoïdes: 23,5 × 18$\mu$, renfermant un ou plusieurs globules oléagineux hyalins puis jaune pâle; membrane un peu épaissie, *paraissant* finement chagrinée-réticulée.

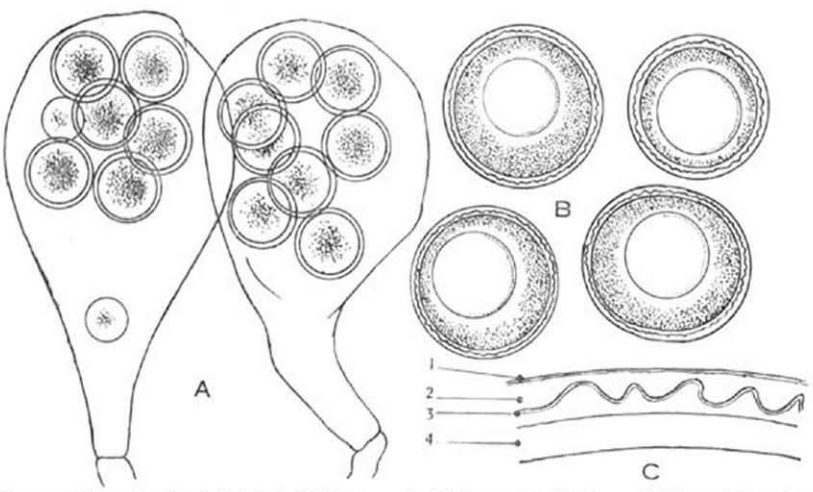


Fig. 4. *Tirmania pinoyi* (Maire) Malçn. — A. Thèques (× 650). — B. Spores figurées en coupe optique pour montrer l'ornementation intratégumentaire (× 1250). — C. Détail très grossi d'une portion de l'enveloppe sporale: 1, feuillet périsporique — 2, coque interpérisporique — 3, membranule plissée formant l'ornementation — 4, épispore.

En réalité, le contour sporal est parfaitement lisse et, malgré des apparences qui laisseraient croire à première vue à une ornementation superficielle, leur rugulosité est intratégumentaire et le demeure jusqu'à la fin. A l'origine, la jeune périspore n'est en effet qu'une coque hyaline et homogène mais, bientôt, une sorte de membranule concentrique, fripée, comme trop grande pour la spore, se différencie *dans son épaisseur*, sous le feuillet périsporique externe, et flotte un moment comme suspendue au-dessus de l'épispore, sur laquelle elle finit par s'appliquer et s'indurer en dessinant les plis enchevêtrés de l'ornementation. Celle-ci est donc et demeure *interne*, et le feuillet périsporique conserve longtemps à la spore sa silhouette circulaire et lisse. C'est seulement chez les éléments âgés qu'il s'affaisse à son tour sur les rugosités intérieures, en provoquant in extremis une irrégularité artificielle de sénescence qui n'a rien de commun avec les verrues, les spinules ou les réseaux des spores de *Terfezia*.

Pas sa chair homogène et ses spores en partie ellipsoïdes et lisses, comme nous venons de le montrer, cette espèce répond beaucoup mieux aux caractéristiques des *Tirmania* qu'à celles des *Terfezia*, et c'est pourquoi nous en faisons un *Tirmania pinoyi*. D'autant qu'elle partage avec le *Tirmania nivea* (= *T. africana*, = *T. ovalispora*), type du genre, la particularité de possèder des thèques à membrane amyloïde, en même temps qu'un péridium fruste, beaucoup plus élémentaire que celui des *Terfezia* authentiques.

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# DIE ARTEN UM RHODOPHYLLUS DYSTHALES (PECK) ROMAGN.

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(Mit drei Abbildungen)

Verschiedene Arten, die in der Literatur mit *Leptonia babingtonii* in Beziehung gebracht worden sind, werden hier aufs neue geprüft.

Dennis, Orton & Hora (1960) haben zu *Leptonia babingtonii* (Blox. apud Berk. & Br.) P. D. Orton folgende Arten als Synonyme gestellt: *Entoloma dysthales* (Peck) Sacc., *Nolanea fumosella* (Wint.) Sacc. und *Inocybe bucknallii* Massee.

Zu *Leptonia strigosissima* (Rea) P. D. Orton stellen sie *Rhodophyllus babingtonii* (Berk. & Br.) Quél. sensu Quélet und Kühner & Romagnesi.

Da jedoch verschiedene meiner Aufsammlungen sowie Typenuntersuchungen zu dieser Auffassung im Widerspruch stehen, möchte ich im folgenden diese Frage eingehender beleuchten. Es handelt sich um folgende Arten, deren Identität bzw. Selbständigkeit zur Diskussion steht:—

*Agaricus* (*Nolanea*) *babingtonii* Blox. apud. Berk. & Br., 1854 (= *A. Nol. Bloxami* Berk.).
*A.* (*Nolanea*) *fulvostrigosus* Berk. & Br., 1878.
*A. dysthales* Peck, 1880.
*A.* (*Nolanea*) *fumosellus* Winter, 1884 (= *A. fumosus* Rabenh., Handb. 504).
*Inocybe bucknallii* Massee, 1905.
*Nolanea strigosissima* Rea, 1905.
*Nolanea hirta* Vel., 1929.
*Nolanea setulosa* Vel., 1939.

Dazu kommt noch die Frage der verschiedenen Interpretation dieser Arten durch neuere Autoren.

Im folgenden seien die wesentlichen Merkmale aus den Originaldiagnosen herausgehoben:—

*babingtonii*: Hut kegelig-glockig, bis 12 mm, grau, seidig, mit dunkelbraunen Faserbüscheln, Lamellen bauchig, entfernt, grau. Stiel zylindrisch, röhrig, mit dunkelbraunen, fast striegeligen Haaren.

*bucknallii*: Hut glockig-konvex, 12–16 mm, bräunlich, faserig, mit einigen Schüppchen. Lamellen dick und ziemlich entfernt, rostbraun, Schneide fein flockig, Stiel schlank, faserig, bräunlich, 2,5–4 cm. Sporen 15–17/8–9 µm, Basidien groß, 70–80/16–18 µm. Auf Erde unter Gebüsch.

*dysthales*: Hut 6–12 mm, leicht kegelig, dann konvex bis ausgebreitet, stumpf, gerieft, schmutzig braun, kleiig oder schuppig. Lamellen breit, leicht entfernt, bauchig, braun, graubraun, Stiel bis 5 cm × 2 mm, filzig, schuppig, bräunlich. Sporen 15–17 × 7–8 µm. Auf feuchter Erde in Wäldern.

*fulvo-strigosus*: Hut kegelig, bis 18 mm, grau, leicht runzelig. Stiel bis 5 cm × 2,5 mm, kleiig-schuppig, Basis rötlich striegelhaarig. Lamellen grau, angeheftet. Sporen 12–13 × 7–9 µm. Auf Erde in Wäldern.

*fumosellus*: Hut 12–13 × 6–7 mm, fast durchscheinend gerieft, rauchgrau mit rötlichem Ton, bisweilen weiß-flockig. Stiel 6 und mehr cm × kaum 1 mm, zart faserig gestreift, dem Hut gleichfarbig, am Grunde weißflockig, steif, knorpelig. Lamellen bis 5 mm breit, fast dreieckig, sehr gedrängt, erst grau, dann rotbraun, mit zart gekerbter, schwärzlicher Schneide. An schattigen Stellen, unter Gesträuch, auf trockenem, schlammigem Boden am Rande von Sümpfen und Teichen.

*hirta*: Hut 5–10 mm, stumpf kegelig, häutig, mit durchscheinenden Lamellen, grau, Scheitel schwarz, abstehend haarig. Stiel 1 mm dick, blaß, flaumig, Basis lang-haarig. Sporen 12–15 µm lang. Auf trockenen, steppigen Kalkböden.

*setulosa*: Hut 10–16 mm, stumpf kegelig, dann konvex, gebuckelt, dunkel grau, Scheitel schwärzlich, gänzlich haarig. Stiel 2–3 × länger als der Hut breit, blaß, durchscheinend, gänzlich kleiig-körnig, oben dunkel. Lamellen entfernt, dicklich, grau, oft anastomosierend. Sporen 15–18 µm. In feuchtem und schattigem Gebüsch.

*strigosissimus*: Hut 4–8 × 3–5 mm, kegelig, rötlichbraun, dicht mit rötlichbraunen, striegeligen Haaren bekleidet, Haare 450–600 × 15–20 µm lang, septiert, Spitze stumpf. Stiel 1,5–2,5 cm × 1 mm, gleichfarbig, dicht mit ähnlichen Haaren bekleidet. Lamellen braun, dann grau, 1 mm breit. Sporen 15–17 × 7–8 µm. Zystiden an der Schneide spindelig oder lanzettlich, 60–70 × 10–12 µm, Scheitel spitz. An altem Kiefernholz.

Die eingangs zitierte Synonymisierung Ortons wurde durch einen Artikel von Dennis (1948) veranlaßt. Dennis hatte den Typus mit der Beschriftung „*A. Babingtonii* Blox. *Ag.* (*Nolanea*) *Bloxami* Rev. A. Bloxam Twycross Nov. 21, 1851" untersucht, diesen aber ganz von Milben zerfressen und von einem dematiaceen-artigen Pilz befallen gefunden. Dennis konnte daran keine Sporen mehr finden. Er untersuchte dann eine zweite Kollektion (Collyweston-Kollektion), die bei Berkeley in Notices 903 erwähnt ist und mit „*Ag. Babingtonii* B., Kings Cliffe, Oct. 2, 1860" beschriftet ist. Diese Kollektion weist Sporen von 16–20 × 8–10 µm auf, sowie ziemlich kurze, angeschwollene Haare auf dem Hut und Stiel (einzelne Zellen bis 25 µm dick), am Stiel etwas länger. Pearson nahm an, daß diese Kollektion *N. fumosella* (Winter) Sacc. (= *N. strigosissima* Rea) entspräche.

Während eines Studienaufenthaltes in England hatte ich 1952 Gelegenheit, den

Typus von *N. babingtonii* (1851) nochmals genauer zu prüfen und nach sorgfältiger Suche war es mir gelungen, an dieser Kollektion doch noch Sporen zu finden, ebenso auch Haare, die eindeutig braun gefärbt sind und genau der Diagnose von Berkeley entsprechen. Daraus geht nun eindeutig hervor, daß die beiden erwähnten Kollektionen von 1851 und 1860 nicht die selbe Pilzart repräsentieren. Während die erste (1851) also als *N. babingtonii* betrachtet werden muß, eine Art die durch braune Haare und kleinere Sporen (9–12 × 6–7 µm) gekennzeichnet ist, stellt die Kollektion von 1860 mit großen Sporen (16–20 × 8–10 µm) und anscheinend farblosen Haaren wohl sicher *N. dysthales* dar.

Im Herbst 1965 konnte ich oberhalb des Kapfensees bei Mels in der Schweiz einen Pilz aus der Gruppe finden, der braune Haare und kleinere Sporen aufwies und meines Erachtens gut mit dem Typus von *N. babingtonii* übereinstimmt, auch wenn die Sporenmaße jene der wenigen Sporen des Typus leicht überschreiten. Ich gebe daher im folgenden eine neue Beschreibung der Art:—

RHODOPHYLLUS BABINGTONII (Blox. apud Berk. & Br.) Quél.

Hut flach gewölbt, 5–6 mm breit, bis 2/3 des Radius durchscheinend gerieft, Scheitel und Riefungen schwarzgrau, sonst etwas heller grau, ziemlich dicht von hell bräunlichen Haaren überkleidet und dadurch faserig-haarig.

Lamellen entfernt, L = 10, l = 1–3, ± gerade angewachsen, grau, Schneide etwas dunkler grau, kaum 1 mm breit.

Stiel 3 cm lang, 0,7 mm dick, heller grau als der Hut, mit hell bräunlichen Haaren ziemlich dicht bekleidet.

MIKROSKOPISCHE MERKMALE: Sporen 10,5–12,5(–13,5) × 6–7(–7,5) µm, meist 5–7(–8) stumpfe Ecken sichtbar (Fig. 1d). Basidien 4-sporig, 38–42 × 10–11 µm. Ohne Cheilozystiden. Haare auf dem Hut in Büscheln, bis über 200 µm lang, mehrfach septiert, nach oben die Glieder immer dicker werdend, basale Glieder 5–6 µm, terminale 9–20 µm dick, stumpf endigend (Fig. $3a_1$, $a_2$). Endglieder bisweilen eiförmig, übrige ± zylindrisch, an den Septen eingeschnürt. Haare vom Stiel dünn. Die Haare des Hutes mit braun inkrustierter Membran, jene des Stieles ebenfalls, jedoch blasser.

STANDORT: Unter Farnen, *Petasites* u.a. Pflanzen auf feuchtem, nassem Boden, Koll. 66/304, oberhalb des Kapfensees ober Mels, Schweiz, 6. 10. 1966.

ANMERKUNG: Meines Wissens ist diese Art seit Bloxam nicht wieder gefunden worden. Die Beschreibung bei Rea ist wohl aus Berkeley & Broome übernommen.

Dieser kleinsporigen, braunhaarigen Art stehen nun die eingangs angeführten Literaturarten gegenüber. Von diesen wird *N. strigosissimus* ebenfalls als braunhaarig aber großsporig, *N. fulvostrigosus* mit rötlich striegelhaariger Basis, die anderen ± großsporig und weißhaarig oder ohne Angabe der Haarfarbe angeführt.

RHODOPHYLLUS DYSTHALES (Peck) Romagn.

Die erste und meines Wissens auch einzige ausführliche Beschreibung unter dem Namen „*Leptonia dysthales* (Peck) Atk." findet sich in einer Arbeit von Humblot (1926: 78–80, Taf. 5 Fig. 2). Diese Beschreibung und Abbildung stimmen gut mit

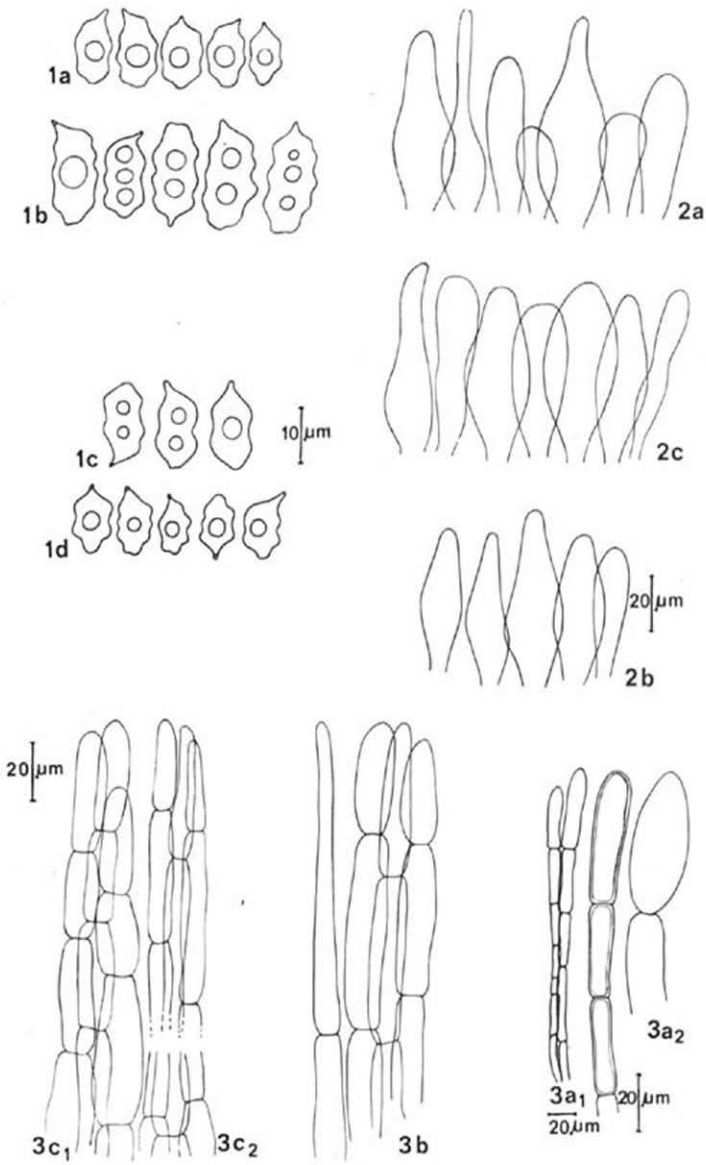


Fig. 1. Sporen von: a. *Rhodophyllus* sp. 66/257. — b. *R. dysthales* 66/24. — c. *R. dysthales* 51/169. — d. *R. babingtonii* 66/304.

Fig. 2. Zystiden von: a. *R. dysthales* 51/169. — b. *R. dysthales* 66/24. — c. *R.* spec. 66/257.

Fig. 3. $a_1$, $a_2$. Haare der Hutoberfläche von *R. babingtonii* 66/304. — b. Haare der Hutoberfläche von *R. dysthales* 66/24. — $c_1$. Haare der Hutoberfläche von *R.* spec. 66/257. — $c_2$. Haare der Stieloberfläche von *Rhodophyllus* spec. 66/257.

jenen der amerikanischen Autoren [Peck, Kauffman (Ag. Mich. 580), Murrill] überein und *R. dysthales* scheint auch in Europa die häufigste Art der Gruppe zu sein. Ich gebe im folgenden eine Beschreibung nach meinen Funden:

Hut 2–6(–7) mm breit, 2–5 mm hoch, glockig, glockig gewölbt, kegelig-glockig, oft auch spitz, hygrophan, dunkel graubraun bis schwarz, dicht wollig-faserig filzig von weißlichen Haaren überkleidet, trocken heller graubraun, feldmausgrau, sepiabraun, manchmal feucht gerieft, meist jedoch feucht nur schwach oder nicht durchscheinend gerieft.

Lamellen dicklich, fast entfernt bis ausgesprochen entfernt, L = 10–14, l = 1–3, abgerundet, gerade oder auch leicht bogig herablaufend angewachsen, 0,5–1(–1,5) mm breit, graubraun, dem Hut ± gleichfarbig, älter mehr grau und durch die Sporen dann etwas rosa bestaubt, Schneide ± gleichfarbig.

Stiel dem Hut gleichfarbig und faserig bis weiszhaarig wollig wie die Hutoberfläche, 1–3 cm lang, 0.5–0,7 mm dick, zylindrisch, gerade oder verbogen. Fleisch graubraun. Geruch unbedeutend oder fast etwas blütenartig (nach Primelblüten).

MIKROSKOPISCHE MERKMALE: Sporen 15–18–20 × 7–9 µm, unregelmäßig stumpf höckerig-eckig, mit 1–3 Öltropfen (Fig. 1b, c), Basidien 40–45(–50) × 11–12,5(–14) µm, Sterigmen kurz. Cheilozystiden flaschenförmig, 50–65(–80) × 15–22(–30) µm oder blasenförmig oder zylindrisch (und dann meist kürzer) (Fig. 2a, b). Haare der Hutoberfläche 12–18(–20) µm dick, septiert, frisch hyalin, im Exsiccat etwas blaß gelbbräunlich werdend, z.T. liegend, Abschnitte 50–80 µm lang, andere mit verjüngten Endgliedern (bis ca. 8 µm dick) und mit bis 150 µm langen Abschnitten. Huthaut aus radiär angeordneten Hyphen von 10–12 µm. Dicke, Pigment braun, die Hyphen inkrustierend.

STANDORT: meist auf nacktem Boden unter Erlen, Buchen, an Wegböschungen an feuchteren Standorten. Koll. 51/169, Issanger. Halltal, Tirol, 66/24, Ellbachtal, Tirol.

ANMERKUNG: Wohl als sicher identisch mit *R. dysthales* müssen *Inocybe bucknallii* Massee und *Nolanea nodospora* Atk. angesehen werden. Sehr wahrscheinlich ist auch *Nolanea setulosa* Vel. synonym.

Die von Romagnesi beschriebene var. *homomorphus* von *Rhodophyllus fumosellus* (Wint.) J. E. Lange dürfte nach dem unten gesagten wohl auch eher in die Verwandtschaft von *R. dysthales* gehören.

## RHODOPHYLLUS FUMOSELLUS (Wint.) J. E. Lange

Unter diesem Namen findet sich in der neueren Literatur nur die Beschreibung von J. E. Lange, wenn man von jener bei Pilát absieht, die sich sicher auf *R. strigosissimus* bezieht. Bei dem Pilz Langes fällt die Entscheidung schwer, ob es sich um eine selbständige Art handelt oder ob sie zu *R. dysthales* gehört. Langes Pilz scheint insgesamt mehr ins Braune gehende Farbtöne aufzuweisen. Dies besagt aber nicht sehr viel, da man nicht weiß bei welchem Feuchtigkeitszustand des Bodens, der Luft, der Fruchtkörper etc. die Beschreibung abgefaßt und das Bild gemalt wurde.

Andererseits scheint es mir mehr und mehr sicher, daß Langes Pilz nicht jenem von Winter entsprechen kann. Es sind vor allem zwei Merkmale, die mir dafür ausschlaggebend erscheinen. Winter (1883: 853) schreibt: „... Lamellen ge-

schweiftherablaufend, locker angewachsen, bis 5 mm breit, fast dreieckig, sehr gedrängt, ... mit zart gekerbter, schwärzlicher Schneide." Leider sagt Winter nichts über die Sporen aus und der Typus scheint nicht zu existieren. Die sehr breiten und gedrängt stehenden Lamellen und die schwärzliche Schneide sind Merkmale, die sonst bei keiner Art dieser Gruppe zu beobachten sind, die so bezeichnend sind, daß ich sie nicht als geringe Abweichungen betrachten kann, wie dies Lange tut.

Ich bin also nunmehr der Meinung, daß *R. fumosellus* im Sinne Langes mit *R. dysthales* identisch sein könnte. Auch eine Synonymie mit *R. strigosissimus*, wie Horak (1968: 500) meint, ist nicht ausgeschlossen. Hingegen ist wohl *A.* (*Nolanea*) *fumosellus* Winter eine davon sicher verschiedene, derzeit verschollene Art.

### RHODOPHYLLUS STRIGOSISSIMUS (Rea) Horak

Diese Art ist, ähnlich wie *R. babingtonii*, durch schon im frischen Zustand braune Haare, zugleich aber durch größere Sporen gut festgelegt. Von neueren Beschreibungen bezieht sich eindeutig die von Pilát (1953: 58) unter dem Namen „*Pouzaromyces fumosellus* (Wint.) n.c." gegebene auf diese Art.

Der Reasche Typus ebenso wie die Kollektion von Pilát wuchsen auf moderigem Holz (vermutlich *Pinus silvestris*?) Nach Pilát und Horak (1968: 500) seien hier die mikroskopischen Merkmale herausgehoben:—

Sporen 14–19 × 8–9 µm, Cheilozystiden zylindrisch-spindelig 60–150 × 10–22 µm oder birnförmig, 45–55 × 20–30 µm, Haare am Hut 300–700 µm lang, basal 4,5–15 µm dick, in ein brennhaarförmiges Ende auslaufend. Haare des Stieles bis 700 µm lang, basal bis 15, an der Spitze 4,5–6 µm dick, purpur- bis rost-braun (Abbildungen siehe bei Pilát und Horak).

Bemerkenswert ist auch die Angabe, daß der Stiel elastisch, fest und nicht gebrechlich ist, ein weiteres Merkmal, das die Art von den anderen Vertretern der Gruppe unterscheidet.

### RHODOPHYLLUS sp.

(oder Varietät von *R. dysthales*?)

*Nolanea hirta* Vel. (1929: 28)??
*Nolanea dysthales* sensu Nathorst-Windahl (1945: 142).

Hier möchte ich noch auf eine gegenwärtig nicht genügend geklärte Form hinweisen. Bei der Aufsammlung im Feld (wobei mehrere Dutzend Fruchtkörper gesammelt wurden), wurde die Art für *R. dysthales* gehalten und daher keine weiteren Notizen gemacht. Bei der mikroskopischen Prüfung erwiesen sich die Sporen jedoch erheblich und konstant kleiner. Ein Versuch, die Art im darauffolgenden Jahr am selben Standort nochmals zu finden, schlug fehl. Sie ist makroskopisch in Farbe und

Form und hinsichtlich des weißlichen Haarbesatzes von Hut und Stiel dem *R. dysthales* sehr ähnlich. Es seien im folgenden daher nur die mikroskopischen Daten gegeben:—

Sporen 10,5–13(–14) × (6,5–)7–8 μm. (Fig. 1a). Basidien 4-sporig, 40–45 × 12 μm Cheilozystiden blasenförmig bis breit spindelig, dazwischen keulige Elemente, 45–65 × (10–)14–30 μm (Fig. 2c). Lamellentrama dickhyphig, Hyphen 14–18 μm, von braunem Pigment inkrustiert. Haare der Hutoberfläche aus Büscheln von 10–18 μm dicken Hyphen bestehend, relativ kurzgliedrig, frisch hyalin, am Exsiccat in KOH blaß bräunlich (Fig. $3c_1$). Hyphen der Huthaut braun inkrustiert. Haare der Stieloberfläche dünner (7–9 μm) und langgliedriger (Abschnitte bisweilen über 100 μm lang), Basalglieder dicker bis 14 μm und mehr (Fig. $3c_2$), in KOH blaß bräunlich, frisch hyalin.

STANDORT: Unter *Alnus* auf Erde, zahlreich, oberhalb Göltschach, Sattnitz, Kärnten Koll. 66/257, 26.9.1966.

Ziemlich sicher gehören hierher auch die beiden von Nathorst-Windahl (1945: 142) unter dem Namen *N. dysthales* (Peck) Atk. zitierten Funde mit Sporen von 12–15 × 6,5–7,5 und 11–12 × 5,5–6,5 μm. Hingegen könnte die dort auch zitierte Aufsammlung von H. Svensson aus dem Gebiet von Karlstad mit Sporen von 9–10 × 6–7 μm eventuell zu *R. babingtonii* gehören. Leider ist über die Färbung oder Pigmentierung der Haare sowie über Zystidenverhältnisse nichts angegeben.

Es erscheint nicht ganz ausgeschlossen, daß es sich dabei um *N. hirta* Vel. handeln könnte, für die Velenovsky Sporen von 12–15 μm Länge angibt. Was dabei etwas stört, sind die Standortsangaben.

### NOLANEA FULVO-STRIGOSA (Berk. & Br.) Sacc.

Diese Art dürfte den oben besprochenen Arten zwar nahe stehen, jedoch nicht in deren allernächste Verwandtschaft gehören.

Dennis, Orton & Hora (1960: 104) stellen dazu als Synonyme: *R. dysthales* (Peck) Romagn. sensu Favre (1948) und *R. araneosus* (Quél.) Quél. sensu Kühner & Romagnesi (1953). Diese Synonymie scheint uns einer nochmaligen genaueren Überprüfung zu bedürfen und ich beabsichtige, auf diese Art in einem späteren Artikel eingehender zurückzukommen.

Zusammenfassend ergibt sich also folgendes Bild:—

A. Haare im frischen Zustand braun:

1. Sporen 9–11(–13,5) × 6–7 μm . . . . . *Rhodophyllus babingtonii* (Blox. apud Berk. & Br.) Quél. (R. *dysthales*, Kollektion Svensson; Nathorst-Windahl 1945?)

2. Sporen 14–19 × 8–9 μm . . . . . *Rhodophyllus strigosissimus* (Rea) Horak [*Pouzaromyces fumosellus* (Wint.) Pilát, 1953; *Rhodophyllus babingtonii* sensu Quél., Kühn. & Romagn. ??; *Rhodophyllus fumosellus* (Wint.) sensu J. E. Lange?]

B. Haare im frischen Zustand hyalin, weiß.

3. Sporen 15–20 × 7–9 μm . . . . . *Rhodophyllus dysthales* (Peck) Romagn. [*Inocybe bucknallii* Massee; *Naucoria setulosa* Vel.; *Naucoria nodospora* Atk.; *Rhodophyllus fumosellus* (Wint.) sensu J. E. Lange?]

4. Sporen 10,5–13(–14) × (6,5–)7–8 μm . . . . . *Rhodophyllus* sp. (oder Varietät von *dysthales*?; *Rhodophyllus dysthales* sensu Nathorst-Windahl, 1945; *Naucoria hirta* Velenovský ??)

Ungeklärt: *Agaricus* (*Nolanea*) *fumosellus* Winter.

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# SPORE ORNAMENTATION IN RAMARIA AS DEPICTED BY SCANNING ELECTRON MICROGRAPHS[1]

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(With Plates 24–26)

Scanning electron micrographs of *Ramaria* spores show three distinct ornamentation patterns: (1) spiny ornamentation; (2) raised patches or warts; and (3) longitudinally or obliquely oriented ridges. These observations fully support none of the provious taxonomic schemes at the subgeneric level, and some nomenclatural adjustments are recommended.

Although a number of papers have illustrated basidiospores with scanning electron micrographs, only one has shown a spore of *Ramaria* (Perreau & Heim, 1969). Bigelow & Rowley (1968) and Grand & Moore (1970) offered photos of spores of *Gomphus floccosus*, which recent authors have placed in the Gomphaceae with *Ramaria*, and Pegler & Young (1971) have shown spores of *Gymnopilus* and *Hebeloma*, which Petersen (1968) conjectured as perhaps related to the Gomphaceae.

Corner (1970) described three subgenera within *Ramaria*. Subgenus *Echinoramaria* was based on spiny spore ornamentation, while subgenera *Lentoramaria* and *Ramaria* were characterized by a combination of habit, hyphal construction of the fruit body, and spore ornamentation. Although for any student of the genus these designations were obvious and clear, such groupings were really based on experience, with the characters hardly definitive or empirically measurable. Similarly, Petersen (1967) suggested four subgeneric complexes, also based on character combinations, and that scheme was of dubious usefulness. In order to clarify some emerging concepts of subgeneric classification, spores of representative species of *Ramaria* were examined under the scanning electron microscope to corroborate data already gathered in observations with bright field and phase contrast microscopy with the aid of cotton blue staining (Petersen, 1967, 1971a, b, c).

Spores for examination were obtained from spore prints from specimens in herb. TENN. Spore prints on glass or wax-impregnated paper were found preferable to those on paper. Spores were transferred directly to double-faced cellophane tape which had been mounted on standard 3/4 inch aluminum studs, and then coated with vaporized carbon and gold in vacuo using a Denton vacuum coater equipped with a random rotating head. The spores were viewed on an AMR model 900

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scanning electron microscope and photographed with a Polaroid Land camera.

Using these methods, three clearly discernable subgeneric groups may be identified on spore ornamentation characters as follows:

COMPLEX 1.—*Ramaria grandis* (Pk.) Corner was chosen to represent the echinulate-spored group because spore ornamentation is gross in this species and good spore prints were readily available. Line drawings of such spores [Coker, 1923; Corner, 1950 under *R. zippelii* (Lév.) Corner] had already shown the spiny ornamentation but subsequently Petersen (1967) illustrated spores stained in cotton blue, in which the ornamentational spines stained much more strongly than the interspine areas.

Scanning electron micrographs of such spores (Pl. 24 Figs. 1–3) completely corroborate the data gathered with cotton blue and bright field microscopy. Not only are some spines longer than others, but some are partially joined by low, raised isthmuses. The spines (Fig. 3) are seen as extensions of the spore surface, rather than protrusions through an outer layer as suggested for *Clavulinopsis helvola* (Pers. per Fr.) Corner. The apiculus, marked in the figures, seems accompanied by a collar-like neck, but this feature is obscure, as it also is with the light microscope. Likewise the type of apiculus as categorized by Pegler & Young (1971) remains unknown.

Although such spores are obviously different from those described below, additional representatives of this group must be observed, especially those with smaller, more delicate spore ornamentation, for instance *R. ochraceo-virens* (Jungh.) Donk.

COMPLEX 2.—A spore of *Ramaria subbotrytis* (Coker) Corner is illustrated (Pl. 25 Figs. 4, 5). Spore ornamentation consists of raised patches or warts on the spore surface, either discrete or somewhat meandering. In cotton blue, it is these raised patches which stain most strongly, as evidenced by comparison of the photo with line drawings of stained spores with similar ornamentationl patterns (see Petersen, 1967, 1971a). Based on such comparisons, it would appear that high magnification (2500 × or higher) and cotton blue staining reveal all of the ornamentation seen under higher magnification by scanning electron microscope examination.

Perreau & Heim (1969) illustrated a spore of *R. stricta* (Pers. per Fr.) Quél. as seen through the SEM, and the ornamentational pattern was very similar to that of *R. subbotrytis*. This is supported by observations with the light microscope. Such similarities detract from definitive or diagnostic differences between Corner's 1970) subgenera *Lentoramaria* and *Ramaria*, but also mitigate against resurrection of the name *Clavariella* Karsten, based on *C. apiculata* (Fr.) Karsten ast ype, as suggested by Petersen (1971b).

Only one confusing variation of this ornamentational pattern has been observed. In some species [i.e. *R. xanthosperma* (Pk.) Corner] the raised pattern takes the form of irregular ridges often oriented longitudinally or obliquely on the spore. Such patterns superficially resemble the striate appearance described below. Care in observations, however, readily reveals the true ornamentation type.

COMPLEX 3.—As the type species of *Ramaria*, *R. botrytis* (Pers. per Fr.) Bourd.

Pl. 26 (Figs. 6–8) was chosen as representative of the "striate spored" complex. Line drawings and descriptions (Coker, 1923; Corner, 1950) had suggested such ornamentation, but later drawings (Petersen, 1967; Marr, 1968) showed the pattern more clearly under cotton blue staining. All drawings, even with stain, had indicated that the stained areas (not nearly as cyanophilous as in the preceding complexes) were raised, perhaps as folds of a thin outer spore wall. When such drawings are compared with SEM images, however, it is clear that the areas which stain with cotton blue are not raised, but are the narrower, attenuate, sometimes reticulate sunken areas between the longitudinally or obliquely arranged raised striae. This is in contrast to the situation described in complex 2 above, where the raised ornamentational patches stain more strongly than the lower spore surfaces. Although additional spores must be examined, such a discrepancy indicates that a wider separation between complexes 2 and 3 may be warranted. In such an event, complex 2, hitherto grouped under subgenus *Ramaria* by Corner (1970), would require a new name. Thus far, the only name available is "Laeticolores Marr" (1968), but this name has not been validly published.

Figure 8 shows the abaxial spore surface in *R. botrytis*, on which the obliquely oriented ridges diverge downward adaxially. Such a divergent pattern is also observable under the light microscope with cotton blue stain.

Such "ground truth" gained under the SEM thus far substantially corroborates the observations already made with the light microscope. Several tentative conclusions seem more evident: (1) subgenus *Echinoramaria* seems well founded, and with further investigations may require generic rank (in which case the unfortunate name *Phaeoclavulina* Brinkmann is available); (2) little distinction may be made between subgenus *Lentoramaria* and subgenus *Ramaria* sensu Corner, and further attempts to ease the taxonomy of this interface must be made; and (3) separation of subgenus *Ramaria* sensu Petersen (striate-spored species) from "Laeticolores Marr" nom. inval. seems obvious on spore ornamentation and staining patterns.

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## EXPANATION OF PLATES 24-26

### PLATE 24

Figs. 1–3. *Ramaria grandis* (Pk.) Corner, TENN 36164. figs. 1, 2: × 5000; 3: × 10,000.

### PLATE 25

Figs. 4, 5. *Ramaria subbotrytis* (Coker) Corner, TENN 31279. Fig. 4: × 5000; 5: × 10,000.

### PLATE 26

Figs. 6–8. *Ramaria botrytis* (Pers. per Fr.) Bourd., TENN 31138. Figs. 6, 8: × 5000; 7: × 10,000.

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# NEW OR INTERESTING RECORDS OF BRITISH HYMENOMYCETES—V

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(With five Text-figures)

In this paper the new species *Myxarium crystallinum* is described and its relationships with *Tremella grilletii* and *Sebacina sphaerospora* discussed. The two latter species are transferred to the genus *Myxarium* Wallr. An account of a third British gathering of *Tremiscus helvelloides* is given, together with a detailed review of its world-wide distribution, since it is one of the species included in the European Mapping Scheme for fungi.

## A NEW SPECIES OF MYXARIUM WALLR.

**Myxarium crystallinum** Reid, *sp. nov.*—Figs. 4a, b

Sporophora oculo nudo tenuia, caesio-cinerea ad instar *Corticii*, 4.5 cm longa, 1.5 cm lata; oculo armato pustularum minimarum, turbinatarum gelatinosarum, nitentium, dense confertarum efformata. Pustulae 120–150 $\mu$ altae, 100–200 $\mu$ latae, ad substratum anguste affixae et in vivo discretae, saccharo-crystallis similis; in sicco coalescentes et reticulum irregulare efformantes. Hyphae indistinctae, angustae, gelatinisatae, fibulatae, muris tenuibus praeditae. Dikaryophyses non visae. Basidia myxarioidea, bispora. Probasidia ad 25 $\mu$ longa, apice 7–8 $\mu$ lata, et septo basali fibulato provisa. Sporae ellipticae vel late ellipticae 6.0–7.75 × 4.2–4.75 $\mu$ vel globosae vel subglobosae, 4.75–5.2 $\mu$. On very rotten stump, possibly *Alnus*, Vann Lake, Ockley, Surrey, coll. Dr. Petch (TYPUS).

*Fructifications* appearing to the naked eye as a thin, resupinate, corticioid, blue-grey film, covering an area 4.5 × 1.5 cm, but under a lens this can be seen to consist of myriads of minute, densely crowded, glistening, gelatinous, turbinate pustules, 120–150 $\mu$ high and 100–200 $\mu$ wide, each with a narrow point of attachment. These pustules, which resemble tiny grains of sugar, remain discrete even when in close contact, at least until dried, whereupon they coalesce to form an irregular reticulum (sub lente). Each consists of an erect spreading fascicle of rather indistinct, thin-walled, narrow, gelatinized, clamp-bearing hyphae, with scattered basidia in the apical portion. *Dikaryophyses* not preserved. *Basidia* myxarioid, 2-spored. The basidial initials, up to 25 $\mu$ long, are at first club-shaped, with a basal clamp-connexion; the enlarged apical portion 7–8 $\mu$ wide, becomes divided into two by a longitudinal septum and is cut off from an enucleate (?) stalk-cell, 15–18 $\mu$ long and 1.2 $\mu$ wide, without clamp formation. *Spores* varying in shape from elliptical or broadly elliptical, 6.0–7.75 × 4.2–4.75 $\mu$, to more or less globose, 4.75–5.2 $\mu$, with a small apiculus, and germinating by repetition.

HABITAT: on very rotten stump, possibly *Alnus*, Vann Lake, Ockley, Surrey, coll. Dr. Petch, Oct. 1972 (TYPE).

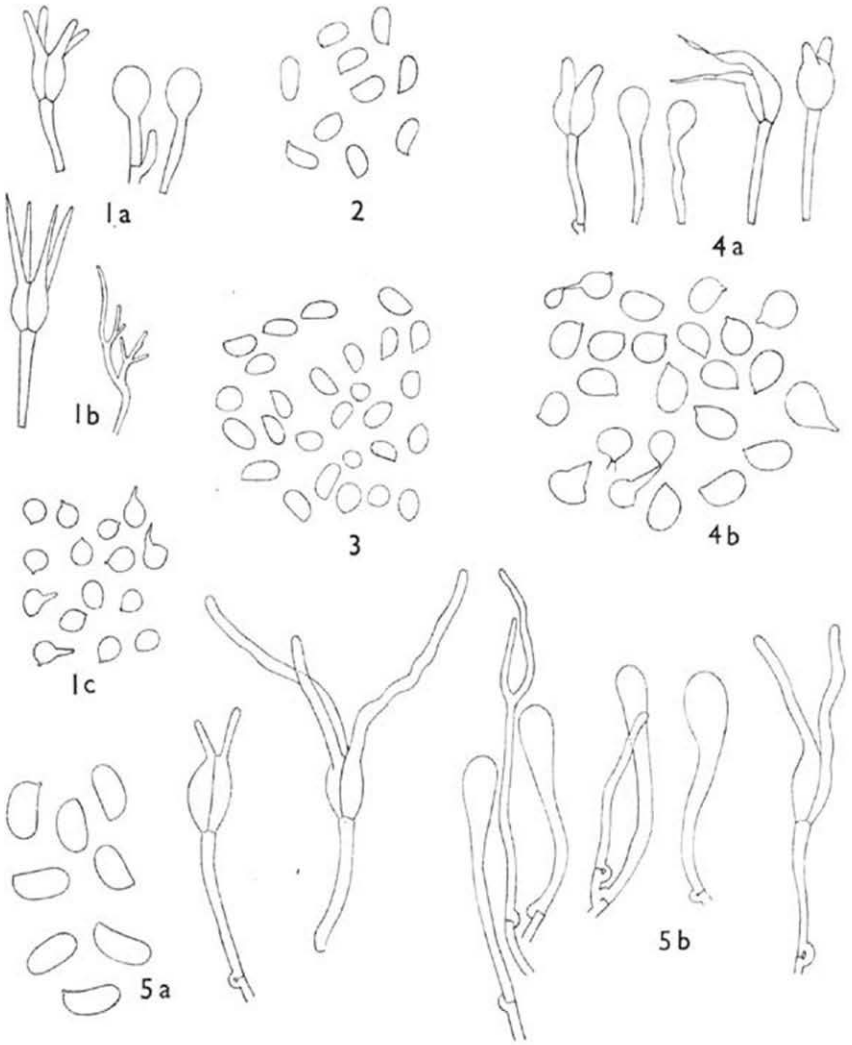


Fig. 1. *Sebacina sphaerospora*. — a. Two mature basidia and two probasidia. — b. Dikaryophysis. — c. Spores (Galzin No. 16069, K).
Fig. 2. *Tremella glacialis* Spores (Galzin No. 18518, K).
Fig. 3. *Stypella minor*. Spores (Rogers No. 335, K).
Fig. 4. *Myxarium crystallinum*. — a. Basidia and probasidia. — b. Spores (Type).
Fig. 5. *Tremiscus helvelloides*. — a. Spores. — b. Basidia, probasidia, and dikaryophyses (Bircher Common, Aug.-Oct. 1971). (All approx. × 570).

There is possibly an existing record of this fungus in the literature from Denmark under the name *Sebacina sphaerospora* Bourd. & Galz. (Christiansen, 1959).

*Myxarium crystallinum* belongs with a group of species which Donk (1966) included as "species incertae sedis" at the end of the genus *Tremella* Pers. ex St-Amans. These species were listed by Donk under "Microtremella" but he noted that this denomination "must be seen as that of a term rather than a name: it makes it possible to designate a group of tremellaceous fungi of a certain particular habit but no more; it does not even imply that all its members are known to possess sphaero-pedunculate basidia." The species involved are *T. albescens* (Sacc. & Malbr. apud Sacc.) Sacc., *T. coriaria* Bres. apud Strass., *T. fusispora* Bourd. & Galz., *T. grilletii* Bourd., *T. rosea* Höhn., *Sebacina sphaerospora* Bourd. & Galz., and *T. translucens* Gordon. Of these species *T. coriaria* was said to have spores "obovatis, saepe uno latere depressis, 12–15 × 8–10 $\mu$" while those of *T. fusispora* were described as "fusiform, 12–21 × 5–8 $\mu$", those of *T. rosea* as "ovata vel subsphaeroidea, 8–9 $\mu$ crassa" and those of *T. translucens* as "ellipsoideis, basi oblique apiculatis, 7.1–11.8 × 3.7–6.2 $\mu$, plerumque 9 × 5 $\mu$." From these data it is clear that these species may be readily distinguished from *M. crystallinum* in having larger and often differently shaped spores. The original material of *T. albescens* lacked spores. This leaves *T. grilletii* and *S. sphaerospora* for more detailed consideration since they would seem to be most closely related to *M. crystallinum*.

From the original diagnosis of *T. grilletii* it is clear that there is little to separate it macroscopically from *M. crystallinum*, but the spores were said to be "oblongues un peu courbes, obtuses et arrondies à l'extrémité, obliquement apiculées à la base, qui est un peu moins large . . . Leur longueur est de $0^{mm}$, 008 à 10 sur $0^{mm}$, 003 à 5 de largeur." This was later modified by Bourdot & Galzin (1928) to read "spores oblongues subcylindriques un peu déprimées ou arquées, 6 – 10 × 3 – 5 $\mu$." Indeed in his original article Bourdot figured the spores as subcylindric or elliptic varying to allantoid. It is now customary to regard *T. glacialis* Bourd. & Galz. and *T. minutissima* Höhn. as synonyms of *T. grilletii*, and I have been able to examine an authentic collection of the former in K (Champignons de l'Aveyron, on *Populus*, Bordeaux, leg. Galzin No. 18518, Oct. 1915). This consists of minute, crowded, gelatinous sugar-like pustules exactly as in *M. crystallinum* but with elliptical to broadly elliptical spores, 5.75–7.5 × (2.2–) 3.0–3.75 $\mu$ (Fig. 2). This compares with Bourdot & Galzin's observations in which the spores were originally described as "oblongae, base acutae, saepe lateraliter subdepressae, 5–8 × 3–5 $\mu$." Later they added that the spores were "souvent un peu déprimées latéralement" and they figured them with much the same shape as those of *T. grilletii*. On available evidence it therefore seems justifiable to relegate *T. glacialis* to synonymy under *T. grilletii*. However, the spores are smaller and proportionally more elongate than those of *M. crystallinum*.

The second species, *S. sphaerospora*, was originally described by Bourdot & Galzin (1924) as "indeterminata, ceraceo-gelatinosa, granuloso-tuberculosa, subplicata, opaleo-fuscescens, denum mucosa, sicco evanescens v. rufescens, haud nitens." There

is no suggestion that the fructification originates as tiny, discrete pustules and this is one of the reasons which no doubt led Bourdot & Galzin to describe the species in *Sebacina*. Indeed in an authentic collection in K (Champignons de l'Aveyron, Bourdot No. 14094, on *Alnus*, Lubotis, leg. Galzin No. 16069, Sept. 1914) the fructification consists of a thin, continuous, smooth, gelatinous film, up to 180 $\mu$ thick. In section this can be seen to comprise a narrow basal layer of indistinct, horizontal, thin-walled, clamp-bearing hyphae, from which other hyphae curve upward to form the bulk of the tissue. It should be noted in contrast that Wells (1961) who had also studied two authentic specimens of this species found that these and other collections so named in the Mycological Herbarium at the State University of Iowa "all show a tuberculate structure in cross section, at least in certain portions of the fructifications. There is present in each specimen a basal layer . . .." It is not altogether clear from this whether the tuberculate structure referred to was merely a surface irregularity or whether a tubercular or pustular origin was to be inferred—the mention of a basal layer of horizontal hyphae is evidence against the latter possibility. To return to the Bourdot collection in K (see Fig. 1a–c), this was found to have branched dikaryophyses and 4-spored, myxarioid basidia; the probasidia measured 17—20 $\mu$, and although no basal clamp-connexions were seen they were presumably present since clamps were demonstrated on the vegetative hyphae. The apical region of the mature basidium measured 8.0–10.2 × 5.0–6.5 $\mu$ and the enucleate (?) stalk cell about 12.75 $\mu$. Spores were abundant, 3.5–4.75 $\mu$. and were almost uniformly globose, many having germinated by repetition (Bourdot & Galzin gave the spore size as 4–6 × 3.5–5.5 $\mu$). From this it would seem that *S. sphaerospora* differs from *M. crystallinum* in forming a continuous gelatinous film with a distinct, if narrow, basal layer, and also in having 4-spored basidia and small spherical spores.

A complication in regard to the interpretation of *S. sphaerospora* is that Wells gave it as his opinion that this species merely represented the nearly confluent phase of *Stypella minor* Moll. sensu Martin and in this he was followed by Donk (l.c.) who argued that Martin's (1934) interpretation of *S. minor* was unlikely to have been that of the original author. An Iowa collection in K of *S. minor* (on aspen bark, Turkey Creek, Johnson Co., coll. D. P. Rogers, No. 335, 28 Oct. 1933) which clearly consisted of minute, discrete pustules when fresh, bears abundant spores of somewhat variable shape ranging from elliptical, broadly elliptical or ovate, 4.5–6.2 × 2.75–3.5 $\mu$, to occasionally globose 3–4 $\mu$ (Fig. 3). The evidence from this collection of a large preponderance of elliptical spores, together with Martin's illustration of similarly shaped spores from material he referred to *S. minor* suggests that *S. minor* sensu Martin might well be more appropriately listed in synonymy under *T. grilletii* than under *Sebacina sphaerospora*. In contrast *T. gangliformis* Linder, commonly regarded as based on *Stypella minor* sensu Martin, although having a pustular origin, was said to produce spores which were "subglobose to ovoid and obliquely apiculate 4–5 × 5.5–6 $\mu$." Unfortunately no material of this species was available for study and until the spore shape is checked one cannot feel alto-

gether confident in placing it in synonymy along with *S. minor* sensu Martin under *T. grilletii* or on account of its pustular origin with *Sebacina sphaerospora.*

From the foregoing study of *T. grilletii* and *S. sphaerospora* it is clearly inappropriate to retain them in the genus *Tremella* on account of their having myxarioid basidia—a feature not shown by members of the genus *Tremella* sensu stricto. They are in my opinion better assigned to the genus *Myxarium* Wallr. and the transfers are accordingly made as follows:—

**Myxarium grilletii** (Bourd.) Reid, *comb. nov.* (basionym: *Tremella grilletii* Bourd. *in* Bull. Soc. bot. Fr. **32**: 284. 1885).

**Myxarium sphaerosporum** (Bourd. & Galz.) Reid, *comb. nov.* (basionym: *Sebacina sphaerospora* Bourd. & Galz. *in* Bull. trimest. Soc. mycol. Fr. **39**: 263. 1924).

## An account of Tremiscus helvelloides from Shropshire

### Tremiscus helvelloides (DC. ex Pers.) Donk — Figs. 5a, b

*Tremella helvelloides* DC., Fl. franç,. Ed. 3, **2**: 93. 1805 (devalidated name); *Tremella helvelloides* DC. *ex* Pers., Mycol. eur. **1**: 100. 1822. – *Guepinia helvelloides* (DC. ex Pers.) Fr., Epicr. Syst. mycol. 566. 1828. – *Gyrocephalus helvelloides* (DC. ex Pers.) Keissl. *in* Beih. bot. Zbl. **31**: 461. 1914. — *Phlogiotis helvelloides* (DC. ex Pers.) Martin *in* Am. J. Bot. **23**: 628. 1936. – *Tremiscus helvelloides* (DC. ex Pers.) Donk *in* Taxon **7**: 164. 1958.

*Tremella rufa* Jacq., Misc. austr. **1**: 143. 1778 (devalidated name); *Tremella rufa* Jacq. *ex* Pers., Mycol. eur. **1**: 103. 1822. — *Guepinia rufa* (Jacq. ex Pers.) Quél., Ench. Fung. 202. 1886. – *Gyrocephalus rufus* (Jacq. ex Pers.) Bref., Unters. Gesammtgeb. Mykol. **7**: 131. 1888.

*Gyrocephalus juratensis* Pers. *in* Mém. Soc. linn. Paris **3**: 77. 1825.

*Fruitbodies* caespitose in a cluster of about 12 sporophores, each 3–8 cm high, basically erect, stipitate, spathulate, with a flattened pileate margin, the sides of the stalk enrolled to give a pseudoinfundibuliform structure slit down one side almost to the base and somewhat resembling the apothecia of *Otidea* spp. The fructifications are reddish-fawn, of firm gelatinous texture with creamy-buff outer surface. The flesh is creamy-buff, translucent, up to 3 mm thick, and consists of narrow, branched, clamp-bearing hyphae, up to 2.5 $\mu$ wide, lacking well-defined walls and lying more or less parallel in a gelatinous matrix. There is no distinctly differentiated cuticle on the upper (inner) side. Hymenium, up to 100 $\mu$ thick, is inferior and consists of a dense mass of dikaryophyses and scattered basidia. *Dikaryophyses* 1.5–2.0 $\mu$ wide, originate from a clamp-bearing septum, and are mostly simple, although sometimes branched toward the apex. *Basidia* myxarioid, originating as elongate-clavate structures, 36–40 $\mu$ long, 4.5–7.2 $\mu$ wide at the apex, but tapering to a long narrow base only 1.75–2.0 $\mu$ wide, and terminating at a clamp-bearing septum. Eventually the apical portion swells and becomes more or less globular or ovate and is cut off from an elongate, enucleate (?) stalk cell, 22–25 $\mu$ in length. The swollen apical portion, which lacks a clamp-connexion, measures 11.2–13.0 × 7.2–8.0 $\mu$, and soon becomes divided by a longitudinal septum, each half then gives rise to an elongated sterigma. The basidia are mostly 2-spored but a very occasional 3-spored basidium was seen. *Spores* 8.75–11.2 × (4–)4.75–5.0 $\mu$, varying from elliptical or elongate-elliptical, to slightly allantoid. Germination not observed.

HABITAT: Growing in a line 4 feet long on sawdust, Bircher Common, Herefordshire, coll. E. Blackwell, Aug.–Oct. 1972.

The occurrence of this fungus in the West of England is remarkable since it is typically a mountain species of coniferous forests. There are two previous records from the British Isles; the first, by Cooke (1891) but without locality, and the second by Crossland (1914) from Sandsend, Yorkshire, but unfortunately no specimens appear to have been kept.

In Europe it is known from the Pyrenees in the West: SPAIN: Prades, Castellfullit (Maire, 1935); Salardu (Singer, 1947); without locality (Bertaux, 1964) and FRANCE: Haute Garonne: Joueou (Boidin, 1957b). Romagnesi (1967) also observed that it is "pas rare en été et en automne dans l'humus ou les mousses des pâturages humides et des bois de conifères, mais presque uniquement en montagne, ou du moins dans l'est de la France"—there are records as follows, Moselle: Metz (Anon., 1965a). Vosges: St. Die (Anon., 1966). Jura: (Quélet, 1872). Saône-et-Loire: Château d'Arlay (Bigeard & Jacquin, 1898), de Changey près Saizy (Gillot & Lucand, 1891). Ain: Outriaz (Maublanc, 1949). Isère: Grande Chartreuse (Tulasne, 1872, Maublanc, 1949). Loire: (Jimmy-Sibert, 1971). Lyon Region: (Maublanc, 1924; Anon., 1965b). Haute Savoie: (Boidin, 1957a). Savoie: Aix les Bains (Malençon, 1959; Maublanc, 1938). Haute Alpes: Briançon (Remy, 1965). In addition there are collections in K from Jura: Desmazières- Plantes Cryptogames de France, Series II, 1853–1860, No. 661. Isère: St. Pierre de Chartreuse, coll. N.Y. Sandwith, 6 Oct. 1949; Dauphiné Mts. Lyon Foray, coll. A. A. Pearson, Sept. 1947. Alpes Maritimes: coll. J. B. Barla, 1889 (Roumeguère, Fungi Selecti Exsiccati, No. 5333). SWITZERLAND: where it is said to be very common (Neuhoff, 1938), (Secretan, 1833; Trog, 1844; Anon., 1936; Favre, 1960; Oefelein, 1969). There are specimens in K from Neuchâtel, prope Corielles, coll. Dr. Morthier, Oct. 1873; Neuchâtel, coll. Dr. P. Morthier, Aug. 1878 (de Thümen, Mycotheca Universalis, No. 1609); Zürich, coll. G. Winter (Roumeguère, Fungi Selecti Exsiccati, No. 5111); Thun, Dorfhalden, coll. Trog, Sept.; Bad Ragaz (Fuckel, Fungi Rhenani, No. 2487); Engadin, coll. Miss Lewis, 1887; Les Bioux, Lac de Joux, coll. A.D. Cotton, Aug. 1903; without locality, coll. Miss M. Miles, Aug. 1904. ITALY: without locality (Bresadola, 1932; Balletto, 1972). Lombardia, Veneti and Trentino (Neuhoff, 1938); Valtellina (Pirola, 1966). Trentino: Sella, Mt Rivere Vezzena (Anon., 1970). There is a specimen in K from Val Visdende (Belluno), Aug. 1901 (D. Saccardo, Mycotheca Italica, No. 819). YUGOSLAVIA: Laibach (Neuhoff, 1938); Croatia: Gorski Kotar (Tortic, 1968, who noted it amongst the most common fungi in that area). There is a specimen in K from Croatia: Triglav, 1000–4000 ft., coll. Mrs. M. Leathes, 1923. ROMANIA: (Eliade, 1965, data for 17 collections, mostly from the Carpathian Mts in the east of the country, from the regions of Bacau, Brasov, Cluj, Ploiesti and Suceava; Toma, 1967 data for 3 collections); Moldova (Chifu et al., 1965); Basinul Stina de Vale (Bechet et al., 1968). CZECHOSLOVAKIA: Tatra Mts (Neuhoff, 1938). Moravia & Slovakia: (Pilát, 1957, data for 7 collections), Unicov and Sechovice (Kriz et al., 1961); Vrátna Dolina (Kunc. 1965). The following specimens are in K: Montibus Carpatorum Centralium, haud rara, leg. Kalchbrenner (Rabenhorst, Fungi Europaei, No. 131); Weisskirchen, leg. F. Petrak,

Aug. 1921 (Flora Moravica); Frayn in Mähren, leg. & det. Dr. J. Hruby, Aug. 1930 (Petrak, Flora Bohemiae & Moraviae Exsiccata, No. 2344); Valle rivuli Hoverla Podkarpatská Rus., leg. & det. A. Hilitzer, 25 Aug. 1934 (K. Kavina – A. Hilitzer, Cryptogamae Cechoslovenicae Exsiccatae, No. 131); Corveny Klastor, near Prague, coll. J. Ramsbottom, 9 Sept. 1960; Slovakia: Harmanecka dolina, Banska Bystrica, coll. F. Kotlaba, Z. Pouzar & D. A. Reid, 27 Sept. 1965; High Tatra, coll. B. Hawkes, 18 Aug. 1965. AUSTRIA: without data (Neuhoff, 1938, who states that it is very frequent); Attergau (Thirring, 1962); Tirol, Fritzens (Trentepohl, 1970). The following specimens are preserved in K: Salisburgia, non frequens, leg. Dr. Sauter, 1872 (de Thümen, Fungi Austriaci, No. 667) Tirolia Centralis: Trins in valle Gschnitz, 1200 m, coll. A. Kerner (Flora Exsiccata Austro-Hungarica, No. 766); Austria Inferior: prope Purkersdorf, leg. F. de Höhnel (Mus. Palat. Vindebon. Kryptogamae Exsiccatae, No. 1713b); Stiria prope Aussee, Sept., leg. L. et C. Rechinger (Mus. Palat. Vindobon. Kryptogamae Exsiccatae, No. 1713); Igls, Innsbruck, coll. A. D. Cotton, July 1922; Brannenburg, coll. P. James. Sept. 1956. GERMANY: Most of the records are from the central and southern mountainous areas: Bavaria: Augsburg, nicht raren; Algaü (Britzlemayr, 1887; Stangl, 1969, 1970), (Killermann, 1922– several collections cited from the Regensburg area), Weismain and Durrbacher Wald (Ade, 1923). Württemberg: (Neuhoff, 1938, data for 6 collections); Rheinwald Rappenworth (Vollmer), 5 Oct. 1943; Albtal bei Marxzell (Findeisen), 9 Sept. 1946 (Stricker, 1950). Baden: (Neuhoff, 1938, data for 3 collections). Thüringen: Blankenhain (Neuhoff, 1938); Schneptenthal, Friedrichroda (John, 1964). It should be noted that Bresinsky & Dichtel (1972) have published a map of the distribution of the species in West Germany. This confirms the distribution outlined above but in addition shows a remarkable record from the Baltic coast, seemingly from the Norden region of Ost Friesische—a very flat area. There is also a specimen in K from Württemberg: Untersontheim, coll. Kemmler, 1858 & 1859 (Rabenhorst, Fungi Europaei Exsiccati, Klotzschii Herbarii vivi Mycologici Continuatio, Editio Nova, Series Secunda, 1859–, No. 1316). POLAND: for a summary of all records until 1967 see Skirgiello (1967) from which it is obvious that with one exception all the collections are from the extreme south; the exception being from Danzig: Starogard. In addition there are records from Zakopane: Dolina Koscieliska, Sept. 1946, Aug. 1958; Dolina Malej Laki, Aug. 1958 (Rudnicka – Jezierska, 1965). Tatry: Dolina Mietusia; Pieninski Park Narodowy (Anon, 1968; Guminska, 1969). LATVIA: Riga (Stoll, 1923); Odsen and Wenden (Neuhoff, 1938); without localities (Raitviir, 1967). ESTONIA: without localities (Kalamees, 1966; Raitviir, 1967). RUSSIA: Leningrad area: Gatschinam (Weinmann, 1836; Fries, 1874; Karsten, 1882). NORWAY: records are mostly from around Oslo but there are also a few from the central region (Eckblad, 1960; Torkelsen, 1972). SWEDEN: there are only 3 records from the mainland: Västmanland, Medelpad and Jämtland, but the fungus is very common on the island of Gotland from which there are about 18 records (Nilsson, 1958). Outside Europe it is known from ASIA: PAKISTAN: Murree; Kagan Valley; Sharhan; Shogan; Swat, Kalam, common (Ahmad, 1972). RUSSIA: Primorsk

Region (Raitviir, 1967). MANCHURIA: Kirisamedani, Mt Tyôhakusan, 12 Sept. 1942 (Kobayasi, 1953). JAPAN: Hokkaido; Mt Daisetu, 4 Aug. 1913; Nakagawa experimental Forest. Honshu: Nagano Prefecture, Kamikôti, Aug. 1954; Saitama Prefecture, Mt Ryôgami, Sept. 1954 (Kobayasi, 1953; Ito, 1955, Imazeki & Hongo, 1965; Anon., 1969.) NORTH AMERICA: Ontario, Michigan, Manitoba, Nova Scotia to British Columbia, south to New York and California (Martin 1952). There are specimens in K from CANADA: without locality, coll. Carleton Rea, 19 Sept. 1921; Western Manitoba: Clear Lake, coll. G. R. Bisby, 17 Aug. 1935. UNITED STATES: Idaho: Seven Devils Range, coll. L. Hawker, 10 Aug. 1962. California: Woodside (Coastal), coll. Mrs. Newhall, 1 Sept. 1934, very rare (Fungi of Pacific Coast States, E. E. Morse); Dr. Harkness, No. 473. New York: Taughanrock Falls, coll. Carleton Rea, 15 Sept. 1962. MEXICO: Estado de Mexico and Estados de Morelos (Romero et al., 1970; Lowy, 1971). PUERTO RICO: near Mayaguez (Lowy, 1971). BRAZIL: Sao Paulo, Serra de Mar (Lowy, 1971).

There are a number of published illustrations of *Tremiscus helvelloides* amongst which may be cited the following: Atkinson (1901: fig. 208), Bresadola (1932: pl. 1130), Gillet (1874: pl. 707 [= 304 & 517]), Imazeki & Hongo (1965: pl. 57 fig. 334), Jacquin (1778: pl. 14), Kalamees (1966: fig. 217), Lloyd (1922: pl. 206 fig. 2178), Maublanc (1959: pl. 213 fig. 2), Michael-Hennig (1960: fig. 204), Neuhoff (1936, 1938: pl. 1 pl. 7 figs. 6–15), Patouillard (1889: fig. 688), Peter (1964: fig. 319/349), Pilát (1957: pl. 37 & 38a, Poelt & Jahn (1964: pl. 24), Prihoda (1952: pp. 181 & 183), Quélet (1872: pl. 20 fig. 4, Romagnesi (1963: pl. 330; 1967: pl. 307c), Torkelsen (1972: fig. 38).

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# TYPE-STUDIES IN THE POLYPORACEAE—I

## Tropical species described by C. H. Persoon

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The type specimens of 20 tropical polypores described by C. H. Persoon have been examined. Eleven species are accepted, seven are reduced to synonymy, while one name is a nomen nudum. One type is so poorly developed that no conclusive determination is possible. The combination *Trametes marianna* (Pers.) Ryv. is proposed.

Persoon described many polypores, but he restricted his own collecting to Central Europe. The only extra-European collections he ever saw were those sent to him from Paris which had been collected by C. Gaudichaud during his journey around the world. The fungi described by Persoon were published in the book Gaudichaud (1827) wrote about the expedition. With the exception of a few specimens from the more ample collections, the material was returned, and today the types are in the Paris herbarium (PC).

Many of Persoon's species later passed into oblivion. However, since they were among the first tropical polypores described, they are very important. I therefore examined the types both macro- and microscopically during a short stay in Paris in 1972. In the following enumeration the species are arranged alphabetically according to specific epithet. The number given refers to the page in the original publication, and the locality indicated is the type locality.

The fungi were collected at the following places:

(a). Rio de Janeiro in Brazil;
(b). Rawak Island—a small island near Waigeo Island, north-west of New Guinea, about 0° S, 130° E;
(c). Mariana Islands—a large group of islands situated in the Western Pacific between 10–20° N and 140–150° E.

No descriptions or drawings of microscopical characters of the accepted species are given here. This will be done separately on loose sheets containing descriptions of tropical polypores in general. Those interested in these descriptions are requested to write the author for information.

POLYPORUS APIARIUS—p. 169, Rawak

The species is a true *Hexagonia*, and it was transferred to this genus by Fries as early as 1838. M. Fidalgo in her monograph on *Hexagonia* (1968a: 41) selected the specimen in Persoon's herbarium in Leiden as holotype; the specimens in Paris then become isotypes.

The typification of *Hexagonia* has been much disputed (cf. Donk, 1960 and 1969, Fidalgo, M., 1968a and b). I agree with M. Fidalgo in her acceptance of *H. crinigera* Fr. as selected type species for the genus. This selection was made by Clements & Shear in 1931 and, being the first, it must be followed (Int. Code of Bot. Nomencl. Art. 8). The species is typical within the Friesian emendation of the genus, while the selection cannot be said to be based on a misinterpretation. Donk (op. cit.) preferred *H. mori*, which was the original and only species of the devalidated genus of Pollini. In my interpretation of the Code as regards typification of revalidated names, it is of no interest or consequence to know what species Pollini included in his genus. What counts is Fries' emendation of the genus, and it is evident from this that it is not drawn up from *H. mori* (which he did not know), but from the group represented by species like *H. hirta*, *H. crinigera*, *H. wightii*, etc., i.e. true *Hexagonia* species in the strict sense, and the group from which Clements & Shear made their selection. The taxon represented by *H. mori* (Poll. ex Fr.) Fr. is a *Polyporus* s. str. originally described as *Favolus europaeus* Fr. and *Cantharellus alveolaris* DC. ex Fr.

The generic name should be spelled *Hexagonia*, not *Hexagona*. The latter is given as an example of an orthographic error. (Art. 73 of the Code).

My concept of the genus is wider than that of M. Fidalgo. She places the main emphasis on the trichoderm of the pileus and excludes all species not having this. Personally, I attach more importance to the microscopic characters. My concept of *Hexagonia* therefore includes species with a trimitic hyphal system having hyaline clamped generative hyphae, hyaline to faintly coloured binding hyphae, and distinctly brown skeletal hyphae. The spores are hyaline, cylindrical, smooth and large, viz., in the range of 10–20 $\mu$ long.

Most species have large hexagonal pores. The most closely related genus is *Coriolopsis* Murr., which has the same hyphal configuration, but shorter spores and smaller pores, although there are a very few transitory species.

POLYPORUS AURISCALPIUM—p. 169, Rio de Janeiro

This is an *Amauroderma* species, as already noted by Lloyd (1912). The type is almost sterile and only 12 spores were found; they are pale yellowish, more or less globose, with a diameter of 6–7 $\mu$.

POLYPORUS BIVALVIS—p. 173, Rawak

The type is a typical specimen of the widespread and common *Hexagonia tenuis* (Hook.) Fr., a most variable species, especially in regard to the pore size. Repeatedly

new species have been described on the basis of different pore sizes—a character that clearly breaks down when many specimens are compared. The pileus surface is glabrous and zoned in brown shades, but it may also be covered from the base with a thin reddish cuticle. The extent of this cuticle may vary from a small band near the base to a complete cover. However, this reddish cuticle is of no taxonomic value. In some collections there may be a variation from specimens devoid of this cuticle to such that are more or less covered with it.

POLYPORUS CORRUGATUS—p. 172, Rawak

The type represents *Trametes scabrosus* (Pers.) Cunn. as already noted by Montagne (1834).

POLYPORUS DERMOPORUS—p. 170, Rawak

The type is a typical specimen of *Favolus brasiliensis* (Fr.) Fr., as already noted by Léveillé (1846: 144—with the printing error "desmoporus"). There are two authentic specimens in Paris: one in herb. Montagne and one in the general herbarium sub "Favolus". The latter is selected as lectotype.

POLYPORUS FLACCIDUS—p. 171, Mariana Islands

This species is unknown to me. The type is a small dimidiate specimen about 1.5 cm wide from base to margin and about 2.5 cm long, with a thickness of about 1–2 mm. The pileus surface is glabrous, ochraceous to pale fulvous, with a few wrinkles and small pits. The context is the same colour as the pileus surface, 0.5 mm thick, and soft. The tubes are soft, with a depth of 0.5—1.5 mm. The pores are thin-walled, slightly irregular, 4–6/mm, partly collapsed (pressure during collecting?)

Hyphal structure dimitic or trimitic. Skeletal hyphae 2.5–3.5 $\mu$ in diameter, hyaline and thick-walled; binding hyphae (?) moderately branched; no generative hyphae with septa seen. Spores and cystidia not seen.

The general impression is that of a very poorly developed specimen of *Favolus spathulatus* (Jungh.) Lév., even though some objections can be raised. The fruitbody with its semicircular form is not typical of *F. spathulatus*, even if this shape could be ascribed to a young state. However, the colour, the texture, and the pores are all within the range of variation for these characters in *F. spathulatus*. The hyphal structure in this species is difficult, and it seems to me that this is a species in which the distinction between skeletal hyphae and binding hyphae breaks down. Further, it is very difficult to find septate hyphae in *F. spathulatus*, and in some specimens apparently both simple septa and clamps are present. The generally branched hyphae observed in *P. flaccidus* could represent branched generative hyphae devoid of septa or true binding hyphae. Until more material is available, the name *P. flaccidus* should be dropped from consideration.

POLYPORUS FUSCO-BADIUS—p. 172, Mariana Islands

The type specimen is typical of the common and widespread species *Trametes scabrosus* (Pers.) Cunn. This was already noted by Montagne (1834).

POLYPORUS FUSCO-PURPUREUS—p. 172, Mariana Islands

This is a species of *Nigroporus* as this genus is typified by *N. vinosus* (Berk.) Murr. (type examined). A later name for Persoon's species is *Polyporus calignosus* Berk. (type examined). Cunningham (1965: 236) transferred the latter to *Phellinus*. However, *P. fusco-purpureus* is dimitic and has clamped generative hyphae (as in *P. vinosus*, cf. Fidalgo & Fidalgo, 1967: 847); also, the colour of the skeletal hyphae is different from that of *Phellinus*.

The spores of *P. fusco-purpureus* are light brownish, ellipsoid, 2–3(–3.4) × 1–2 μ. Closely related is *Nigroporus roseo-albus* (Jungh.) Ryv., but the spores of this species are larger. Otherwise both species have the pileus umber to fuscous, often zoned and with a distinct cortex, and the context light purplish to brownish.

POLYPORUS LATERALIS—p. 175, Rawak

The type consists of a stipitate specimen with the pileus glued to the sheet. The pileus is semicircular, with a radius of about 3 cm and a thickness of about 3 mm. The surface is exposed only a few mm along the margin, and seems to be glabrous and ochraceous. The stipe is attached laterally, is 2.5 cm long, and has a diameter of about 2.5 mm. The surface is glabrous, with a black, thin cuticle over a hard ochraceous core. The context is pale ochraceous, while the pore surface is pale brown (probably distinctly lighter in fresh state). The pores are entire, thin-walled, round, and 7–9/mm. The hyphal structure is dimitic, with clamped generative hyphae and strongly branched arboriform binding hyphae. Spores were not seen.

The species belongs in *Polyporus* s. str., as I define it. The specimen may represent a young *Polyporus picipes* Fr., which is a variable species with regard to both stipe attachment and pileus colour. The European and African specimens I have seen had a generally darker, more bay pileus than what I could see from the narrow rim of exposed margin of *P. lateralis*. More collections will be required to decide whether it is a species in its own right, or only one of the many forms of *P. picipes*.

POLYPORUS LEPTOPUS—p. 169, Rawak

This is an *Amauroderma* species belonging to the characteristic group with a shiny laccate pileus surface. The group has been treated by Furtado (1967). The species is known from Asia and Africa.

POLYPORUS LINEATUS—p. 175, Rawak

The type is a typical specimen of the species formerly called *Polyporus zonalis* Berk. (type examined). The characteristic cystidia, partly smooth, partly incrusted, are

abundantly present, with a diameter of up to 21 $\mu$. The spores are scanty, but the 14 found in the hymenium measured 4.5–6 $\mu$ in diameter. The hyphal system is monomitic, with simple septa. *Polyporus lineatus* has recently been transferred to *Rigidoporus* (Ryvarden, 1972b).

Closely related is *Rigidoporus microporus* (Sw. ex Fr.) Overeem (Syn. *Polyporus lignosus* Kl., the types of both examined). However, this species can be separated by the absence of cystidia and its smaller spores; also, the fruitbodies are usually larger and more distinctly zoned.

POLYPORUS MARIANNUS—p. 173, Mariana Islands

This is an earlier name for *Polyporus paleaceus* Fr. (1838). The species belongs in the difficult group around *Trametes modesta* (Fr.) Ryv. *P. mariannus* is characterized by its pileus being glabrous, smooth, and somewhat glossy in broad zones. *Trametes modesta* and closely related species are usually finely adpressed-tomentose, becoming more glabrous and dull only with age. The *T. modesta*-complex was discussed by Fidalgo & Fidalgo (1968).

The glabrous, smooth, and often somewhat glossy surface of *P. mariannus* is due to the hyphae being agglutinated. Cunningham (1965) stated that a cortex is present, but this is not the case in the types of either *P. mariannus* or *P. paleaceus*. According to my experience, the agglutination is usually restricted to a very thin upper layer that does not appear as a cortex when viewed in section. It could be that the agglutination proceeds deeper in older and more weathered specimens.

The following combination is proposed: **Trametes marianna** (Pers.) Ryv., *comb. nov.* (basionym, *Polyporus mariannus* Pers. *apud* Gaudichaud, Voyage Monde 173, 1827).

POLYPORUS NUMMULARIUS—p. 174, Rio de Janeiro

The type has not been traced in either Paris or Leiden. The description runs as follows: "P. orbicularis tenuissimus, pileo subpubescente concentrice zonate griseo pallido, poris distinctis margine acuto inaequaliter prominente." Persoon himself suggests ("probablement") that the species is a variety of *Polyporus versicolor* L. ex Fr.

POLYPORUS POLYZONUS—p. 171, Rawak

The type is a very typical specimen of the common and widespread species usually called *Polyporus occidentalis* Kl., which is the type species of *Coriolopsis* Murr.; since Persoon's name has priority, it has been transferred to that genus (Ryvarden, 1972b). *Coriolopsis* is a genus close to *Trametes*, the principal difference being the brown skeletal hyphae that are responsible for the brown colour of all species of *Coriolopsis*. *Coriolopsis polyzona* is very widespread, and has repeatedly been redescribed under various names. A long, but still not complete, list of synonyms was given by Fidalgo & Fidalgo (1966).

DAEDALEA REPANDA—p. 168, Rawak

The type specimen is a very large and typical specimen of *Lenzites elegans* (Spreng. ex Fr.) Pat., and this was already noted by Murrill (1908). The species is very widespread in the tropics and has repeatedly been redescribed under various names. A long, but still not complete, list of synonyms can be found in Fidalgo & Fidalgo (1966).

POLYPORUS SACCATUS—p. 169, Mariana Islands

No type has been traced in either Paris or Leiden, and the specimen may be lost. The description runs as follows: "Pileo tenui glabro zonato infundibuliformi subnitente ligneo-pallido poris tenuissimus pallidis, stipite brevi glabro."

In the text Persoon suggested that his species may be the same as *Boletus katui* Ehrenb., which has generally been accepted as a synonym of *Polyporus xanthopus* Fr., and Fries (1838) regarded both species as identical with the latter.

POLYPORUS SCABROSUS—p. 172, Mariana Islands

This is a very widespread, common species. It is polymorphic, especially as concerns the pileus, which may vary from pure white and finely tomentose to deep red and glabrous, as the hyphae begin to agglutinate to a thin, reddish cuticle that, spreading from the area of attachment, finally covers the whole pileus. Owing to this variation, Persoon alone described the species three times, viz. as *P. scabrosus*, *P. corrugatus*, and *P. fusco-badius*. Montagne (1834) was the first to note their identity, and Fries (1838) placed the last two in synonymy with the first (*P. scabrosus*) which then became the correct name for the species. The species belongs in *Trametes*, as I define the genus.

POLYPORUS SERPENS—p. 173, Mariana Islands

Nomen nudum, not *P. serpens* Fr., 1821.

The specimens in Paris represent the species now called *Polyporus latus* Berk., 1839 or *Coriolopsis latus* (Berk.) Ryv. (type examined). Further synonyms are *Trametes acupunctata* Berk., *Polyporus luteo-olivaceous* Berk. & Br., and *Polyporus aratus* Berk. (all types examined).

As it is a later homonym of *P. serpens* Fr., *P. serpens* Pers. cannot be used.

POLYPORUS TORNATUS—p. 173, Mariana Islands

The species belongs in *Ganoderma* as indicated already by Bresadola (1912). Steyaert (1972) concluded that *G. applanatum* and *G. tornatum* had better be treated as two separate species in spite of the fact that the microscopical characters are identical. To me, *G. tornatum* clearly falls within the range of variation we must allow for *G. applanatum*.

POLYPORUS VESPACEUS—p. 170, Rawak

The specimen at Paris is better developed and more typical than the one at Leiden, and is therefore selected as type.

This species is a very variable one owing to the hymenium varying from true lamellae (*Lenzites aspera* Kl., type examined) to hexagonal pores (*Hexagonia albida* Berk., type examined), with all intermediates. Lloyd (1912: fig. 314) gave a most convincing picture, which shows that this variation may occur in fruitbodies from the same mycelium. The pileus surface is white to cream, typically finely asperulate, but it may also be more or less smooth. The hyphal configuration is trimitic; generative hyphae hyaline, with clamps; skeletal hyphae hyaline and thick-walled, while the binding hyphae are moderately to strongly branched with the upper branches typically projecting into the hymenium—appearing almost like cystidia.

The species belongs in *Lenzites*, as I define the genus, owing to its tendency to develop lamellae and the typically branched binding hyphae which are so prominent in *Lenzites betulina* L. ex Fr.—the type of the genus.

*Lenzites vespacea* (Pers.) Ryv. is known from the Western Pacific to Tropical Africa.

The disposition of tropical polypores described by C. H. Persoon is summarized as follows:—

*Polyporus apiarius* = *Hexagonia apiaria* (Pers.) Fr.
*P. auriscalpium* = *Amauroderma auriscalpium* (Pers.) Torr.
*P. bivalvis* = *Hexagonia tenuis* (Hook). Fr.
*P. corrugatus* = *Trametes scabrosa* (Pers.) Cunn.
*P. dermoporus* = *Favolus brasiliensis* (Fr.) Fr.
*P. flaccidus* = Type poorly developed; the name should be dropped from consideration until more material becomes available.
*P. fusco-badius* = *Trametes scabrosa* (Pers.) Cunn.
*P. fusco-purpureus* = *Nigroporus fusco-purpureus* (Pers.) Ryv.
*P. lateralis* Pers. = *Polyporus* (s. str.) *lateralis* Pers.
*P. leptopus* = *Amauroderma leptopus* (Pers.) Furt.
*P. lineatus* = *Rigidoporus lineatus* (Pers.) Ryv.
*P. mariannus* = *Trametes marianna* (Pers.) Ryv. (for recombination, see p. 309).
*P. nummularius* = Type not seen. Probably a synonym of *Trametes versicolor* (L. ex Fr.) Lloyd.
*P. polyzonus* = *Coriolopsis polyzona* (Pers.) Ryv.
*Daedalea repanda* = *Lenzites elegans* (Spreng. ex Fr.) Pat.
*P. saccatus* = Type not seen. Probably a synonym of *Microporus xanthopus* (Fr.) Kuntze
*P. scabrosus* = *Trametes scabrosa* (Pers.) Cunn.
*P. serpens* = Nomen nudum, not *Polyporus serpens* Fr. 1821.
*P. tornatus* = *Ganoderma applanatum* (Pers. ex Wallr.) Pat.
*P. vespaceus* = *Lenzites vespacea* (Pers.) Ryv.

No mycologist has influenced and stimulated me more than did Dr. M. A. Donk. His encouragement and support were decisive when I considered taking up the study of tropical polypores. It is very appropriate, that the present paper, which I hope will be the first of a long series, appears in a number of Persoonia dedicated to his memory.

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# NOTES ON BOLETE TAXONOMY

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(With two Text-figures)

Newly discovered mycorrhizal relationships of boletes (with *Nothofagus*, *Shorea*, *Quercus humboldtii*, *Alnus jorullenses*, *Eucalyptus*, and *Leptospermum*) are discussed. Type studies on *Fistulinella*, *Boletus granulatus* var. *capricollensis*, *Boletogaster*, and *Gastroboletus* are reported. The following new combinations are proposed: subsections *Pictini* and *Spectabiles* in sect. *Solidipes* of *Suillus*; *Suillus ochraceoroseus*; *Chalciporus piperatus*, *C. rubinus*, *C. rubinellus*, and the new section *Eximia* of *Leccinum*, with *L. eximium* (Peck) Sing. The interpretation of *Porphyrellus pseudoscaber* on the basis of topotypical material is indicated.

Recent field and type studies on boletes (Boletaceae and Strobilomycetaceae) have been carried out on both fresh and dried as well as alcohol material. Some of the results as far as they refer to thus far unpublished data or lead to new combinations or new taxa have been found to be of general interest in Basidiomycete taxonomy and will be discussed in the following notes.

## 1. Mycorrhizal relationships

Thus far, ectomycorrhizal associations of trees with South American and Asiatic as well as tropical African boletes have been restricted to introduced trees, particularly *Pinus* and to a few isolated ectotroph associations with *Alnus jorullensis* (*A. jorullensis*/*Gyrodon monticola*) and *Salix humboldtiana* (*S. humboldtiana*/*Leccinum griseum*) in Argentina, not counting of course, the associations with Pinaceae and Fagales, sometimes *Tilia*, in the extratropical regions of Asia and South America. In the latter continent we know even now only two associations between *Nothofagus* and Boletaceae: *N. obliqua*/*Boletus loyo* and *N. obliqua*/*Boletus chilensis* (Singer, 1969). But in India, Singer & Singh (1971) have described the ectotrophs *Shorea robusta*/*Pulveroboletus shoreae* Sing. & Singh and *Shorea robusta*/*Xerocomus bakshii*, providing evidence regarding a further, thus far overlooked family of Cormophyta forming ectomycorrhiza with boletes, viz. the Dipterocarpaceae (see also Singer, 1971).

Ectotroph formation has also been indicated by Singer (1963) from the Colombian oak forests, but no boletes had been observed then. During a second visit in the Querceta of Colombia (provinces of Cundinamarca and Valle to Cauca) it was shown that Boletaceae are likewise involved in the ectotrophic mycorrhiza of

*Quercus humboldtii* H. & B. The following species are now known to enter symbiosis with this species of oak: *Boletus fuligineotomentosus* Sing. (see also *in* Sydowia, Beih., in print) and *B. atkinsonianus* Murr. as well as *Phylloporus purpurellus* Sing. (Sydowia l.c.)

A new ectotroph association has been discovered in the *Alnus*-woods of the montane zone of the neotropics: *A. jorullensis/Phylloporus caballeroi* Sing. (Sydowia, in print).

It was formerly not known with certainty that *Eucalyptus* forms ectomycorrhiza with boletes. It has now been established by ecological and anatomical research in the *Eucalyptus* plantations of both Argentina and Chile that *Xerocomus* is involved. We have consequently two new ectotrophs in South America: *E. globulus/Xerocomus brasiliensis* in Argentina (prov. of Buenos Aires) and *E. globulus/Xerocomus chrysenteron* in Chile (prov. Valparaiso). This shows that Myrtaceae are obviously ectomycorrhizal under certain conditions. Ectomycorrhiza has now also been established with *Eucalyptus* and *Leptospermum* in New Zealand by McNabb and Horak which is now confirmed by our observations (see also Singer, 1971).

This latter information is particularly interesting since our (Singer & Moser, 1965) research has definitely shown that the South American Myrtaceae (*Myrceugenia*, *Myrceugenella*, *Nothomyrcia*) are not ectotrophically mycorrhizal. It is furthermore remarkable that *Gyrodon* is often non-mycorrhizal. I have been able to demonstrate that ectomycorrhiza is absent in the undisturbed tropical rain forest of Mexico and Colombia where *Gyrodon proximus* and *G. exiguus* have been collected, the latter obviously a lignicolous species like *Pulveroboletus hemichrysus*.

The wide range of mycorrhizal hosts for *Xerocomus chrysenteron* and *X. brasiliensis* and the absence of mycorrhizal hosts for some Gyrodontoideae and some Pulveroboleti shows clearly that the relative selectivity and the degree of dependency on symbiotic relationships increase gradually from a group of low specialization and/or dependency to a group of high specialization and dependency in Gyrodontoideae, Xerocomoideae and Boletoideae, whereas in Suilloideae even the 'lowest' forms (whatever one's criterium for determining the level of evolutionary progression) are in their vast majority highly specialized Pinaceae/Suilloideae ectotrophs. On the other hand, in the series *Boletus-Tylopilus-Leccinum* even the most recent observations confirm the statement, generally accepted, that here we have obligatory ectomycorrhiza whereby the preferred symbiont becomes, as we progress from *Boletus* to *Tylopilus* to *Leccinum* and *Xanthoconium*, increasingly the frondose tree (Salicales and Fagales), and association with Pinaceae becomes rarer. If then we want to make mycorrhizal association the principal measure of phylogenetic development, we would certainly not consider the Suilloideae the most primitive group (as has been done by Smith & Thiers, 1971) but would agree with Benedix (1963) who thinks that *Boletinus* is relatively more recent ("abgeleitet").

## 2. Types revised at Dahlem and Vienna

A large number of species is based on types now lost or supposedly lost. This is often regrettable because of the different interpretations of classical species by different authors or the impossibility to come to a correct interpretation. Singer & Clemençon (in print) have emphasized the possibilities still existing in Europe to replace, for the study of species whose type specimen is no more existent, the holotype by a topotype—a procedure still often successful in the case of taxa proposed by Secretan, Fries, Schulzer, and Quélet and as we have shown (Machol & Singer, 1972) even in the case of Micheli. On the other hand, fortunately not all type material thought to have been lost is actually lost but only temporarily misplaced. The following examples will illustrate the point I am particularly indebted to the Director of the botanical collections at the Botanical Museum in Berlin-Dahlem and the Botanical Institute in Vienna, for permission to search for and analyse the type material of Boletaceae (and other fungi) at these institutions.

*Fistulinella staudtii* P. Henn. (*in* Bot. Jb. **30**: 44. 1901). – This is based on Zenker & Staudt 229 (B) from Yaundé, Cameroon, still well preserved in the collections of alcohol material. The pileus is now whitish in one, grayish bister in the other carpophore; the stipe is now white, not reticulated and without traces of a veil, 24–32 × 2–2.5 mm and equal or slightly thickened in the lower half but again narrower at the base; pores 3–4 per millimeter, about 1/4 mm wide and now as wide or smaller than the wall diameter, pallid, depressed around the apex of the stipe; a broad sterile band running around the margin of the pileus; ornamentation of the stipe finely punctate-verruculose. Spores fusoid or cylindric-fusoid, smooth, with suprahilar depression and heterotropic, occasionally with a round oil drop, with 0.5–0.6 $\mu$ thick wall which is homogeneous and cyanophilic, 15–20 × 4.5–6.2 $\mu$ basidia about 28–30 × 11–11.3 $\mu$, 2–4-spored; cystidia ventricose-ampullaceous, obtuse, hyaline, 35–43 × 6–13.5 $\mu$; hyphae without clamp connections, hymenophoral, trama bilateral of the *Boletus*-type, with a narrow less gelatinized, melleous mediostratum consisting of filamentous hyphae 1.5–3.7 $\mu$ broad and not divergent, and a broad lateral stratum consisting of hyaline recurved-arcuate-divergent hyphae 3.7–7 $\mu$ broad; epicutis of pileus apparently a trichodermium but with applanate horizontal hyphae predominent in the uppermost tier, 1.2–9 $\mu$ broad, where pigmented, the pigment intracellular, but a (now) subhyaline incrustation also present on some of the hyphae; hyphae of the context of the stipe all inamyloid (now).

This type analysis indicates that the fungus is boletaceous and belongs in the Boletoideae. The spores, rather pale under the microscope, do not permit a conclusion as to the color of the fresh spore print except that it was not white. One cannot help but think that *Fistulinella* which has the same basic characters as *Ixechinus* is indeed synonymous with the latter (as was also concluded by Horak, 1968 on the basis of literature data). The habitat (lignicolous in both *Fistulinella* and *Ixechinus*) and the shape of the stipe would indicate *Pulveroboletus*.

The pale spores, in spite of being larger than usual in *Tylopilus* may suggest that the spore print was ochre or pinkish and that the genus is closer to *Tylopilus*. It is,

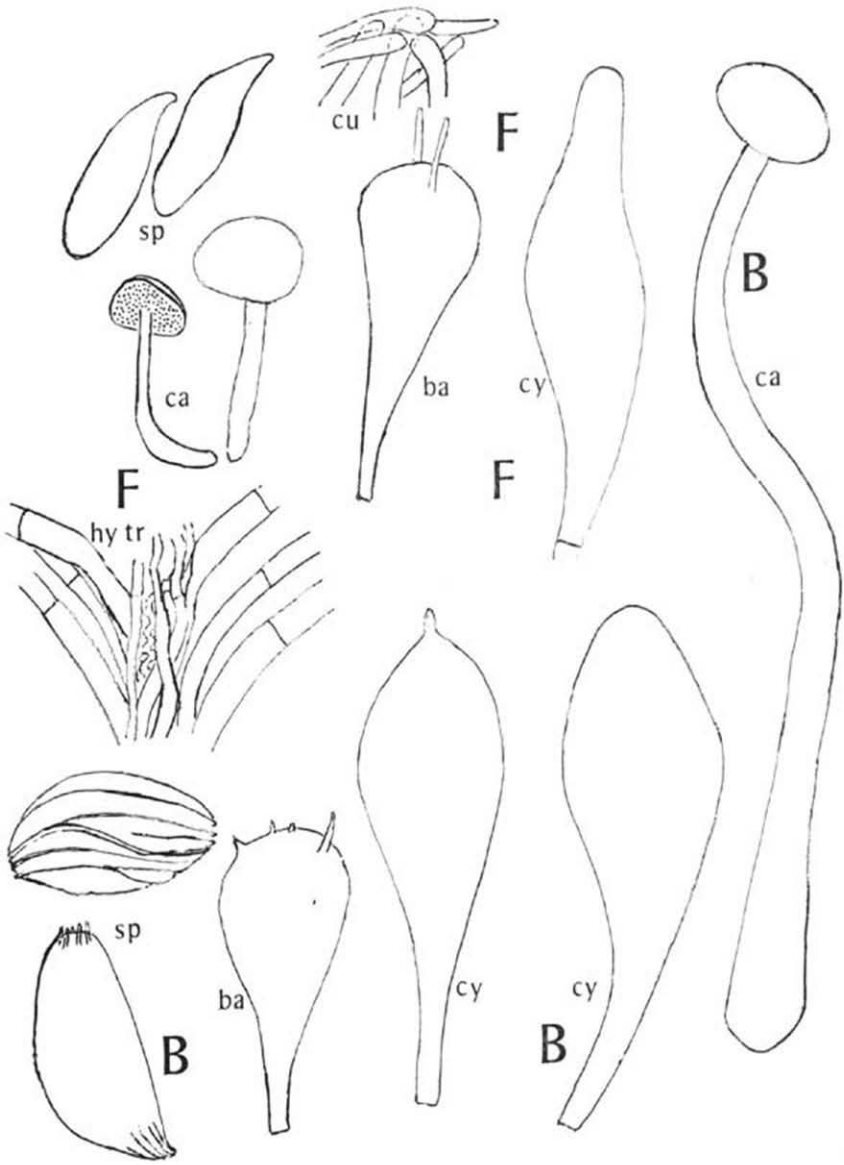


Fig. B. *Boletogaster jalapensis*, type.

Fig. F. *Fistulinella staudtii*, type. ca, carpophore (× 0.8); ba. basidium; cu, fragment of cuticular layer; cy, cystidium; hy tr, section of hymenophoral trama; sp. spores (microscopic elemets × 800); lower left spore schematic, with ornamentation only indicated at the hilar (below) and distal (above) pole.

however, also possible that the combination of stipe size and shape, spore color, and absence of mycorrhizal association (?) might in the end justify a separate genus within the Boletoideae. As for the isolation of the tubes in *Fistulinella* and *Ixechinus*, it is certainly no part of the normal development of the carpophores. Some of the alcohol material of common European boletes (like *Tylopilus felleus*) shows partial separation of isolated tubes; dried material of *Ixechinus* does not. It was M. A. Donk who first directed my attention to this phenomenon. Consequently, the latter can hardly be used as an additional generic character specific to *Fistulinella* and *Ixechinus*.

*Boletus granulatus* var. *capricollensis* Buchs & P. Henn. (*apud* P. Henn. *in* Hedwigia **42**: 215. 1903). — The topotype and authentic material, under *Boletus capricollensis*, the type later relabeled "*Boletus* (*Gyrodon*) *placidus* Bon." (B, sub P 240) is undoubtedly *Suillus placidus* (Bon.) Sing. in spite of the fact that the label says "unter Fichten.'

*Boletogaster jalapensis* (Murr.) H. Lohwag sensu H. Lohwag.—*Ceriomyces jalapensis* Murr. (*in* Mycologia **2**: 248. 1910) was based on Mexican material; it was correctly referred to *Boletellus* by Gilbert, as is shown by the type studies and redescription by me (1945, 1970); Lohwag's genus is based on material from China which was determined *B. jalapensis* by Lohwag. The material was supposed to have been lost but was rediscovered in Vienna (W) by me. Its description runs thus:—

The pileus (20–22 mm) is relatively small in relation to the stipe which before drying must have been 169 × 13, at apex × 4 mm, gradually tapering upwards; otherwise macroscopically quite like Murrill's description. The stipe appears to be slightly sulcate in places but is definitely devoid of a raised network. Spores ellipsoid with slight suprahilar applanation or depression, melleous, later with brown wings on yellowish ground, with ornamentation of type X with the longitudinal wings projecting 0.7–1.7 $\mu$, some of them forked, some shorter, not cross-striate as in *B. ananas*, suddenly rounded off at distant pole, attenuated-concurrent at hilar end, with wall proper up to 1.5 $\mu$ thick, (with ornamentation) 15.2–20 × 8.3–11 $\mu$; basidia 25–31 × 11.7–14.5 $\mu$, (2)–(3)–4-spored; cystidia ventricose, some with apical mucro, hyaline, thin-walled, 30–62 × 11.7–16.7 $\mu$; hyphae without clamp connections; hymenophoral trama bilateral, subhyaline; epicutis of pileus consisting of loosely arranged hyphae which are 2–4.5–(8.5) $\mu$ broad and hyaline to subhyaline in KOH; hyphae of the trama of the base of the stipe longitudinally arranged, without clamp connections, not gelatinized, inamyloid. The collectors note indicates the color as "brunneus, brunneus luteus". Pores 0.2–0.5 mm wide, subirregular in size but subisodiametric; tubes depressed-subfree.

These data show that aside from the still more elongated stipe there are no important differences between Murrill's and Lohwag's *B. jalapensis*, and the microscopical characteristics are in close agreement. The Asiatic specimens cannot be more than a geographic race at most.

*Gastroboletus boedijnii* H. Lohwag [Beih. bot. Zbl. (II) **42**: 273, 1926].—This was likewise based on Chinese material of the Handel-Mazzetti collection and was

considered by Horak (1968) to be "verschollen." However, the type exists at W. It comes from Yünnan around the village Ngulukö near Lidjang, in temperate zone, collected by "Collectores indigeni," early October 1916.

The fungus, as preserved, corresponds well with Lohwag's description and drawing the pileus is now brownish and somewhat finely rivulose-rimulose and minutely fibrillose-asperulate; the stipe is not preserved. Spores fusoid to cylindric, more or less asymmetrical, with a deep melleous-brown episporium and a very pale melleous endosporium (both together 1 $\mu$ thick), smooth, cyanophilic, with a short hilar appendage which is more often obliquely than centrally attached, with or without a suprahilar applanation, inamyloid, cyanophilic; basidia clavate, 23–43 × 6.8–11 $\mu$, 2–3–4-spored, sterigmata straight or recurved, (excepting a minority) not half-sickle-shaped as in typical bolete-basidia but obviously apobasidial; cystidia moderately numerous in the interior of the tubes and on the pores, ventricose and mucronate, hyaline, thin-walled, 20–34 × 5.2–11.7 $\mu$; cheilocystidia smaller than the pleurocystidia, cylindric to clavate, 15–16 × 4–5.5 $\mu$; hyphae of the trama of the pileus in part running radially and 3.3–5.5 $\mu$ broad, filamentous, without clamp connections, inamyloid; hymenophoral trama bilateral consisting of a melleous to hyaline mediostratum of parallel hyphae 4–4.5 $\mu$ broad, without noticeable gelatination and a divergent lateral stratum consisting of somewhat broader or equally broad filamentous hyphae, not paler or deeper colored than those of the mediostratum, partly touching each other (partly not); subhymenium differing from the lateral stratum by the fact that here the hyphae are multiseptate (these up to the base of the basidia also clampless); epicutis of pileus a trichodermium consisting of pigmented hyphae running in all directions and the end-cells more or less ascendant or erect and sometimes in fascicles of parallel elements which may or may not be cystidiform, or broad and short, 5–14 $\mu$ diam. Under the dissecting microscope, the context appears bright yellow.

This is obviously conform with the interpretation of the fungus by Smith & Singer (1959) which was likewise based on the type of *Gastroboletus boedijnii*. I have studied the type in 1971 so the data can be compared with our earlier analysis (l.c., fig. 1, 2–4). It is obvious that here we have a genus which approaches the Boletaceae as much as *Macowanites* approaches *Russula* but still on the secotiaceous level. *Gastroboletus* is an important genus since it is the type genus of the family Gastroboletaceae (Gasteromycètes), see Singer (1962). It is remarkable that, as far as can be determined from the type specimen of *Gastroboletus boedijnii*, the hymenophoral trama is much like the *Boletus*-type established in *G. turbinatus* (Snell) Smith & Sing. and *B. fascifer* Sing. & Smith but in the first of these species perhaps more similar to that of *Truncocolumella*.

### 3. New combinations

A revision of the limits between *Boletinus* and *Suillus* as worked out by Singer (1967) makes it necessary to propose the following new combinations:—

SUILLUS sect. **Solidipedes** (Sing.) Sing. subsectio **Pictini** (Sing.) Sing., *c.n.* Basionym: *Boletinus* sect. *Solidipedes* Sing. subsectio *Pictini* Sing. *in* Revue Mycol. **3**:158. 1938.

SUILLUS sect. **Solidipedes** (Sing.) Sing. subsectio **Spectabiles** (Sing.) Sing., *c.n.*, *st. n.* Basionym: *Boletinus* sect. *Spectabiles* Sing., ibid. p. 157.

**Suillus ochraceoroseus** (Snell) Sing., *c. n.* Basionym: *Boletinus ochraceoroseus* Snell *apud* Snell & Dick *in* Mycologia **33**: 35. 1941.

Data obtained by a recent revision of some species belonging to section *Piperati* of *Suillus*, combined with the findings of Bresinsky & Rennschmid (1971) on the distribution of pigments in this group have made it necessary to separate this section from *Suillus* and to recognize Bataille's genus *Chalciporus*, inasmuch as this will also make the mycorrhizal specialization of the remaining sections of *Suillus* more uniform (see also Benedix, 1963).

**Chalciporus piperatus** (Bull. ex Fr.) Sing., *c. n.* Basionym: *Boletus piperatus* Bull. *ex* Fr., Syst. mycol. **1**: 388. 1821.

**Chalciporus rubinus** (W. G. Smith) Sing., *c. n.* Basionym: *Boletus rubinus* W. G. Smith *in* J. Bot., Lond. **6**: 33. 1868.

**Chalciporus rubinellus** (Peck) Sing., *c. n.* Basionym: *Boletus rubinellus* Peck *in* Rep. N.Y. St. Mus. nat. Hist. **32**: 33. 1879.

The anatomy of the scales of the stipe, the size of the spores and the characteristics of spore color and cystidia make it necessary to transfer *Boletus eximius* to *Leccinum* where it is placed in a new section close to sect. *Roseoscabra*:—

LECCINUM sect. **Eximia** Sing. A sectione *Roseoscabra* differt basi stipitis vix chromeo-lutea. — Typus sectionis: **Leccinum eximium** (Peck) Sing., *c. n.* Basionym: *Boletus eximius* Peck *in* J. Mycol. **3**: 54. 1887.

## 4. On Porphyrellus pseudoscaber

A revision of the species of the *Porphyrellus pseudoscaber* complex has made it clear that here we have two European species, one being *P. porphyrosporus* (Fr.) Gilbert which I have described as *P. pseudoscaber* var. *pseudoscaber* (1967: 109–111) and another which I have described as *P. pseudoscaber* var. *fuligineus* (Fr. in Fr. & Hök) Sing. (p. 112) but which is the true *P. pseudoscaber* (Secr.) Sing. (*B. fuligineus* being its later synonym).

*P. porphyrosporus* (Fr.) Gilbert is the bluing species, usually medium to large, growing in mixed and frondose woods, mostly at lower altitudes. *P. pseudoscaber* is the non-bluing species, usually small to medium, growing in coniferous woods, mostly in the lower montane zone.

The identity of *P. porphyrosporus* in the sense of Fries is easy to establish since Fries himself states that the pores become blue where bruised. Although Fries indicates the habitat as „in . . . pinetis" on sandy roadsides, it must be assumed that as in most such habitats in South Sweden *Fagus* was also present. The identity of *P. pseudoscaber* has been established by material collected by Ch.-Ed. Martin at the type locality

(Chalet-à-Gobet) September 2, 1894 where I have likewise observed it in 1971, in both cases under conifers ("sous les sapins", under *Picea*). The plate made by Martin is still in the Iconothèque Ch.-Ed. Martin at Geneva, Switzerland, and represents the earliest topotype in existence. Descriptive data fully establish the identity with *B. pseudoscaber* Secr. and *P. pseudoscaber* var. *fuligineus* (Fr. in Fr. & Hök) Sing.

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# NOTES ON MICHIGAN BOLETACEAE

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(With seven Text-figures and Plate 27)

Studies have continued on the diversity of the Michigan bolete flora. During the season of 1972 a variety of *Boletus affinis* Peck having a reticulate stipe was discovered and abundant material of *Boletus bicolor* var. *subreticulatus* Smith & Thiers was obtained. *Boletus hortonii* Smith & Thiers was collected on two occasions and a detailed description was prepared. *Boletus rubissimus* sp. nov. is described. Specimens of *Leccinum aurantiacum* from France are reported upon, and color variants in *Suillus* are discussed. In *Tylopilus* amyloid reactions in *T. sordidus* are discussed and *T. subfusipes* is described as new.

Since publishing 'The Boletes of Michigan' (Smith & Thiers, 1971), Smith has continued his study of this group in the state with the result that a number of new problems have been discovered as well as data have been obtained on a number of problems of long standing. In the following account some of the more interesting items resulting from continued field work in the state are presented.

One was the discovery, by Mrs. Florence Hoseney, of a *Tylopilus* growing in connate clusters and having narrow spores and a bitter taste. Another was the discovery of a variant of *Suillus brevipes* in which the pileus stains or flushes green over extensive areas. Also, the taxonomic value of the amyloid reactions in the *Tylopilus sordidus* complex still remain questionable because of the erratic pattern of appearance which they present. The problem, apparently, concerns metabolic products precipitated in a fortuitous manner so that similar results are never obtained in a consistent pattern from one fruit body to another, or even from different mounts from the same basidiocarp. This phenomenon is not restricted to the genus *Tylopilus* in the Boletaceae. Singer (1962) and Snell & Dick (1970) both described the genus *Xanthoconium* as having the stipe entirely smooth. Here in Michigan we have picked up a variant of *Boletus affinis* with the stipe distinctly reticulate.

The specimens cited have all been deposited in the University Herbarium of the University of Michigan (MICH). Color terms within quotation marks are taken from R. Ridgway, 'Color Standards and Color Nomenclature', Washington D.C. 1912.

BOLETUS AFFINIS var. **reticulatus**, *var. nov.*

Pileus 3–5 cm latus, late convexus, siccus, velutinus, ochraceo-brunneus ("Sudan brown"), non-maculatus, cum 'KOH' ferrugineus. Contextus albidus, immutabilis, mitis. Pori fulvo-

ochracei. Stipes 4–7 cm longus, 12–13 mm crassus; subalbidus, reticulatus; reticulum cinnamomeum. Sporae 10.5–14 × 3.5–4.5 μ. Highland Rec. reaction. Area, Oakland County, Michigan, July 24, 1972, A. H. Smith 81176 (typus, MICH).

Pileus 3–5 cm broad, hemispheric to broadly convex, dry, velvety to merely unpolished, evenly colored "Sudan brown" to "buckthorn brown" overall (a rich yellow-brown), margin flush with the tubes; KOH on cuticle ferruginous; $FeSO_4$ no reaction. Context whitish, taste slight, odor not distinctive, with KOH: no color change.

Tubes mature, all dull amber-brown, adnate, plane, spotting rusty ochraceous to dull "Sudan brown," no blue stains evident; pores minute, nearly concolorous with the pileus when mature.

Stipe 4–7 cm long, 12–13 mm thick, equal, solid, distinctly reticulate overall with a brown ("Sayal brown") reticulum on a pallid to brownish ground color, base white and naked at first, the brown color gradually extending baseward until entire stipe is colored.

Spore deposit rusty ochraceous. Spores 10.5–14(–15) × 3.5–4.5 μ, smooth; in profile narrowly inequilateral, in face view suboblong to bluntly navicular, bright ochraceous in KOH, pale rusty brown in Melzer's.

Basidia 4-spored, clavate, 6–7 μ broad, hyaline in KOH. Pleurocystidia scattered, subaciculate, 30–45 × 6–9 μ, hyaline in KOH, in Melzer's many seen to have a ± granular dark yellow-brown content. Cheilocystidia similar to pleurocystidia and hyaline, some clavate cells with golden-ochraceous incrustations also present. Caulocystidia abundant, clavate, 25–38 × 10–18 μ, hyaline and thin-walled in KOH, yellow in Melzer's; small dextrinoid particles and incrustations present and these very abundant on cortical hyphae as revived in Melzer's.

Tube trama with boletoid hyphal arrangement (hyphae diverging from a central strand.). Pilear cuticle a closely packed trichodermium of inflated cells 9–18 μ wide giving an impression of a cellular layer (epithelium) but the terminal cells ± cystidioid and acute to obtuse at apex, these cells up to 15 μ or more wide and the layer yellow in KOH except for the hyaline ultimate and penulatimate cells; dextrinoid debris conspicuous in the cellular layer. Tramal body of wide (12–15 μ) hyphae with fine particles scattered in the intercellular spaces or on the hyphal walls (not as dextrinoid as the particles in the cuticle). Clamp connections none.

Gregarious under oak-beech (old growth stand). Highland Recreation Area, Oakland County, Michigan, July 24, 1972, A. H. Smith 81176 (type, MICH).

OBSERVATIONS.—This variant is clearly a "*Xanthoconium*" in the sense of Singer. It is closest to *Boletus affinis* var. *affinis* but differs sharply in the stipe being reticulate (quite obviously so) to near the base, and in having spores measuring slightly smaller. The degree to which dextrinoid debris occurs in the tissues of var. *reticulatus* is rather striking, but its taxonomic significance remains to be established.

### BOLETUS BICOLOR var. SUBRETICULATUS Smith & Thiers

During the season of 1972 near Oak Grove in Livingston County, Michigan, fruitings of hundreds of basidiocarps were observed, and variation within *B. bicolor*, especially var. *subreticulatus*, was studied in detail. The following characters were observed:—

(1) The reticulum at the apex of the stipe: It is obscure in most young basidiocarps, but evident at maturity and in age, and is to be regarded as a rather con-

stant feature of freshly matured fruit bodies. It is present to the same degree that one finds it in *Boletus sensibilis* Peck. (2) The color of the pileus: It is very close to "brick red" and soon fades so that mature caps have usually lost the deep red tone. In fact about half of all the basidiocarps seen had lost nearly all the red tints (but were, admittedly, past maturity). The red pigment is located in the epicuticular hyphae and as these are pulled apart by the expansion of the pileus, yellow becomes the dominant color. (3) The tubes: They were typically adnate-decurrent and short. They often split instead of separating when broken downward. In var. *bicolor*, they tend to become depressed around the stipe and to separate when broken downward. (4) Staining reactions: The context, tubes and stipe readily changed to blue when injured. (5) Size: The dimensions as recorded on paper may create a false impression as to the proportions of the fruit body. Var. *subreticulatus* typically has a slender stipe in relation to the width of the pileus. Young stages resemble closely Peck's (1872) illustration of the type variety. In none of the basidiocarps did one get the impression of a thick-stiped species as shown in the upper figure of Snell & Dick (1970). However, these authors have dealt with the variants of this species remarkably well in their plate 40 (1970). Their upper figure is of the robust variant of the type variety as I have always known it since my student days. Their central lower figure appears to me to be typical of var. *subreticulatus*. The figures to the left and to the right represent the type variety as illustrated by Peck. The point of all this is that to me the robust variant is a true *Boletus* in the sense of Singer (1962), whereas *B. bicolor* var. *subreticulatus* is a "*Xerocomus*" a genus I do not recognize as distinct from *Boletus*.

### BOLETUS HORTONII Smith & Thiers—Pl. 27

This bolete was first described as *Boletus subglabripes* var. *corrugis* by Peck. The very irregular pilear surface obviously influenced the choice of the varietal epithet. Since no critical account based on fresh specimens is available. the following one is offered:—

Pileus 5–9 cm broad, convex, becoming broadly convex, surface coarsely rugulose-pitted and uneven, often more so toward the margin, color variable–reddish cinnamon with olive-brown areas or rather evenly colored by either of these colors, redder in drying but some pilei retaining olive-buff areas, margin even. Context whitish becoming yellow over the tubes, pinkish under the cuticle, taste mild (or the cuticle slightly acid-bitterish), when cut showing occasional very weakly bluish areas and the line above the tubes becoming bluish green; KOH on cuticle merely brownish.

Tubes about 1 cm deep at maturity, yellow at first, greenish in age, very faintly blue where bruised or cut, adnate or depressed around the stipe; pores minute, yellow at first, olive-green in age, staining slowly to dull cinnamon if bruised.

Stipe 4–8 cm long, 12–18 mm thick, equal, pith white, cortex yellow (and color more pronounced in age); surface bright yellow, naked to pruinose, in age discolored below to ± cinnamon buff.

Spore deposit olive-brown. Spores 13–15 × 4–4.5 $\mu$, smooth, inequilateral in profile, in face view navicular to subelliptic, weakly ochraceous to pale tawny in KOH, yellowish to tan in Melzer's; wall about 0.3 $\mu$ thick.

Basidia 9–10.5 μ broad near apex, clavate, 4-spored, hyaline in KOH and practically so in Melzer's. Pleurocystidia none found. Cheilocystidia narrowly elongate, 40–65 × 2–3 μ (at base) × 4–5 μ at apex, this type typically originating from a ventricose cystidium-like cell as an apical proliferation differentiated by a septum; some aciculate to fusoid-ventricose cells also present on tube edges, these 18–27 × 3–5(–10) μ, hyaline and smooth. Caulocystidia in patches of caulohymenium, dextrinoid when first revived in Melzer's but soon fading, tubular with a blunt apex and measuring 25–50 × 5–8 μ, arising as the terminal cell of a filament or as an apical prolongation of a ventricose cell 10–15 μ wide.

Tube trama of hyphae divergent from a central strand (the boletoid type), hyaline to yellowish in KOH and in Melzer's respectively. Pilear trama of interwoven hyphae 8–20 μ wide, yellowish to hyaline in KOH or Melzer's but with a strong "fleeting amyloid" reaction. Hyphae of stipe cortex perpendicular, 7–25 μ wide, walls of some hyphal cells thickened to 2 μ or more and the wall distinctly amyloid under the microscope (but often only in the region near the septa or in the thickened part of the wall, many cells entirely inamyloid and thin-walled), some cells with both deep red and blue present in different areas. Clamp connections not found.

Gregarious on humus in low oak woods, Highland Recreation Area, Oakland County, Michigan, July 24, 1972, A. H. Smith 81172, 81188. The collections were made in the same woods but about a mile apart.

OBSERVATIONS.—The above description is drawn entirely from the collections cited to avoid any possible confusion. The positive features which cause me to identify these collections as *B. hortonii* are the rugose-pitted roughened pileus, the aspect of *Boletus subglabripes*, the very slight bluing reaction, the spore size, and the details of the pileus cuticle. On the other hand, the characters noted in these collections which appear to distinguish them from the type of *B. hortonii* are the elongated narrowly clavate proliferations from ventricose cells—here termed cheilocystidia, and which appear to be a secondary development—and the amyloid reactions of the cortical cells of the stipe in freshly dried mature basidiocarps.

At the present time, however, I do not feel justified in using these features in establishing a 'new species'. Since the proliferations of the cuticular cells of the pileus are a feature of Peck's type, and since the elongated cheilocystidia of the 1972 collections are most numerous on the older basidiocarps for the present I interpret them as an expression of one and the same genetic set of factors. At least this seems to be the sensible course to follow until a much larger sample of the species is availabke for study.

The amyloid reaction on the hyphae of the stipe was demonstrated on old but not on young material. Also, it tends to fade in an hour or so. I was unable to demonstrate it on other collections (from Massachusetts and Ohio as well as from Michigan) which have been in the herbarium for a number of years. This is unusual for the iodine reactions generally are more reliable on dried material that has been in the herbarium for many years than on fresh or recently dried specimens. No amyloid reaction was found on the cortical hyphae of the stipe of *Boletus subglabripes*. Because of these considerations, I prefer to study the problem further. One point, however, was clearly emphasized by the 1972 collections: *Boletus subglabripes* and *B. hortonii*

are very closely related, and have no close relationship to the genus *Leccinum* other than the fact they are boletes. The stipe in *B. hortonii* is less distinctly ornamented than that of *B. subglabripes*.

### Boletus rubissimus, *sp. nov.*

Pileus 4–9 cm latus, convexus demum late convexus, impolitus, siccus, canescens, rubissimus ("Pompeian red"), demum ad marginem sulphureus vel ochraceo-roseus. Contextus pallide luteus, immutabilis, mitis. Pori laete lutei, 2–3 per mm. Stipes 7–9 cm longus, 16–23 mm crassus, sursum laete luteus, deorsum flavus, tactu caeruleus, pruinosus; pruina laete rosea. Sporae 9–11 × 3–4 $\mu$. Highland Recreation Area, Oakland County, Michigan, July 25, 1972, A. H. Smith 81187. (typus, MICH).

Pileus 4–9 cm broad, convex becoming broadly convex, surface unpolished and dry when very fresh with a hoary sheen, "Pompeian red" over all at except the bright yellow ("sulphur yellow" or more ochraceous) margin, disc retaining the pinkish red tones. Context thick, pale yellow, taste mild, not staining blue when cut or only weakly so and then in very limited areas. KOH on pilear cuticle: slowly yellow on the pink surface; $NH_4OH$: no color change on pilear cuticle; $FeSO_4$: on context gray.

Tubes (all young) 2–4 mm deep, bright yellow, staining a grayish blue when injured, depressed around the stipe; pores minute (2–3 per mm in young material), lemon-yellow becoming dingy near maturity.

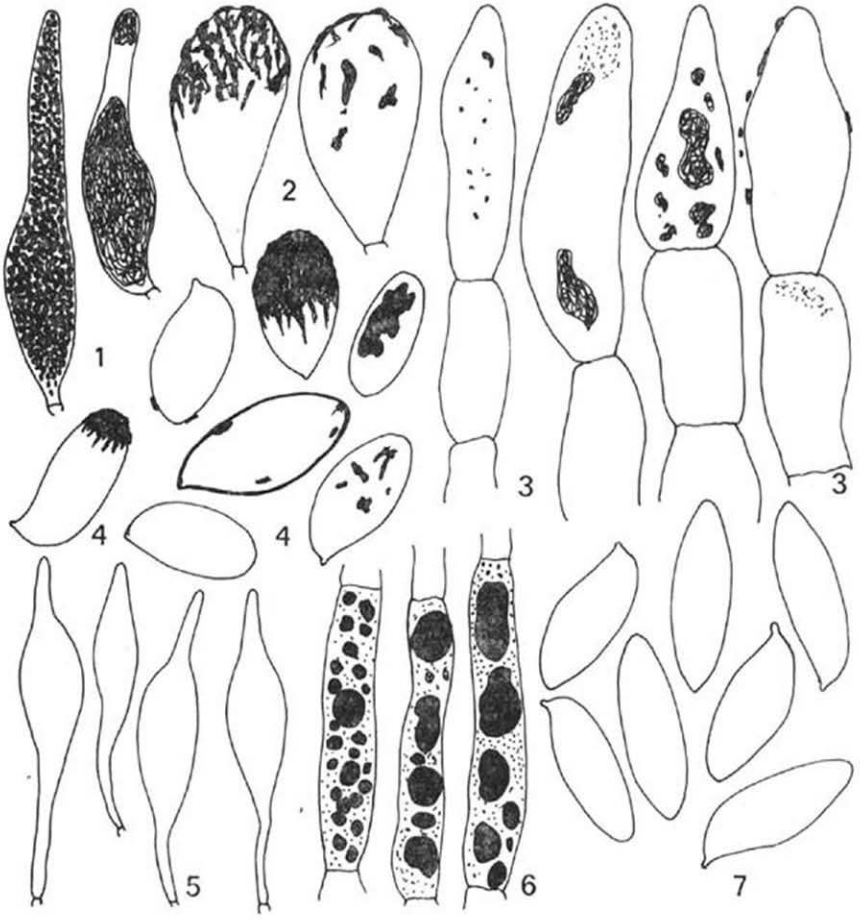
Stipe 7–9 cm long, 16–23 mm thick, equal, solid, pale yellow above, flavous below, when cut turning blue in local areas near base and these eventually reddish stained, paler yellow above; surface flushed pompeian red over lower portion and pruinose, yellow above and there finely reticulate, yellow mycelium around base.

Spores 9–11 × 3–4(–4.5) $\mu$, smooth, yellowish in KOH and yellowish hyaline in Melzer's, in profile somewhat inequilateral, in face view almost oblong varying to narrowly ellipsoid, wall thin (–0.2 $\mu$ thick).

Basidia 28–34 × 7–9 $\mu$, 4-spored, clavate, hyaline in KOH and yellowish in Melzer's. Pleurocystidia numerous, 37–55 × 9–14 $\mu$, fusoid-ventricose and tapered to an acute apex, hyaline in KOH or in Melzer's, thin-walled, smooth, content not distinctive ('empty'). Cheilocystidia either similar to pleurocystidia or smaller (20–35 × 4–10 $\mu$) and aciculate to clavate, remaining yellow in KOH (on fresh material) for sometime before fading, some yellow incrusting material seen on some cells (but this not characteristic). Caulohymenium of cystidia and basidia, the cystidia 28–56 × 7–17 $\mu$, mostly fusoid to fusoid-ventricose and many with yellow content (in KOH), varying toward clavate (apex obtuse and neck lacking), thin-walled, smooth; flexuous filamentose elements also present in the layer.

Tube trama of hyaline thin-walled hyphae 6–9 $\mu$ wide, tubular or an occasional hypha with inflated cells up to 15–20 $\mu$ wide, wall in both types thin and hyaline, arrangement boletoid (hyphae divergent to subhymenium). Pileus trama of compactly interwoven hyphae 8–15 $\mu$ wide, walls thin and hyaline. Cuticle of pileus a basal layer of interwoven hyaline (in KOH) hyphae 3–7 $\mu$ wide from the upper surface of which arrises a trichodermium in patches of narrow hyphae (2–3.5 $\mu$), sparingly septate and with end-cells having parallel walls (in optical section) and the apex blunt, walls smooth and thin. Clamp connections none.

Scattered among bushes of *Vaccinium* under oak, Highland Recreation Area, Oakland County Michigan, Juli 25, 1972, A. H. Smith 81187 (type, MICH).




Figs. 1–4. *Tylopilus sordidus* (a variant). — 1. A pleurocystidum with granular amyloid content and one with coagulated amyloid content (revived in Melzer's). — 2. Cheilocystidia with amyloid material adhering to surface. — 3. Cells from pilear trichodermium with amyloid content and amyloid incrusting material. — 4. Spores with amyloid incrusting material and amyloid content.

Figs. 5–7. *Leccinum aurantiacum*. — 5. Pleurocystidia. — 6. Hyphae from pilear cuticle showing pigment globules and granules. — 7. Spores.

Spores as reproduced approximately × 600; hyphae and hyphal end-cells approximately × 425.

OBSERVATIONS.—The salient features of this bolete are the fine reticulation over the uppermost portion of the stipe, the most beautiful deep pink color of the pileus imaginable (and which is persistent over the disc), the short spores, and the weak and sporadic color change to blue in the context of the pileus and upper part of the stipe. It is a fifth species in the stirps *Regius* of *Boletus*. *Boletus speciosus*, *B. peckii*, and *B. pseudopeckii* are the others. *B. rubissimus* differs from *B. speciosus*, the most similar one of the group, in shorter spores (9–11 × 3–4.5 μ compared to 11–15 × 3–4 μ), in having a weak and spotty change to blue except for the young tubes, and in the hoary sheen of young pilei along with the rather inconspicuous reticulation on the stipe. *Boletus pseudopeckii* is readily distinguished by its dull red pileus at first soon becoming brown, by its spores (10–14 × 3.5–4 μ), by the lack of any trichodermial development of the pilear epicutis, and more extensive development of the reticulum over the stipe. *Boletus regius* has spores 11–16 × 4–5 μ, and quite a different pattern of pigmentation, but the color change to blue in both appears to be rather similar (see Singer, 1967: 40). *Boletus peckii* differs in the strongly reticulated stipe (as described by Peck), a bitter taste (as reported by Coker & Beers), in having very few pleurocystidia and in having the hyphae of the pilear trichodermium 4–8 (–10) μ wide in sharp contrast to the 2–4 μ width of the hyphae as found in *B. rubissimus*.

LECCINUM AURANTIACUM (St-Amans) S. F. Gray—Figs. 5–7

Smith, Thiers & Watling (1966) published an account of this species based largely on American collections, but no neotype was designated. In fact it would have been inappropriate to do so, since the name originated with Bulliard and we did not study material from his area. But over the years there has been much confusion regarding the application of Bulliard's name — and I am afraid this confusion has been carried into the modern literature, see Singer, 1967, and Smith, Thiers & Watling, 1966.

Bulliard's (1809, 1812) plates 236 and 489 fig. 2, show an orange-red *Leccinum* with no overlapping sterile pilear margin, a feature which Smith & al (1966) used to distinguish the section *Leccinum* with *L. aurantiacum* as the type. Singer (1967) made the same mistake since he listed *B. versipellis* Fr. as a synonym of "*Leccinum aurantiacum* (Bull. ex St-Amans) S. F. Gray." (Fries described *Boletus versipellis* in 1838, p. 424 as follows: " . . . velo membran. annulari inflexo appendiculato . . ." a statement which clearly indicates an appendiculate pilear margin).

This situation was again brought to mind by a collection made south of Dôle, France, in the company of Dr. Vincent Demoulin of Liège, Belgium. We found a collection of three basidiocarps in perfect condition which answered perfectly to Bulliard's illustrations. To make a long story short, a description of this material follows:—

Pileus 8–12 cm broad, hemispheric to convex, becoming broadly convex, surface dry and dull, ferruginous (orange red) to deep ferruginous red (dark red), cuticle

continuous at first but toward the margin with minute appressed squamules, margin not distinctly appendiculate (a very narrow inconspicuous sterile zone present). Context white quickly changing to watery-vinaceous to vinaceousgray to bluish fuscous, odor and taste pleasant.

Tubes 1.3–1.5 cm deep in mature pilei, depressed around the stipe, whitish to "ivory yellow" (very weakly yellowish) to grayish, staining as in the context if injured; pores small, whitish to (temporarily) ivory yellowish, dark gray or brownish in age, if rubbed lightly staining yellowish, if severely injured changing as in the context.

Stipe up to 12 cm long and 3.5 cm thick, enlarged evenly downward, ground color white; ornamentation black in age, white at first and becoming reddish to reddish brown before blackening, darkened areas may be in a subreticulate pattern, no blue staining evident.

Spores 12–15 × 3.5–5 $\mu$, smooth, narrowly inequilateral in profile, in face view narrowly subfusoid, apex lacking a pore, color in KOH dull cinnamon, in Melzer's pale dull cinnamon. Basidia 4-spored, 9–12 $\mu$ wide at apex, hyaline in KOH. Pleurocystidia 34–56(–63) × 9–14 $\mu$, fusoid with acute apex, thin-walled, smooth, hyaline and 'empty' as revived in KOH. Pileus cuticle of appressed hyphae containing a dissolved red to orange pigment and 5–10 (12–20) $\mu$ wide, wall in wide hyphae with an irregular hyaline outer thin sheath (revived in KOH).

OBSERVATIONS.—The pileus dries rusty reddish as in American collections placed under this name. Smith & al. (1966) used, as one of the distinguishing features of the 'type' variety of *L. aurantiacum*, the fact that the intracellular pigment in many cuticular hyphae, when revived in Melzer's, rounded up into 'pigment globules' which were 0.5–10 $\mu$ in diam. The collection from France also shows this character clearly. But the American '*L. aurantiacum*' and Bulliard's species differ sharply in the degree to which the sterile pilear marginal membrane develops, and in its behavior as the pileus expands. If we formulate a concept from Bulliard's plates with microscopic characters added from the collection south of Dôle, France, we have the following: (1) pileus margin not distinctly appendiculate; (2) pileus ferruginous red (orange-red); (3) ornamentation of stipe passing from white through reddish to reddish brown before becoming blackish; (4) tubes pallid (whitish) or so lightly tinted yellow as to be scarcely yellow at all; (5) pigment globules in some of the cuticular hyphae of the pileus as revived in Melzer's; and (6), the cut flesh changing through reddish to fuscous. I believe that a neotype should be selected to 'anchor' Bulliard's name to a fungus with the above six essential features, or perhaps in the interim, regard Bulliard's two published plates as a substitute for the type. Our collection is not sufficient to establish a neotype and make the proper distribution of specimens. But it does serve, along with the account by Kühner & Romagnesi (1953: 40) which emphasizes the color of the intracellular pigment, to clearly show that a *Leccinum* with a red pileus and a non-crenate pilear margin does exist, and in my estimation must be regarded as the type-variant of the species. The American variant previously designated as the type differs in the distinctly appendiculate pilear margin as previously stated.

*Leccinum insigne* has the color of *L. aurantiacum* in its type variant, but the pigment is not stable and breaks down in drying so that dried specimens can be distinguished

at a glance. Both have some very wide epicuticular hyphae which form the fibrils noted near the margin. Both the American and European *L. aurantiacum* have pigment globules in some of the cuticular hyphae, but these are absent in the type of *L. insigne*. Thus the two species are more readily distinguished in the herbarium than in the field.

### SUILLUS BREVIPES (Peck) Kuntze

Smith & Trappe (1972) published an account of collections of *Suillus imitatus* Smith & Thiers, in which the pilei became flushed with olive to dark bluish green, yet signs of deterioration of any kind in the basidiocarp were absent. In some instances pilei that were entirely dark green were observed. We thought that *S. imitatus* was the only species in which this change occurred, but on October 13, 1971, at Midland, Michigan, under *Pinus resinosus* it was observed in *S. brevipes* (Smith 80863). Four out of five basidiocarps in the group showed splashes of dull green on the pileus. These varied in extent with the individual fruit body but in no case did they cover more than half of the pileus.

*Suillus imitatus* is an annulate species not closely related to *S. brevipes* within the genus *Suillus*. Therefore the possibility that only one species is involved in this green-staining phenomenon is ruled out. The only common environmental factor was that in both instances the collections were found after periods of cold rain. No freezing was involved that I am aware of though night temperatures had been low in each area.

The variant of *S. imitatus* was formally described as a variety but the designation of *forma* as a category might be more logical in view of the Michigan find. Before making any formal changes, however, it would be advisable to know more about the nature of the change and its possible occurrence in still other species.

The microscopic data on Smith 80863 are as follows: Spores 7–8 × 2.8–3.2 $\mu$, smooth, in face view oblong to narrowly boat-shaped, in profile obscurely inequilateral, nearly hyaline in KOH. Basidia 15–21 × 5–6.5 $\mu$, clavate, 4-spored. Pleurocystidia in clusters surrounded by rusty brown incrusting material or some of this in the cells themselves, the cystidia 4–6 $\mu$ wide, cylindric, and variable as to length. Cheilocystidia not seen (edge may be identified of copious incrustations obscuring cellular detail). Pellicle of pileus an ixocutis as revived in KOH. Clamp connections not found.

### TYLOPILUS SORDIDUS (Frost) Smith & Thiers—Figs. 1–4

Smith & Thiers (1971) commented on the amyloid reactions of tissues in a collection (Hoseney 538) identified as this species (but with reservations). On July 25, 1972 at the Highland Recreation Area, Oakland County, Michigan, a collection (Smith 81193) was made in which the basidiocarps shed further light on the amyloid reactions of species in this genus. Four basidiocarps were found growing solitary, each 100 yards or more from the others, along a trail through hardwoods. All were

studied individually before being grouped under the above mentioned collection number. One basidiocarp was just past the button stage, two were mature, and one was old. In the youngest stage amyloid debris or adhering amyloid material or amyloid cell content was difficult to find, but after much searching, three examples of it were found in the fresh material in the pilear cuticle. It was also sparingly demonstrated again after the specimen had been dried. In the mature group material was found capping some cheilocystidia, it was rare (but present in places) in the pilear cuticle, it occurred in a few pleurocystidia as a granular content, and in or on some immature basidiospores. In the old specimen amyloid material distributed as described above occurred with greater frequency in both fresh and dried specimens. When found capping cheilocystidia or spores, rod-like extensions of amyloid capping material (resembling chromosomes stained with crystal violet) were evident. Within the spores there was no pattern for the amyloid bodies observed either as to shape or age of spore. Very rarely a spore with interior amyloid bodies was found in which the apex was capped by amyloid material.

The characteristic inflated cheilocystidia of *T. sordidus* were present in all basidiocarps, but the large thick-walled spores mentioned by Smith & Thiers (1971) were absent to very rare and were demonstrated satisfactorily only in the oldest basidiocarp. In all the basidiocarps the context stained blue slowly and then reddish, the tubes were gray in all, and the stipe was pruinose but not reticulate.

The collection discussed here is still regarded as a variant of *T. sordidus*. The behavior of the amyloid material suggests that it is a transient stage in the development of the basidiocarp or possibly a product produced in small amounts which accumulates as the basidiocarps age. Since the location of the material cannot be predicted, i.e. on cystidia, on or in spores, or in cells of pileus cuticle or on them, it does not meet the criteria of a valid taxonomic character. It must also be remembered that the presence of this material has been noted for a number of species of the Boletaceae.

## Tylopilus subfusipes, *sp. nov.*

Pileus 4–8 cm latus, convexus, glaber, subviscidus, variegatus (pallidus et griseo-brunneus vel subspadiceus), pelliculosus; contextus amarus, inodorus, subgelatinosus; tubuli albidi demum incarnati; pori griseo-albidi demum incarnati, tactu tarde brunnei: stipes 4–6 (–8) cm longus, 10–15 mm crassus, deorsum attenuatus, non-reticulatus, pallidus vel sordide brunneus, udus, tactu incarnato-brunneus; sporae in cumulis incarnatae; 10–13.5 × 2.9–3.3 $\mu$. Prope Pinckney, Michigan, Livingston County, August 11, 1972, Florence Hoseney 2226 (typus, MICH).

Pileus 4–8 cm broad, convex to plane, the margin wavy and turned up in age, glabrous, tacky to subviscid fresh, surface mottled to variegate (color uneven, pallid in some areas, dingy yellow-brown elsewhere and with some areas grayish brown — reminding one of a medium-dark pileus of *B. griseus* Frost in Peck); pellicle often separable as a thin hyaline layer. Context watery-mottled, soft, taste bitter, odor not distinctive, with $FeSO_4$ olivaceous.

Tubes separable from pileus, 4–5 mm deep, whitish, becoming delicate pink,

adnate to subdecurrent; pores about 2 per mm, staining rusty vinaceous then a dingy brown when bruised.

Stipe 4–8 cm long, 10–15 mm at apex, tapered to a point below (connate), surface uneven but not reticulate, ground color whitish but obscurely streaked or flushed pinkish brown, not viscid but feeling wet to the touch, where cut staining dingy pinkish brown.

Spore deposit dingy pink, about as in *T. felleus* (Fr.) Karsten. Spores 10–13.5 × 2.9–3.3 $\mu$, smooth, apex lacking apical differentiation, color in KOH hyaline and nearly so in Melzer's; shape in face view suboblong to narrowly subfusoid, in profile narrowly inequilateral.

Basidia 4-spored, clavate. Pleurocystidia clavate to submucronate, 9–13 $\mu$ broad, content reddish in Melzer's in fresh material but amorphous and ochraceous in dried material (in both Melzer's and KOH), imbedded in the hymenium. Cheilocystidia basidiole-like but mostly yellow revived in KOH or Melzer's.

Pileus cuticle a thick tangled layer of hyphae 3–5 $\mu$ broad and appearing to be separated by slime, yellowish in Melzer's; no amyloid debris, incrustations, or distinctive cell-content seen. Clamp connections not present.

Cespitose-gregarious under oak, near Pinckney, Livingston County, Michigan, Aug. 11, 1972, Florence Hoseney 2226, (type MICH).

OBSERVATIONS.—The pellicle of the pileus, the connate stipes, the very narrow spores and yellow cystidial content as revived in Melzer's along with lack of reticulation on the stipe, distinguish this species among the bitter ones with vinaceous spore deposits. The wet consistency and 'feel' along with the very soft subgelatinous tissues (pileus and tubes) are also striking features.

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## EXPLANATION OF PLATE 27

*Boletus hortonii*. Smith 81188, × 1.

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# PENICILLIUM DONKII SP. NOV. AND SOME OBSERVATIONS ON SCLEROTIAL STRAINS OF PENICILLIUM FUNICULOSUM

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(With one Text-figure)

A description and drawings of a new species of *Penicillium*, *P. donkii*, are presented. *Penicillium purpurogenum* Stoll var. *rubri-sclerotium* Thom is considered a synonym of *P. funiculosum* Thom. Some observations are recorded, especially in connection with the cultural appearance of sclerotial strains of *P. funiculosum*.

From arable soil in Alaska a number of cultures were isolated by L. K. Oliver and sent to the 'Centraalbureau' for identification. Among these one strain of *Penicillium* turned out to be sufficiently different from all known members of the genus to warrant its description as a new species. Since this isolate is characterized by dark brown, soft, sclerotium-like structures, it is compared with two other species of *Penicillium* which are also known to produce brown or black pseudoparenchymatous sclerotia: *P. novae-zeelandiae* and *P. funiculosum*.

**Penicillium donkii** Stolk, *sp. nov.*—Text-fig. 1

Coloniae in agaro Czapekii 25 °C, fere celeriter crescunt, modice floccosae, medio elato, albae vel bubalinae, conidiis griseo-viridibus abundantibus; nonnumquam pauca corpora alba setosa sclerotialia adsunt. Reversum primo roseolum, deinde brunneum. Coloniae 20 °C lentius crescunt, numerosa corpora alba setose formant, penicilli paucis intermixta.

Coloniae in agaro maltoso 25 °C celeriter expansae, stratum laxe textum modice sporulans formant; reversum brunneum transparet; corpora setose nulla vel rara. 20 °C corpora setosa abundant, penicillis intermixta.

Hyphae vegetativae primo hyalinae, demun luteolae, 2–6 μm diametro.

Conidiophora plerumque e hyphis aeriis, marginem versus nonnumquam e hyphis submersis oriuntur, simplicia, septata, hyalina, 20–300 × 2–3 μm, parietibus levibus vel fere levibus, sursum dilatata, 4–5.5 μm diametro. Penicilli monoverticillati. Phialides 10–12 verticillatae, e basi cylindrica et tubo conidiifero subito constricto, circa 1 μm longo, constant, 7.5–10 × 2.2–2.5 μm. Conidia subglobosa vel paene ellipsoidea, diluta viridia, 2.0–2.7 × 1.5–2.3 μm, levia vel fere levia, columnas ad 200 μm longas formant.

Corpora sclerotialia brunnea, plerumque discreta, globosa, 60–120 μm diametro, mollia, pseudoparenchytamosa, multis hyphis septatis, hyalinis, fere rectis, deorsum ramosis, radiantibus ad 300 μm longis, 1.5–2 μm crassis, circumdata, quae corpus brunneum omnino complectuntur. Status perfectus ignotus.

TYPUS CBS 188.72, isolatus a L. K. Oliver e solo agresti in Alaska.

Colonies on Czapek agar growing fairly rapidly, attaining a diameter of 4–4.5 cm within two weeks at 25 °C, azonate, consisting of a thin, loose-textured, more or

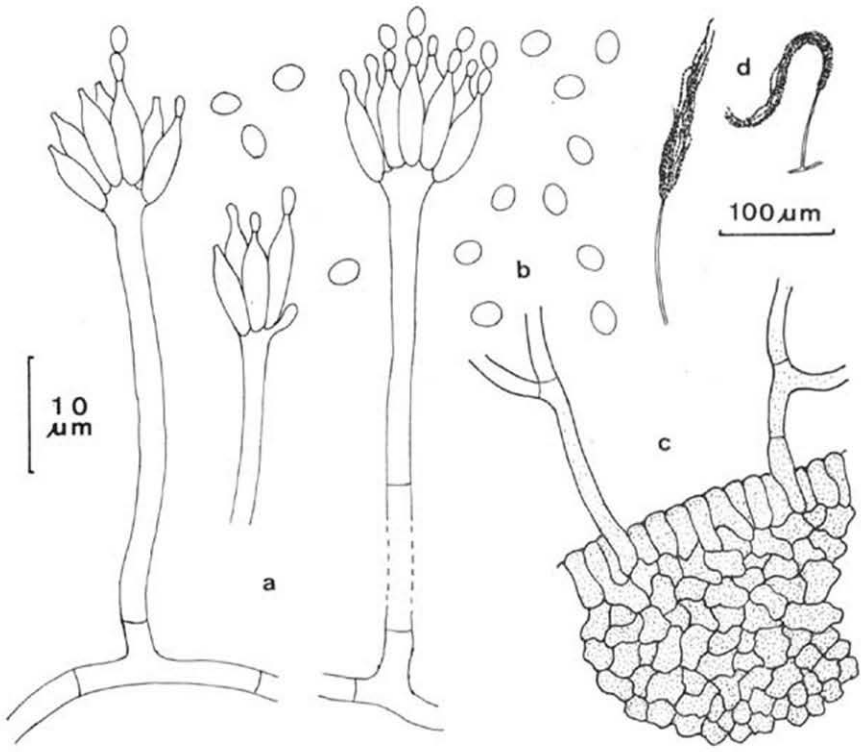


Fig. 1. *Penicillium donkii*, CBS 188.72. — a. Penicilli. — b. Conidia. — c. Section through a sclerotium-like body. — d. Habit sketches of penicilli showing conidial columns.

less floccose, basal felt; central areas raised, close-textured, nearly sterile, white to Vinaceous-Buff (Ridgway, Pl. 40; Rayner, 17'''d), bearing abundant conidial structures in marginal and sub-marginal areas, occasionally producing a few, white, setose, sclerotium-like structures; surrounded by a narrow, brownish zone, consisting mainly of submerged hyphae. Conidial areas greyish green, ranging from Celandine Green to Storm Gray, becoming Grayish Olive in age (Ridgway, Pls. 47, 52, 46; Rayner, 33''''b, 35''''', 21''''). Exudate lacking. Reverse at first pinkish, near Light Pinkish Cinnamon, later showing brown shades ranging from Snuff Brown to Bister, becoming Clove Brown in age (Ridgway, Pls. 29, 40; Rayner, 15''d, 15''k, 15''m, 17'''m). Colonies at 20 °C growing more slowly, developing numerous white, setose, sclerotium-like bodies, usually produced near the agar surface, but sometimes also occurring within the aerial mycelium, intermixed with a few penicilli; colour white to greyish.

Colonies on malt agar attaining a diameter of 6.5 cm within two weeks at 25 °C, zonate, consisting of a loose-textured felt, light-sporing throughout; dark brown, near Chaetura Drab, becoming Chaetura Black in age (Ridgway, Pl. 46; Rayner

17''''k, 17''''m), owing to the brown colour of the reverse showing through; setose bodies lacking or scanty. Reverse dark brown like the surface. Colonies at 20 °C consisting mainly of a layer of white, setose, sclerotium-like bodies, embedded in and overgrown by a loose aerial network, bearing abundant conidial structures, surrounded by a broad, brownish marginal zone consisting mainly of submerged hyphae. Reverse like at 25 °C.

Vegetative hyphae at first hyaline, later becoming yellowish brown, smooth-walled, 2–6 μm in diameter.

Conidiophores arising usually from the basal felt and from overgrowing aerial mycelium, in marginal areas sometimes developing from submerged hyphae, unbranched, septate, hyaline, variable in length, ranging from 20–300 μm in length by 2–3 μm in diameter, with walls smooth or nearly so, rarely covered with a few encrustations, apices enlarged, about 4–5.5 μm in width. Penicilli monoverticillate. Phialides in crowded whorls up to 10 or 12 in a verticil, consisting of a cylindrical base tapering abruptly to a short conidium-bearing tube (about 1 μm long), measuring 7.5–10 × 2.2–2.5 μm. Conidia subglobose to ellipsoidal, pale greenish, 2–2.7 × 1.5–2.2 μm, smooth or nearly so, forming well-defined, sometimes slightly twisted columns up to 200 μm in length.

Sclerotium-like bodies usually discrete, globose, 60–120 μm in diameter, hyaline when young, but soon becoming brown, soft, pseudoparenchymatous, consisting of comparatively small, irregular cells, about 2–3 μm in diameter, with the surface cells radially arranged; bearing numerous, septate, hyaline (at the base slightly brownish), radiating, fairly straight hyphae, up to 300 μm in length by 1.5–2 μm in diameter, a few times branched at the basal parts, completely obscuring the brown inner bodies and giving the structures a conspicuous white appearance even in old cultures. Perfect state not observed.

The species is mesophilic, optimum temperature 20–25 °C, maximum temperature somewhat above 35 °C. Development of setose bodies is more pronounced at 20 °C than at 25 °C.

TYPE CULTURE: CBS 188.72, isolated by L. K. Oliver from arable soil in Alaska.

The species is named after the late Dutch mycologist Dr. M. A. Donk.

*Penicillium donkii* cannot be placed satisfactorily in any of the series of the genus proposed by Raper & Thom (1949). The structures of the penicilli, the conidial columns, and the shape of the phialides are reminiscent of the *P. thomii* series. However, the soft, brown, sclerotium-like structures of the present species are quite different from the true sclerotia characteristic of the species of the *P. thomii* series. The sclerotia of the latter are typically very hard and gritty, consisting of large, almost colourless, polygonal cells with very thick walls. The dark brown, sclerotium-like bodies of *P. donkii* are suggestive of the reddish brown sclerotia produced by occasional strains of *P. funiculosum* Thom and the black sclerotia characterizing *P. novae-zeelandiae* Beyma. The sclerotia of the latter two species are much larger. They are pseudoparenchymatous and consist of large, thick-walled, brown cells, which are quite different from those of *P. donkii*. Moreover, they are not surrounded by long, conspicuous, radiating hyphae. In addition, *P. donkii* differs from the two species mentioned in producing monoverticillate penicilli.

Although classified by Raper & Thom in the *Biverticillata-Symmetrica*, *P. novae-zeelandiae* does not produce the lanceolate phialides characteristic of this section. The

penicilli of *P. novae-zeelandiae* are in much better agreement with those of the *P. raistrickii* series, but the sclerotia of *P. novae-zeelandiae* are quite different from those occurring in this series on account of their structure and black colour.

### PENICILLIUM FUNICULOSUM Thom

*Penicillium funiculosum* Thom *in* U.S. Dept. of Agr., Bur. Anim. Ind. 118: 69. 1910.
*Penicillium purpurogenum* Stoll var. *rubri-sclerotium* Thom *in* Mycologia **7**: 142. 1915.

*Penicillium purpurogenum* Stoll var. *rubri-sclerotium* was introduced by Thom (1915) for strains which have the deep red reverse in common with the parent species, but differ from *P. purpurogenum* in developing dark red to dark brown sclerotia on the surface of the agar. The type strain of this variety (CBS 270.35 = NRRL 1064) has lost its capacity to produce sclerotia and no longer develops its characteristic red reverse. The strain now produces fairly deep, funiculose, broadly spreading colonies. Examination of CBS 270.35 proved the conidial structures and the conidia to be quite different from those of *P. purpurogenum*. The conidiophores and especially the penicilli show greenish brown colours, thus agreeing completely with the corresponding structures of CBS 329.48 (= NRRL 1032a) regarded by Raper & Thom (1949) as representative of *P. funiculosum*. In addition, the conidial structures of CBS 365.48 (= NRRL 1066), identified by Raper & Thom (1949) as *P. purpurogenum* var. *rubri-sclerotium*, are also identical with those of *P. funiculosum*. The rate of growth and the red colour of the reverse of these sclerotial strains agree very well with Thom's original description of *P. funiculosum* (1910, p. 69) and with CBS 329.68.

As there is no character other than the production of sclerotia to separate *P. purpurogenum* var. *rubri-sclerotium* from *P. funiculosum*, a character that becomes useless as soon as the sclerotial strains have lost their sclerotia, the maintenance of this variety seems to have little sense.

Colonies of new isolates of sclerotial strains of *P. funiculosum* (CBS 883.72 and CBS 884.72) grow rapidly on most media but especially on malt agar. They are velvety or nearly so, at least near the margin, while trailing hyphae or strands of hyphae are observed only in the central areas. On Czapek the reverse is deep red. While marginal areas in some strains may be dark brown owing to the production of sclerotia, the latter occur only scantily in others. Sclerotium production is most abundant on malt agar at 25 °C. On this medium sclerotia are abundantly produced throughout the cultures, typically occurring in concentric zones. The sizes of the conidiogenous structures agree with those of the non-sclerotial strains. Conidiophores and penicilli are definitely green to brown coloured. Sclerotia are reddish brown to dark brown, globose to ellipsoid, often confluent, about 200–300 $\mu$m in diameter, pseudoparenchymatous, commonly overgrown by a very thin, inconspicuous weft of hyphae, often bearing a few conidial structures.

Raper & Thom (1949: 619) described an isolate of *P. funiculosum* (NRRL 1132) which produced reddish brown to dark brown sclerotium-like bodies resembling

those of the strains considered by them to represent *P. purpurogenum* var. *rubri-sclerotium*. According to these authors the sclerotia of NRRL 1132 are primarily produced within the substrate, whereas those of *P. purpurogenum* var. *rubri-sclerotium* were stated to develop on the agar surface. However, in the fresh isolates described above the sclerotia develop within the agar as well as on the agar surface.

Sclerotial strains have a strong tendency to degenerate. After a few transfers the colonies become more funiculose while after some years of subsequent laboratory cultivation the number of sclerotia decreases. This ultimately leads to the loss of the capacity to produce sclerotia. However, on Czapek agar some strains produce 'wet' colonies which consist mainly of submerged hyphae.

According to Raper & Thom's conception (1949), *P. funiculosum* is an extremely variable species, especially as regards the appearance of the colony. Broadly spreading as well as restrictedly growing strains belong to it. The colour of the colonies varies depending upon the amount and colour of the aerial mycelium which is usually yellow, red, but occasionally colourless. Moreover, the reverse may show such different colours as pink, red, yellowish or brownish. The older penicilli of the strains are often characterized by a greenish colour which may be lacking in young structures, but very striking in sclerotium-producing strains. The conidia of these strains are all very much alike.

A more detailed examination of a larger number of strains of *P. funiculosum* is necessary to decide on the desirability of a subdivision into varieties, based on cultural appearance and rate of growth.

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# BASIDIAL MORPHOLOGY AND HYMENOPHORAL DEVELOPMENT IN RHIZOPOGON

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(With 14 Text-figures)

Species currently assigned to *Rhizopogon* Fr. & Nordh. can be divided into at least two groups on the basis of basidial morphology and hymenophoral development. It is desirable that two genera should be recognized but problems of typification preclude a formal proposal to this effect. One group contains species with clearly dimerous basidia which are commonly associated with swollen, thickened or gelatinized basidioles and often arise laterally from these. The other is composed of species with clavate or cylindrical non-dimerous basidia which are not associated with modified basidioles. These observations show the potential value of using the developmental anatomy of the hymenophore in the taxonomy of Gasteromycetes. Fresh specimens in various stages of development are desirable; mature or dry specimens usually prove unsatisfactory.

## Introduction

In reference to early work by Fischer on the classification of Gasteromycetes, Lloyd (1902: 5) stated: "It seems to be the tendency of some writers to select the most obscure and difficult points on which to base classification. This has one advantage, it gives an air of greater learning. For our part we feel that a system based on points of difference of the mature plant obvious to the student, is more satisfactory and rational." Lloyd (1902: 4) also said: ". . . it is not a matter of policy to classify plants by minute anatomical differences which only an expert microscopist can trace. . ." Few mycologists would still agree with Lloyd on this issue, yet the fact is that most work on Gasteromycetes still relies heavily on mature fructifications and makes little use of detailed developmental anatomy. One wonders how much this may be due to the lingering influence of Lloyd's sharp pen, and how much to technical difficulties presented by Gasteromycetes. The basidia and other hymenial structures are best seen in young, fresh collections or those preserved in liquid, and usually collapse well before the fruitbodies reach their maximum size. Thus there are difficulties in using dry herbarium material, especially if the collector has carefully selected only older or larger specimens.

What follows is intended primarily to demonstrate the potential value of using hymenophoral anatomy and basidial morphology in the taxonomy of Gasteromycetes, and to show that it is also essential to take development into account. For this purpose a few species of the genus *Rhizopogon* have been studied.

## RHIZOPOGON Fr. & Nordh.

Only three species of *Rhizopogon* have so far been recorded in South Australia: *R. clelandii* G. H. Cunn., *R. luteolus* Fr. & Nordh. and *R. rubescens* Tul. (Cleland, 1935; Cunningham, 1944). Thus it would seem easy to identify the species collected locally by my colleagues in mycorrhizal associations with *Pinus*. However, Smith & Zeller (1966) detected at least fifteen species in the North American flora masquerading under the name of *R. rubescens* and indicated that *R. luteolus*, the type species of the genus, has been similarly confused by various authors. A further complication is that the litter even under a single tree may sometimes harbour more than one species of *Rhizopogon*, each with basidiocarps at various stages of development and thus very difficult to sort out. Or, again, isolated basidiocarps may be found. The problem is this: although the pattern of macroscopic change with aging has been recorded for some species (particularly by Smith & Zeller, 1966), isolated basidiocarps cannot reveal the full pattern and so can only tentatively be determined to species, while a range of material of all ages cannot in any simple way be recognized as belonging to one species unless there is a striking macroscopic character (such as a particular colour reaction to bruising or chemicals) which is present in all stages. It is probably fair to say that microscopic changes with aging, especially in the hymenium, have never been adequately investigated. Yet the importance of basidial morphology as a stable microscopic character has been demonstrated repeatedly with other basidiomycetes and should apply in *Rhizopogon*.

The purpose of this study was to investigate the development of the hymenium, basidia and associated structures in local specimens because the literature shows that these features have not been clearly understood in the past. The hymenium and basidia are difficult to examine in the more gelatinized species. Thin freezing-microtome sections of fresh specimens, mounted in ammoniacal Congo red, teased out and gently squashed under the coverslip, were found to give the best results; but even then it was not easy to determine the exact relationships and morphology of the various elements present. Pickled material gave reasonably good results, but dried specimens were virtually useless for this purpose (see below).

Most accounts of *Rhizopogon* state that the basidia are clavate or cylindrical and usually soon collapse; they usually have 6–8 sessile or subsessile spores, though there have been reports of basidia with 2–4 spores. It is indeed odd that the basidia should be described thus in generic diagnoses, and often in descriptions of species, when illustrations by various authors show that within the genus there are some species with clavate to subcylindrical basidia, e.g. *R. reticulatus* Hawker (1955: Fig. 1), *R. rubescens* sensu Hawker (1954: Fig. 29, $d_1$–$d_5$), and others with clearly dimerous basidia having a ventricose base and a cylindrical prolongation with an expanded apex bearing the spores, e.g. *R. rubescens*, *R. luteolus*, *R. roseolus*, and *R. nigrescens* sensu Coker & Couch (1928: Pls. 106–107). In some cases the descriptions do not match the illustrations for particular species. Smith & Zeller (1966) report the true situation: "... in most species the basidiole is clavate to subcylindric and as the spores

form it may remain clavate, it may elongate to cylindric, or the apex may elongate and the spores form on the narrow apex of the neck."

For the sorts of reasons given above I am still unable to determine local species of *Rhizopogon* and indeed do not yet know how many species are represented by our material. Thus I have to report this work on the basis of collections.

## Details of fresh collections

No. 1: ADW 16239, E. Davison, under *Pinus radiata*, Penola forest, Nov. 1971.

No. 2: ADW 16241, J. H. Warcup, under *Pinus radiata*, Kuitpo forest, Nov. 1971.

Nos. 3, 4, 5, 6: ADW 16242, 16243, 16244, 16245 (respectively), J. H. Warcup, under mixed *Pinus* and *Eucalyptus*, Kuitpo forest, Nov. 1971 (collected separately in areas not close to one another).

No. 7: ADW 16240, J. H. Warcup (E. M. 275), under mixed *Pinus* and *Eucalyptus*, Kuitpo forest, Oct. 1971. (Shown experimentally by Dr Warcup to be mycorrhizal with *Pinus radiata*.)

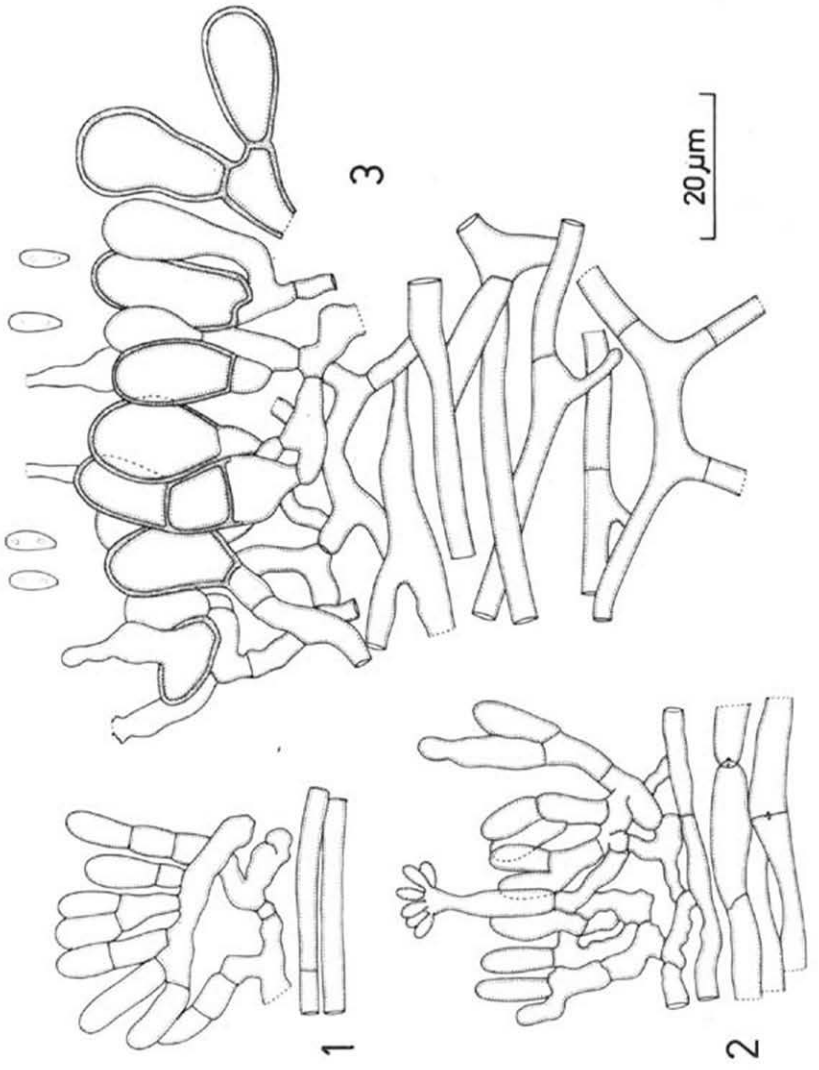
## Development in collection No. 1

This was a large collection of forty-five basidiocarps all found in a restricted area. Although various stages are represented it is certain that all belong to one species, there being a very characteristic bruising reaction common to all stages.

*Basidiocarps* 0.5–3.5 cm diam. *Peridium* externally white when young, later developing bright yellow areas, finally yellow all over, staining vinaceous in all stages when bruised, the bruised parts drying vinaceous-brown, not affected by $FeSO_4$ or ethanol, darkening to medium reddish-brown in KOH; peridium in section composed of a single layer of prosenchymatous hyphae with reddish granules, browning in KOH; hyphae of peridium thin-walled or slightly thickened, without clamps or inflated cells, septate, 3–10 μm wide; epicutis and latex vessels absent. *Rhizomorphs* pale at first, brown when old or dry, composed of hyaline to light brown septate hyphae without clamps, thin-walled, not inflated, mostly 2–5 μm wide, often branching at a wide angle; some central hyphae less branched, 6–11 μm wide, with the wall thickened to 1 μm. *Gleba* soft and gelatinous when fresh, becoming firm but not excessively hard on drying, whitish then pale yellowish and finally medium brown, with small meandering labyrinthiform locules. *Tramal hyphae* thin-walled, 2.5–6 μm diam., much branched, septate, without clamps, with occasional visible dolipores, without latex vessels. *Spores* present in basidiocarps from about 1.5 cm diam., fusoid-ellipsoid, thin-walled, light olivaceous, smooth, non-amyloid, with a truncate base and usually a pair of refractile polar inclusions, borne 6 per basidium, 6–8 × 2–3 μm.

*Hymenial development.*—The hymenium arises vertically from a more or less horizontal layer of hymenophoral hyphae, the vertical branches forming two or three subcymose or irregular ranks. The distal cells of these branches (probasidia) are cylindrical with rounded apices (Fig. 1). Some of these develop into metabasidia by putting out a short prolongation separated by a constriction from the lower part of the metabasidium and terminating in an expansion bearing six sessile basidiospores formed as buds from the apex (Fig. 2). These basidia measure about 6–18 × 4 μm. In a later stage such basidia are still found, but in addition some of the probasidial cells, and some of the proximal cells which bear them, have enlarged

considerably into ellipsoid or more often obovate cells (13–)16–22 × (7–)10–13 μm, with walls thickened to 1 μm or slightly more (Fig. 3). At this stage further basidia arise laterally from some of the enlarged cells and develop a much longer prolongation (more than 10 μm) than the original basidia. The basidia in this species are thin-




Figs. 1–3. — Development of dimerous basidia and hypertrophied basidioles in Collection No. 1.

walled at all times. An old hymenium consists mostly of enlarged thickened cells supported by a narrow hymenophoral layer. The median part of the hymenophoral trama consists of irregularly arranged hyphae which vary greatly in width over a short distance and are intricately branched.

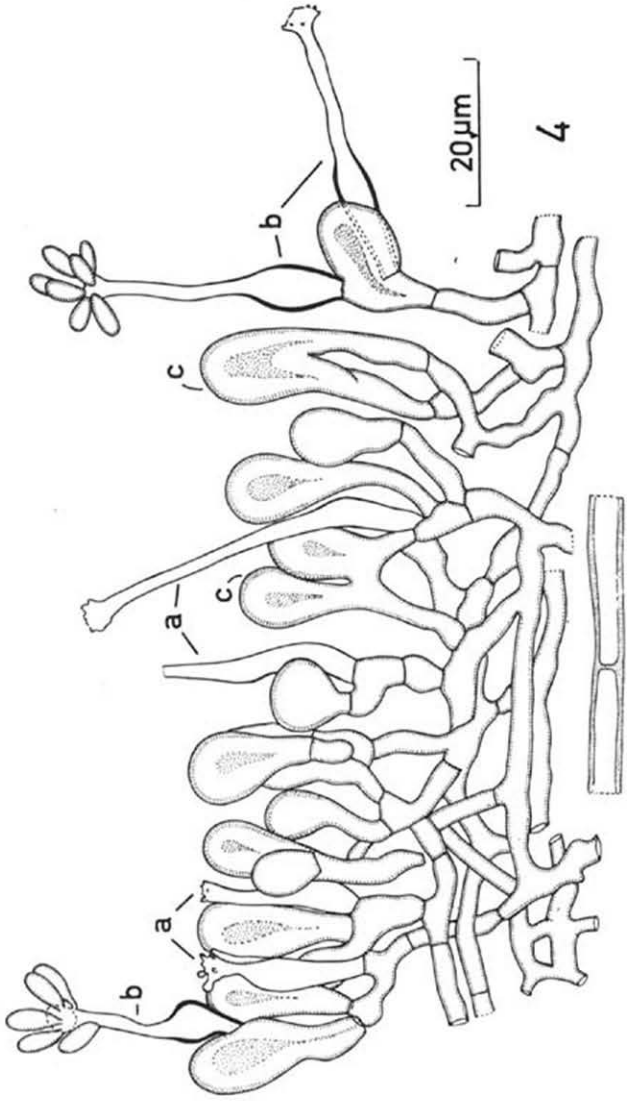
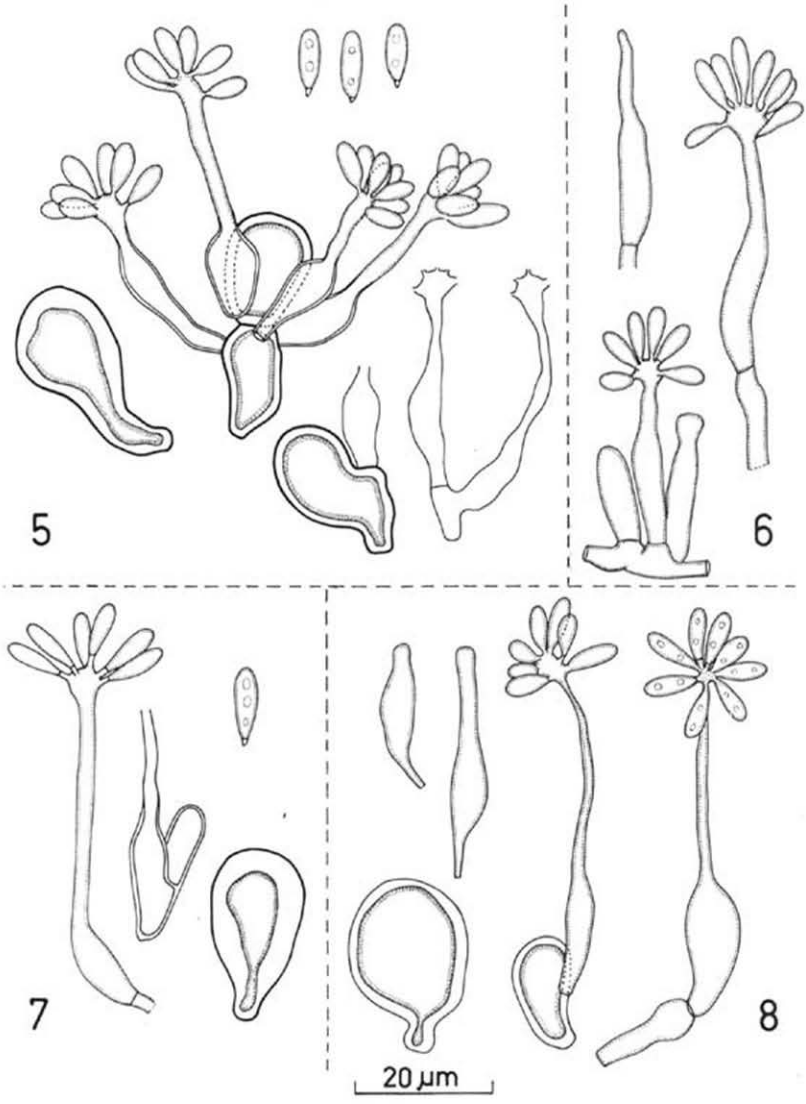



Fig. 4. — Mature hymenium in Collection No. 2. — a. Dimerous basidia arising from hyphae. — b. Dimerous basidia with thick-walled bases arising laterally from swollen gelatinized basidioles. — c. Anastomosed basidioles.




Figs. 5–8. — Collections Nos. 3–6 respectively. See text for details.

The basidia in this species are quite clearly dimerous, whether they arise directly from hymenial hyphae or laterally from the enlarged hymenial cells. The latter type of cell has usually been referred to in the literature as a 'paraphysis' but in origin it is an hypertrophied probasidium or basidiole. The hymenium changes so much in microscopic appearance with aging that young and old basidiocarps would probably be assigned to different species if the pattern of development were not known.

### Other collections with similar hymenia

Fig. 4 (Collection No. 2) shows a mature hymenium in which the basidia arise either directly from hymenial hyphae (4a) or laterally from hypertrophied basidioles (4b). The latter are strongly gelatinized, very thick-walled, and occasionally anastomosed (4c). The basidia are strongly dimerous, sometimes with the ventricose base becoming firm-walled (4b).

Fig. 5 (Collection No. 3) shows dimerous basidia arising either from hyphae or from hypertrophied basidioles. The main points of interest are that several basidia may be formed in a cluster from a single basidiole, and that the basidial walls become appreciably thickened towards the base.

The development of dimerous basidia is shown in Fig. 6 (Collection No. 4). No hypertrophied basidioles were found in this material which consisted of a single basidiocarp. The basal part of the metabasidium was subcylindrical rather than ventricose.

The basidial prolongations shown in Fig. 8 (Collection No. 6) are notable for being unusually tapered towards the distal end, and narrow in comparison with those in other collections.

In Fig. 7 (Collection No. 5) it is seen that the spores are clearly not sessile in this species but are borne on short sterigmata. The spores themselves, as in several other collections examined, are shortly pedicellate at the base, instead of truncate as in Fig. 3.

### Development in collection No. 7—Fig. 9

*Basidiocarps* 1–1.5 cm diam. *Peridium* externally pink, lacking an epicutis, in section composed of a single prosenchymatous layer of thin-walled to slightly thickened hyaline hyphae, 3–5 μm wide but inflated in short-celled portions to 15 μm wide, lacking clamps. *Rhizomorphs* whitish to reddish-brown, composed of parallel thin-walled septate hyphae, 2.5–5 μm wide, with frequent septa, lacking clamps, a few central hyphae becoming 10 μm wide. *Gleba* soft, gelatinous, white when fresh, with small meandering locules. *Tramal hyphae* 2.5–6.5 μm wide, thin-walled, hyaline with frequent septa and exceptionally large dolipores, lacking clamps. *Latex vessels* present throughout the trama though rather scanty, 3–7 μm wide, rarely septate, with homogeneous contents and walls that cannot be distinguished from contents. *Spores* fusoid-ellipsoid, 7.5–8.5 × 3–3.5 μm, hyaline to faintly tinted, not amyloid, thin-walled, smooth, with a truncate base, borne (2–4–)6–8 per basidium on sterigmata up to 2 μm long.

*Hymenial development.*—The hymenial branches arise vertically in 2–3 ranks of

subcymose or irregular branching from the subhymenial hyphae. The distal cells (probasidia) are subcylindrical with rounded apices. The spores develop directly from the apex from bud-like processes whose proximal part remains as a narrow sterigma which is eventually separated from the spore by a septum. The metabasidia

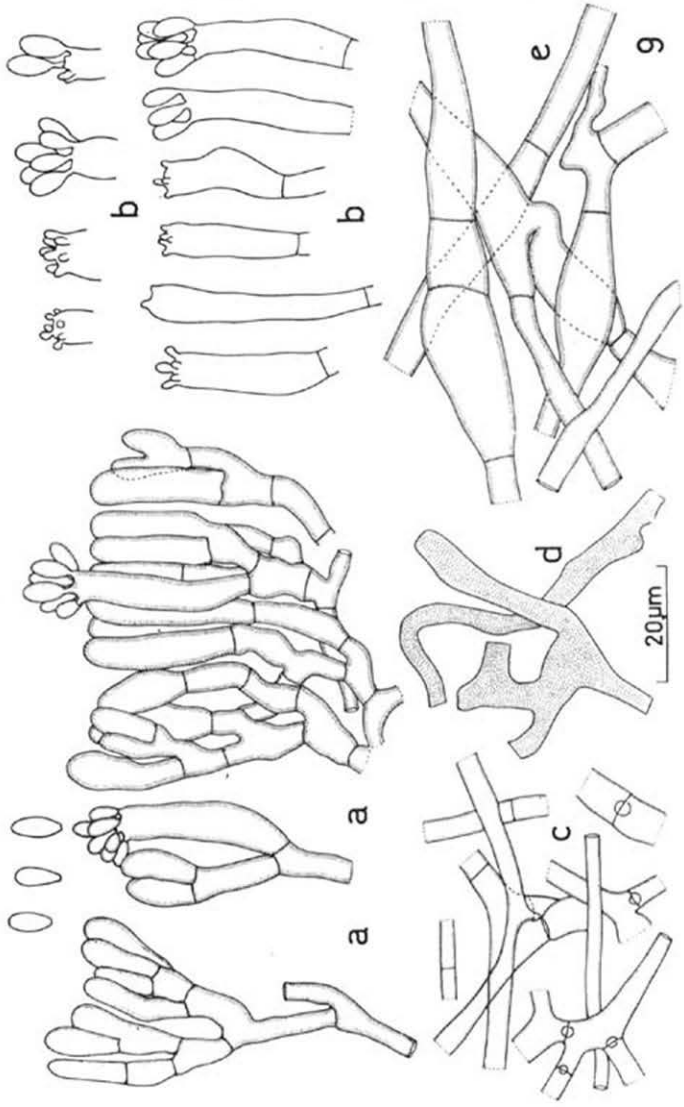



Fig. 9. — Development of the hymenium (a) and cylindrical basidia (a and b) in Collection No. 7. — c. Tramal hyphae with exceptionally large dolipores. — d. Laticiferous hyphae. — e. Peridial hyphae.

in this species are subcylindrical, not dimerous nor constricted, 23–27 × 5.5–7 μm, and they always develop terminally from hymenial hyphae. Hypertrophied basidioles are absent. The hymenium is finally composed of subcylindrical probasidia and scattered fertile subcylindrical metabasidia.

## Information from dried herbarium specimens

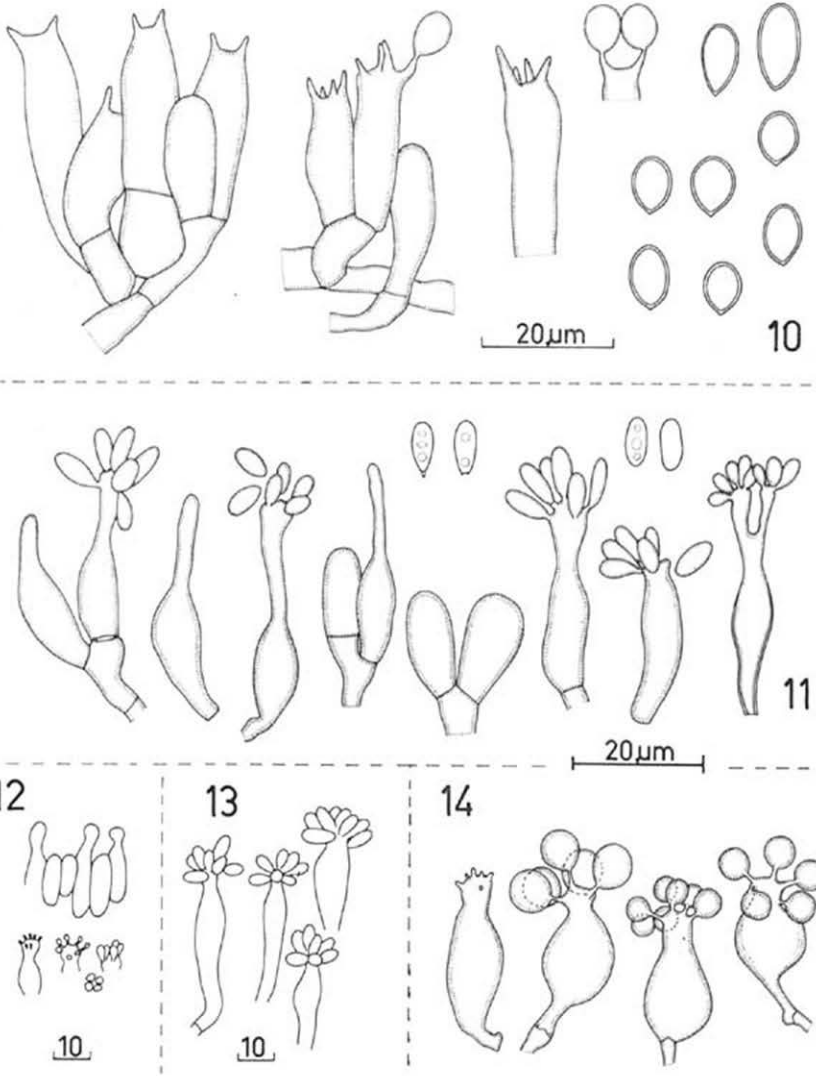
Twenty-one herbarium specimens of *Rhizopogon* species were examined. In only one collection was the state of preservation almost as good as in a fresh specimen. In general, the details of hyphae and spores were quite well preserved, but the hymenial structures had collapsed and were badly distorted. The presence of thickened basidioles, but not their details, could be determined in eighteen collections. In only nine of these was it possible to infer the presence of dimerous basidia from collapsed metabasidial prolongations emerging above the level of the hymenium. In the other collections basidia could not be seen. It was noted that the spores in some collections, even in a single preparation, varied from shortly pedicellate at the base to notched or truncate. Thus dried specimens were found to be of little use for determining details of hymenial structure.

Among the dried material examined was the type specimen of *Rhizopogon clelandii* G. H. Cunn. (Herb. ADW 6009). This, as shown in Fig. 10, has subcylindrical basidia, 19–36 × 7–8 μm, with two or four substantial sterigmata. Its spores are smooth, non-amyloid, thick-walled, non-guttulate, broadly ellipsoidal or pip-shaped, somewhat narrowed towards the small pointed hilum, 8–13 × 5.5–6.5 μm. I consider that it should not be regarded as a species of *Rhizopogon* sensu lato.

## Discussion

Among representatives of the genus *Rhizopogon* sensu lato there are at least two different types of hymenial development with associated differences in basidial morphology. Most species will probably be found to have dimerous basidia and a hymenium in which some or most of the basidioles finally become enlarged, thick-walled or gelatinized, and able to produce further basidia laterally. In this way the hymenium thickens both by swelling and gelatinization of the basidioles and by addition of new basidia, until the glebal locules may become almost filled. I am not certain that this is so in the type species, *R. luteolus*, because there is confusion as to what this really represents. However, the illustrations by Coker & Couch (1928, Pl. 106, Figs. 15, 17) show dimerous basidia, some arising laterally from swollen basidioles, while Morten Lange's (1950) description mentions long basidia projecting above the hymenium (presumably the prolongations from dimerous basidia). Dr. D. M. Dring of Kew Herbarium has favoured me with liquid-preserved material of what he regards as *R. luteolus*. This (Fig. 11) has dimerous basidia, but in the single basidiocarp examined there was no evidence of hypertrophied basidioles, though possibly these might develop in older material.

The other type of development is that where the basidia are subcylindrical to




Figs. 10–14. — 10. *Rhizopogon clelandii* (holotype), showing basidia and spores. — 11. *Rhizopogon luteolus* fide Dring, Scotland, showing dimerous basidia and spores with pedicellate, notched or rounded bases; extreme right, a basidium with two apical prolongations, not uncommon in this material — 12. *Rhizopogon flavum*, Dehra Dun, Bakshi 113/65, showing "waisted" basidia (courtesy of D. M. Dring). — 13. *Rhizopogon* sp., Hampshire, showing "waisted" basidia (courtesy of D. M. Dring). — 14. Basidia and spores of *Geastrum* sp.

clavate, not dimerous, and are not associated with modified basidioles. If hymenial thickening occurs it must be by growth of hyphae from below the layer of current basidia; this was not apparent, however, in the example studied, nor were the glebal locules filled. This type of development appears to be illustrated by Coker & Couch (1928, Pl. 20) for *Rhizopogon parasiticus* Coker & Totten, and also by Hawker (1954, Fig. 29) for *R. rubescens*. However, Coker & Couch's illustration for *R. rubescens* (1928, Pl. 106, Fig. 7) is at variance with Hawker's.

In both types of development the initial basidia are formed at the surface of the hymenium; they are not embedded in either a hyphidial or a gelatinous matrix which, in many genera of Aphyllophorales, appear to be responsible for the development of dimerous basidia (Donk, 1964: 215). Also, in both types the gleba is entirely enclosed by the peridium during development. The basidia in both instances would thus appear to occupy the same sort of ecological situation and be subject to the same types of spatial pressures. This suggests that the differences between the basidia are fundamental and not simply adaptive to the situations in which they occur.

Dr. D. M. Dring has drawn my attention to what he calls "waisted" basidia in *Rhizopogon flavum* Petch and in an undetermined British collection (Figs. 12, 13). These are probably dimerous in their development but notable for the shortness of the apical prolongation. Similar basidia occur as rarities among the elongated dimerous basidia in some South Australian collections but are evidently the dominant form in some species investigated by Dr. Dring.

Among other Gasteromycetes, dimerous basidia are known in *Nigropogon asterosporus* Coker & Couch (1928, Pl. 108, Figs. 4, 5) and in *Galeropsis paradoxa* (a gasteroid *Bolbitius*; Dring & Rayner, 1967). What appear to be dimerous basidia are also well known in *Geastrum* (Fig. 13). The basidia in *Lycogalopsis* E. Fisch. (Martin, 1939) are compared by Martin with those of *Rhizopogon* and *Geastrum* as well as certain Aphyllophorales. The differences between urniform and utriform dimerous basidia (Donk, 1964) are primarily cytological though Donk gives morphological pointers to their differentiation. In the absence of cytological data I would hazard the opinion that the dimerous basidia of *Rhizopogon* are utriform. *Lycogalopsis* basidia are also probably utriform: if so I suggest that they (and the basidia of *Coniophora*) may represent a subtype in which the basidium instead of being ventricose and rounded at the base, is tapered below the ventricose part.

There appears to be a good case for dividing *Rhizopogon* sensu lato into two genera primarily on the basis of basidial and hymenophoral morphology once the problems of typification have been solved. There are several instances in the Aphyllophorales where genera have been so divided and a wealth of confirmatory features found only after the initial division gave the impetus to further investigation.

ACKNOWLEDGMENTS

I am grateful to my colleagues Dr. J. H. Warcup, Dr. Elaine Davison and Mr M. Bumbieris for collecting fresh specimens for examination; also to Dr. D. M. Dring for helpful discussions and for providing materials of use in this study.

In this publication dedicated to Dr. M. A. Donk it is fitting that I should acknowledge my profound indebtedness for the friendly help he has given me for many years, and especially for first interesting me in problems of basidial morphology and terminology, and their application in taxonomy.

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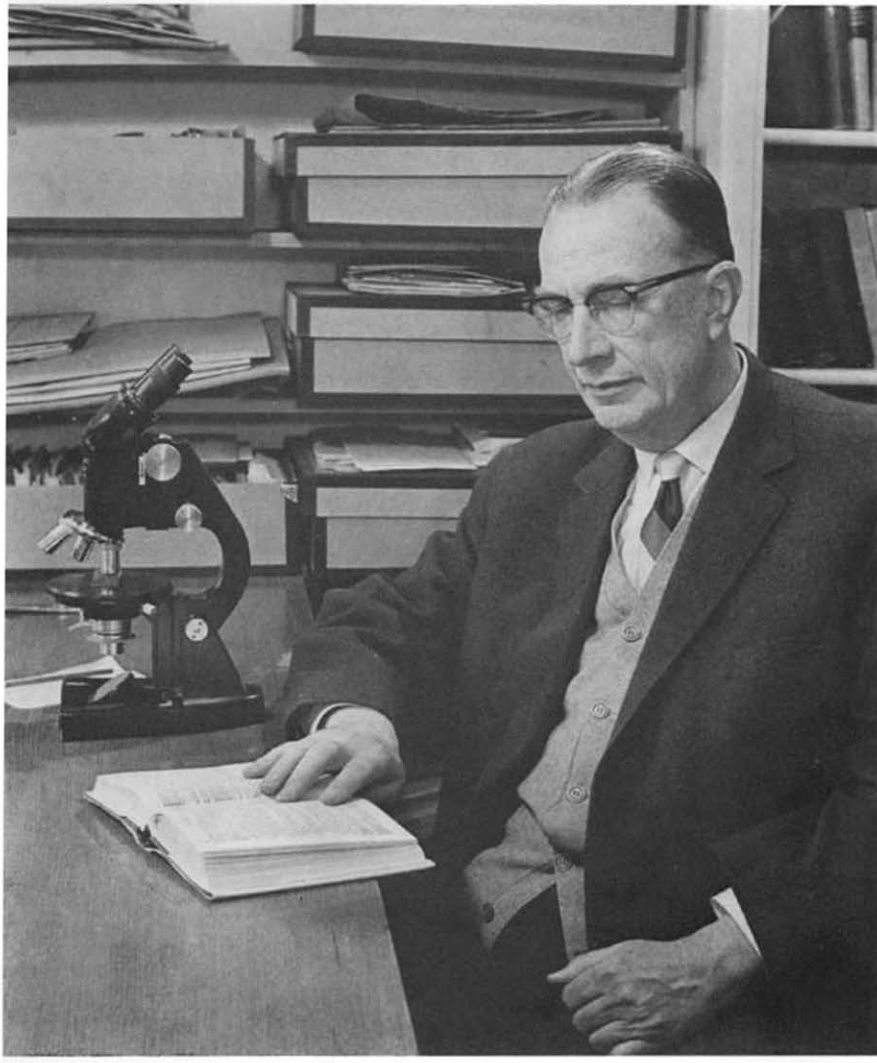
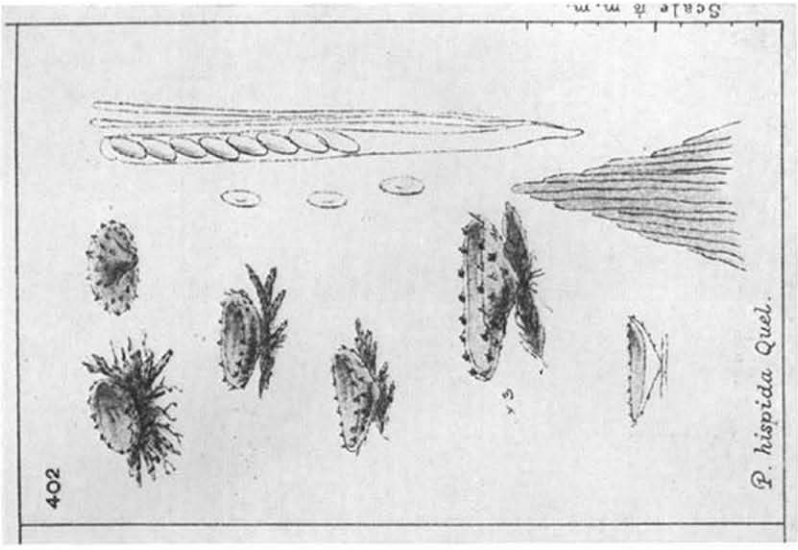


(Photo J. van Brummelen)

DR. M. A. DONK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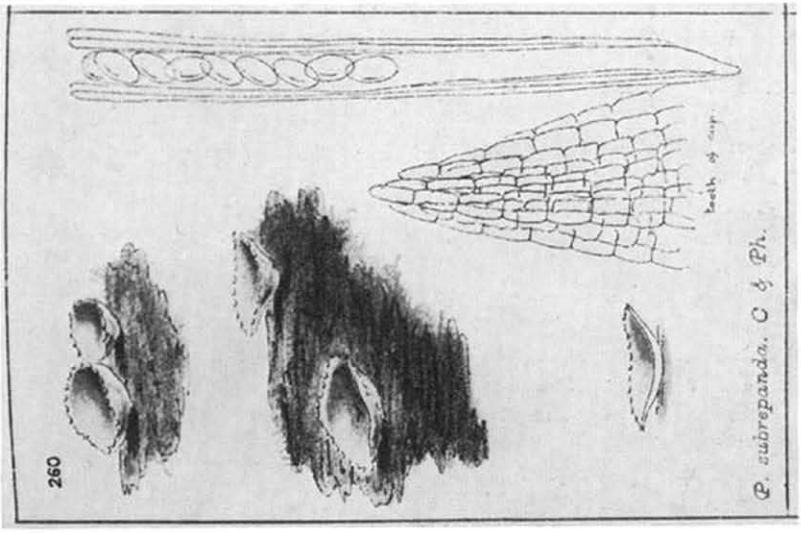
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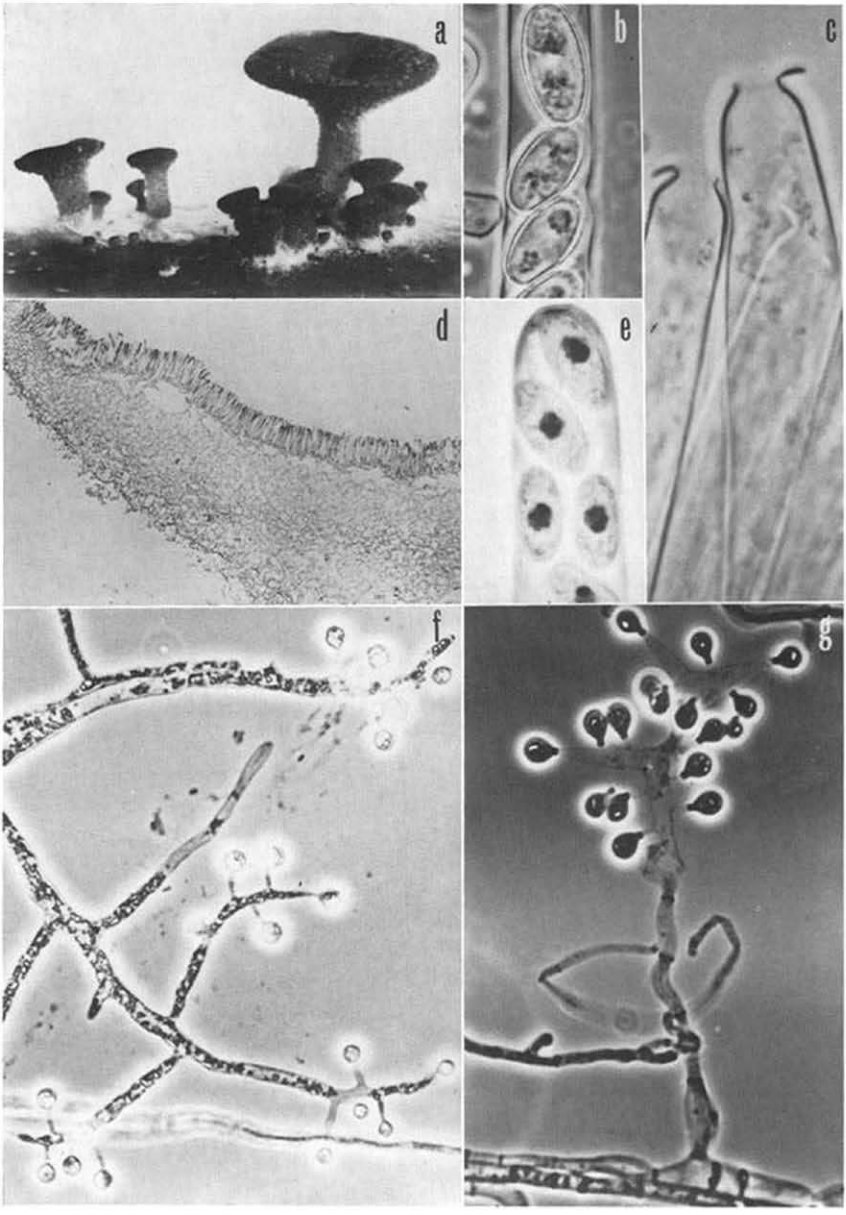
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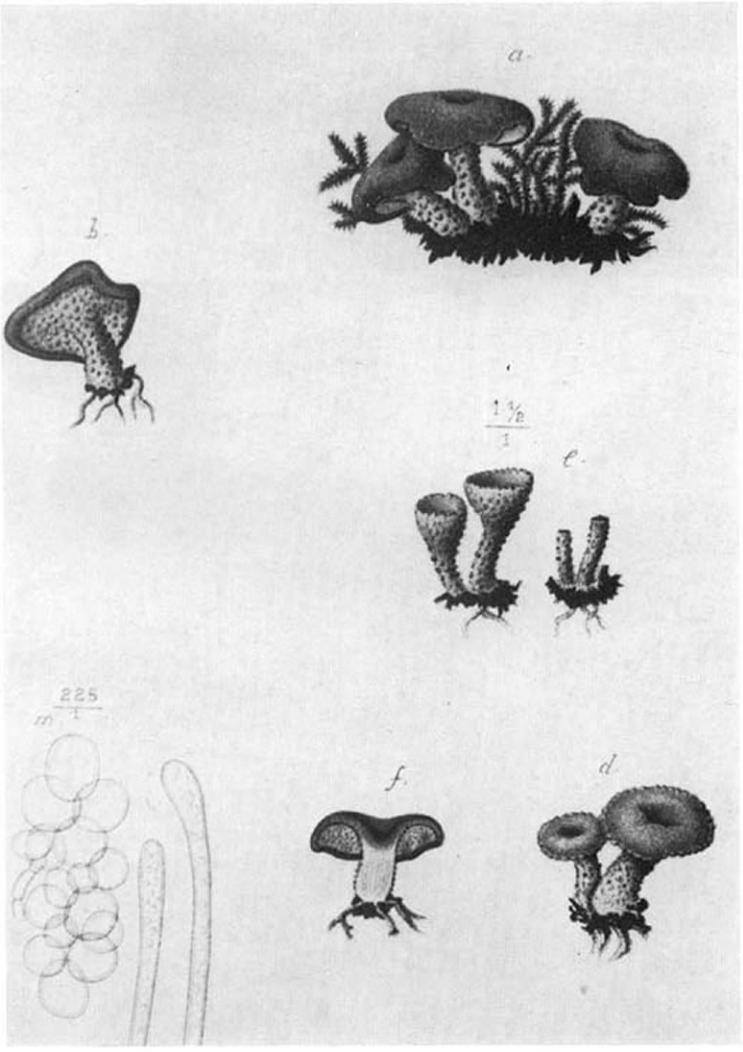
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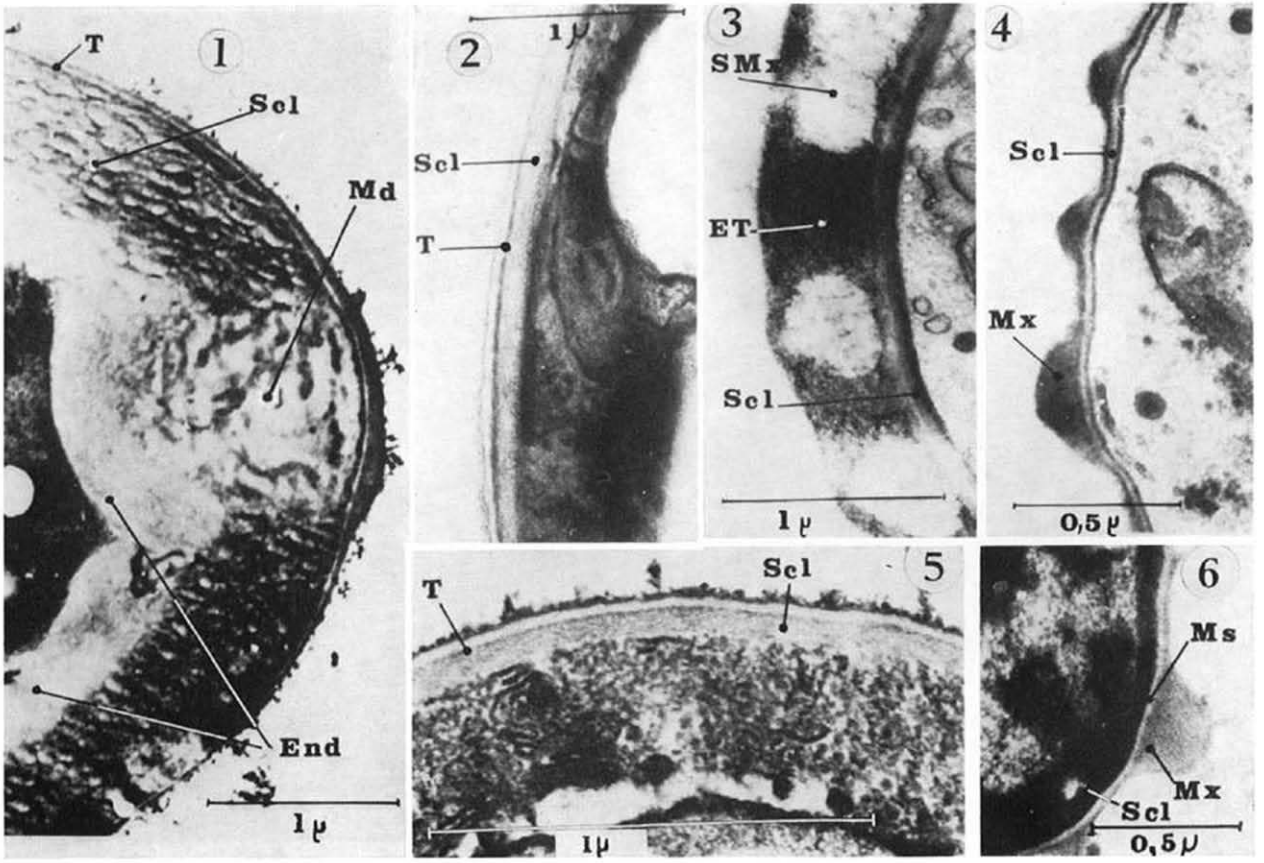
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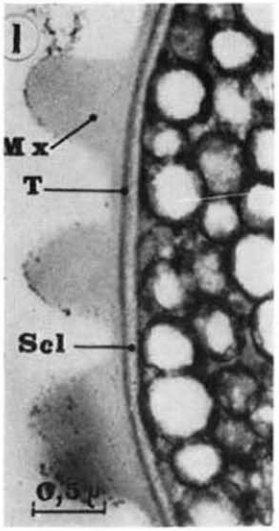
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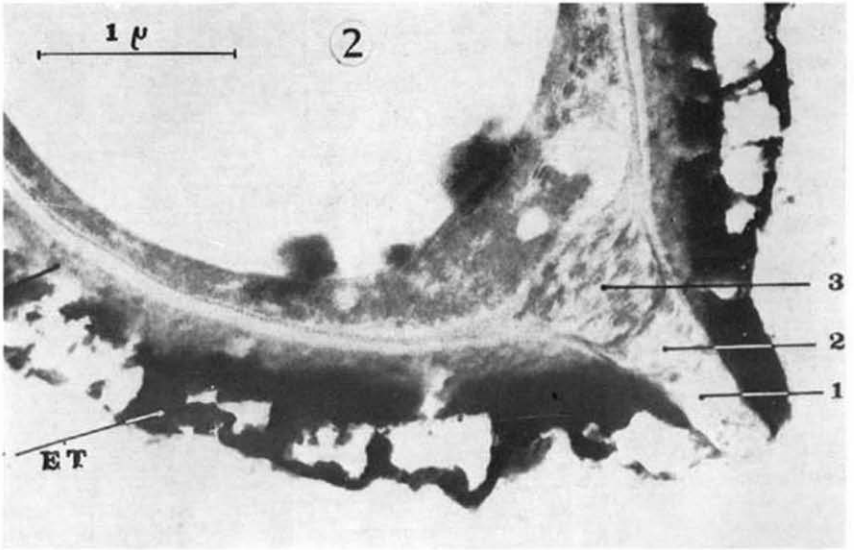
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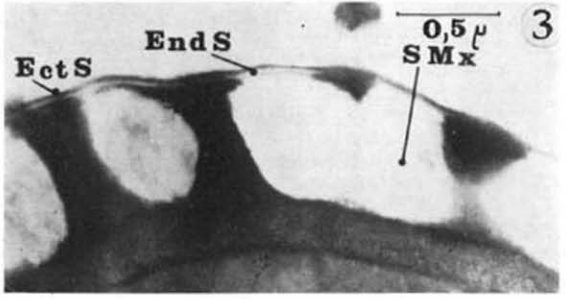
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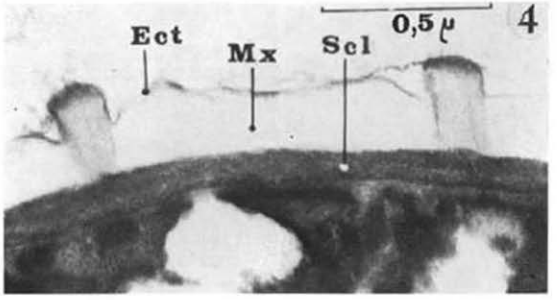
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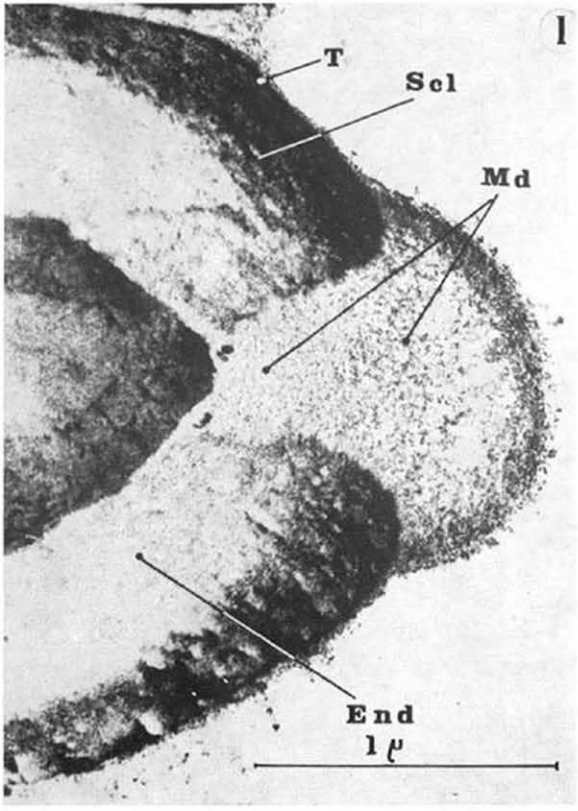
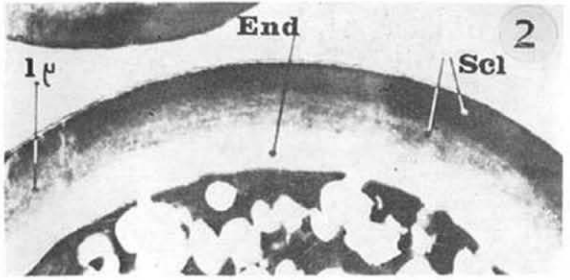
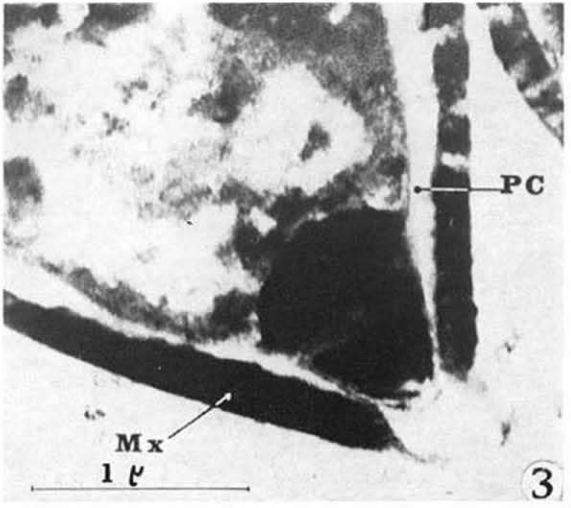
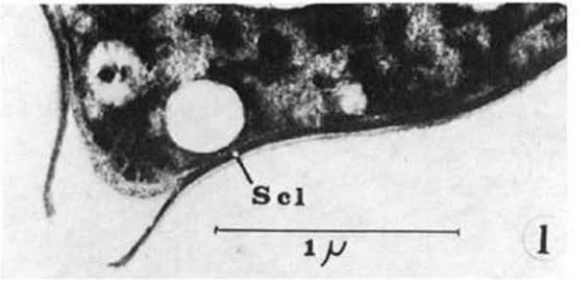
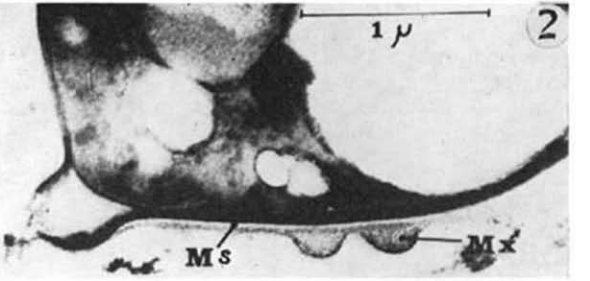
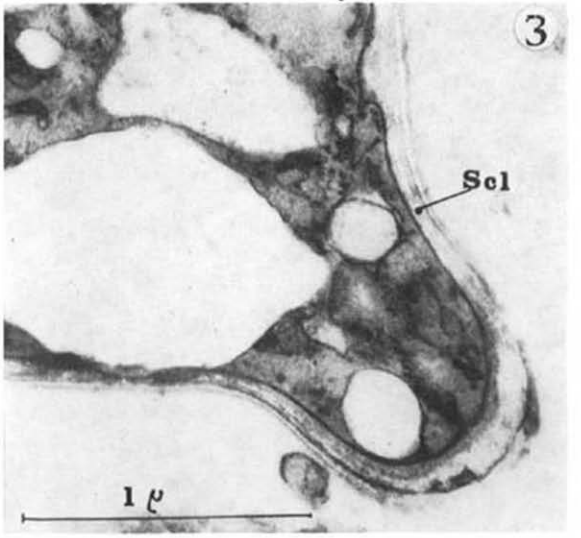

1
T
Scl
Md
End
1 μ

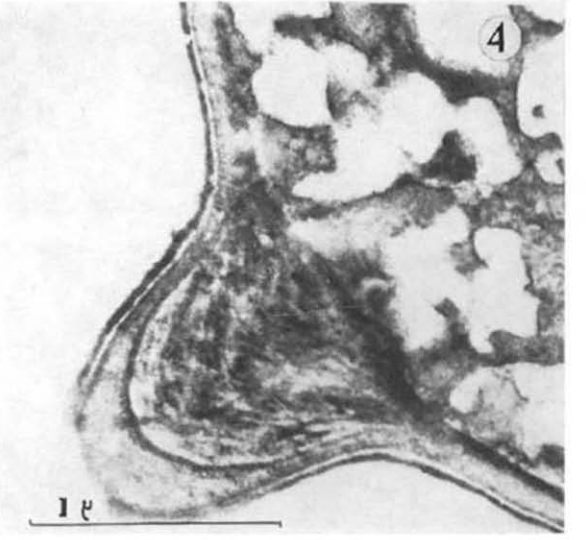

2
End
Scl
1 μ

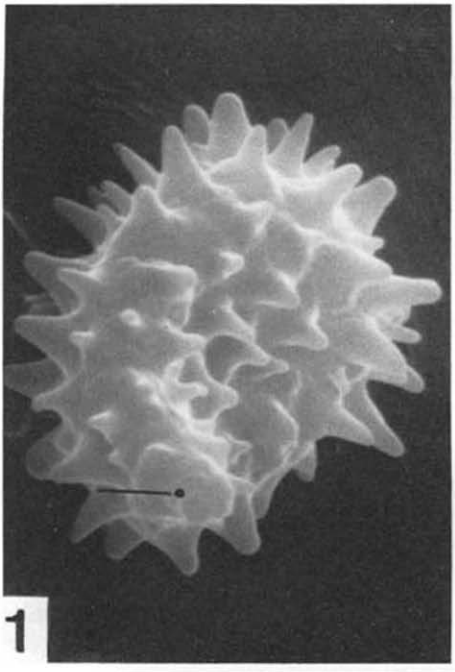

PC
Mx
1 μ
3


Scl
1 μ
1


1 μ
2
Ms
Mx


3
Scl
1 μ


4
1 μ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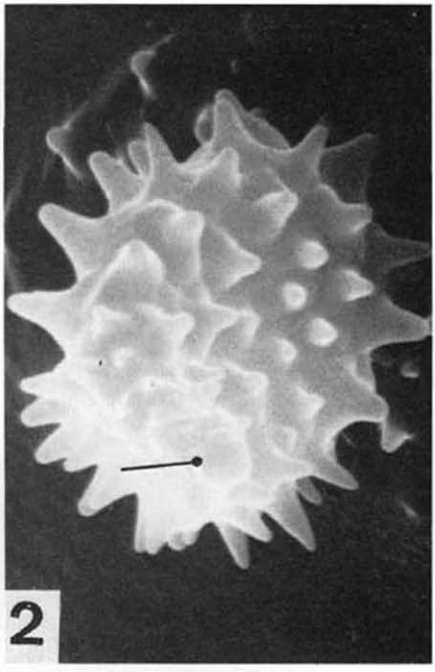
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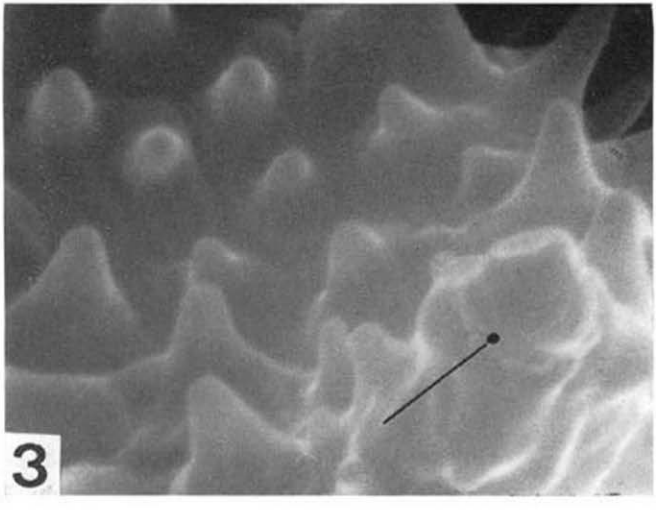
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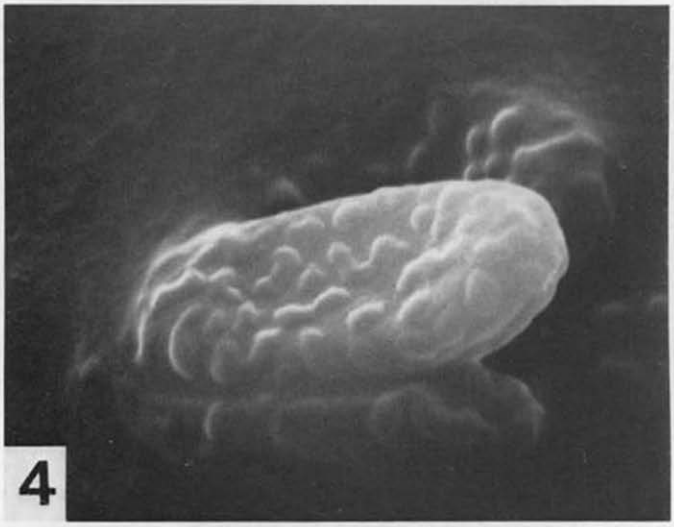
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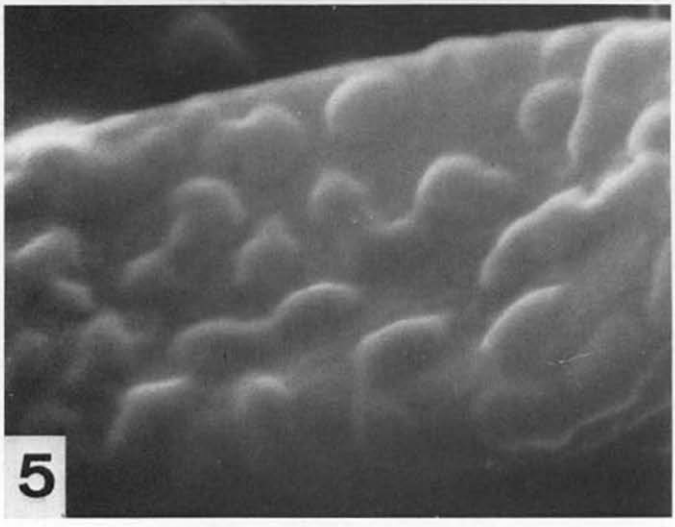
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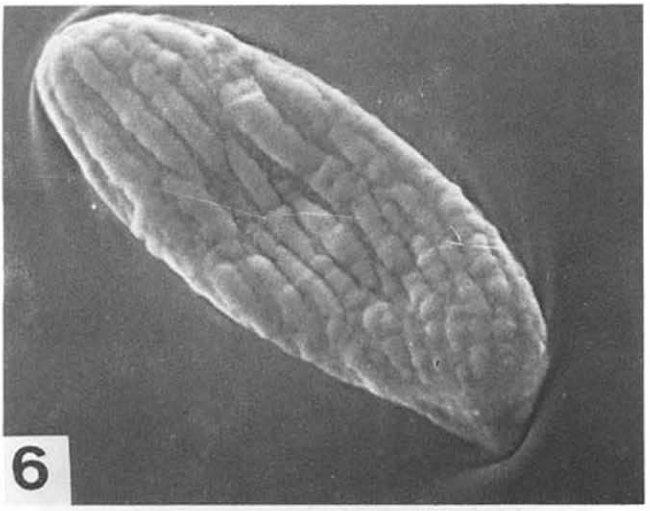
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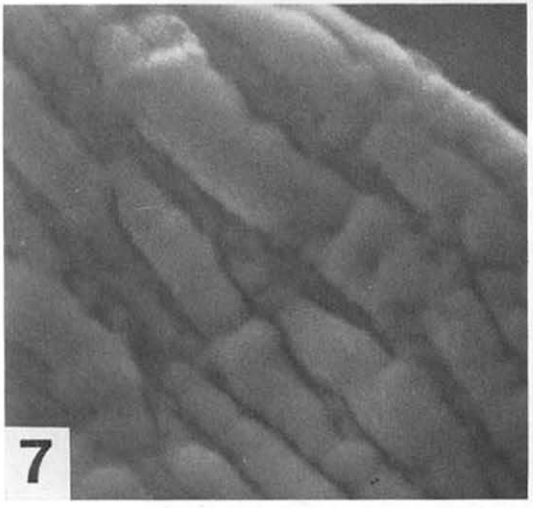
7


8