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NOTES ON THE GENUS PSATHYRELLA—VI

Four controversial species of Psathyrella: P. fibrillosa, P. frustulenta, P. clivensis, and P. obtusata

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(With 34 Text-figures)

Examination of four collections of *Psathyrella frustulenta* sensu A. H. Smith and four of *P. frustulenta* sensu Romagn. revealed that the former species is distinguished from the latter by its strongly developed veil and habitat (woods) and that there are considerable microscopic differences between the two (spore size, number and shape of pleurocystidia, pattern of cellular lining of gill edge). The former species is to be regarded as conspecific with *Agaricus frustulentus* Fries, the latter as conspecific with *P. clivensis* (Berk. & Br.) P. D. Orton. It is argued that the name *P. fibrillosa* was misapplied by J. E. Lange and A. H. Smith to a species for which the name *P. friesii* is introduced. Descriptions of *P. friesii*, *P. frustulenta*, *P. clivensis*, and *P. obtusata* are given.

In the autumn of 1976 we had the good fortune of finding three species of *Psathyrella*, which enabled us to clear nomenclatural problems round *P. fibrillosa* (Pers. ex Fr.) sensu J. E. Lange and sensu A. H. Smith, *P. frustulenta* (Fr.) A. H. Smith sensu A. H. Smith, *P. frustulenta* (Fr.) A. H. Smith sensu Romagn., and *P. obtusata* (Fr.) A. H. Smith. Smith himself already stated that *P. fibrillosa* does not have a clear and widely accepted concept in Europe by present-day mycologists, reason why he used the name tentatively. Close comparison of the Friesian descriptions of *Agaricus fibrillosus* with the descriptions furnished by Lange and by Smith disclosed that the epithet 'fibrillosus' is misapplied by the latter authors. A new name, *P. friesii*, is introduced for the species they describe under that name.

We were enabled to compare our own four collections of *P. frustulenta* sensu A. H. Smith with material of four collections of *P. frustulenta* sensu Romagn. which Prof. Romagnesi very kindly sent us from his own herbarium. Through the courtesy of Dr. R. Watling we received from the herbarium of the Royal Botanic Garden Edinburgh the material of the two collections of *P. clivensis* (Berk. & Br.) P. D. Orton, mentioned by Orton (*1960*: 369) in his description of that species, so that we were able to include this species in our study also.

For our methods of examining the fruit bodies, particularly the microscopic characters, the reader is referred to our previous papers (Kits van Waveren *1968*: 132; *1971a*: 249; *1972*: 24). Spore measurements are given both as a range and

as a mean value added between brackets. For the description of the colours of the macroscopic structures and the spores (mounted in water, NH_4OH 10% or KOH 5% and studied with oil immersion in a rather strongly lit field of view) we used the Munsell Soil Color Charts, edition 1971 (abbreviated in the text to M.), and the code designating its colours.

With regard to the pigmentation of the fruit bodies we have, as previously, confined ourselves to studying only the pigmentation of the hymenophoral trama for reasons given in our earlier paper (Kits van Waveren, *1976*: 346). Again we emphasize the importance of paying special attention to the pattern of the cellular lining of the sterile gill edge. Doing this turned out to be particularly rewarding in *P. obtusata* and *P. clivensis*, where this pattern is very characteristic.

ACKNOWLEDGEMENTS

We are greatly indebted to Prof. H. Romagnesi for very kindly sending us material of four collections of *P. frustulenta* (Pers. ex Fr.) sensu Romagn., and for keeping up a very lively and instructive correspondence with us about this interesting species. We also wish to thank very much indeed the Director of the Herbarium, Royal Botanic Gardens, Kew for enabling us to study the type specimens of *P. cortinarioides* P. D. Orton, and the Director of the Royal Botanic Garden Edinburgh for sending us material of *P. clivensis* (Berk. & Br.) P. D. Orton.

Psathyrella friesii Kits van Wav., *spec. nov.*—Figs. 1, 6–10

Psathyra langei Sing. *in* Collect. Bot. I **3**: 244. 1947 (not validly published).

MISAPPLIED NAMES.—*Agaricus fibrillosus* (Pers. ex Fr.) sensu Lambotte *in* Fl. mycol. Belge I: 216. 1880. — *Psathyra fibrillosa* (Pers. ex. Fr.) sensu J. E. Lange, Fl. agar. dan. **4**: 94, pl. 152 D. 1939. — *Psathyrella fibrillosa* (Pers. ex Fr.) Maire sensu A. H. Smith *in* Mem. N.Y. bot. Gdn **24**: 233. 1972; non *Agaricus fibrillosus* Pers., Syn. fung. 424. 1801; non *Agaricus fibrillosus* Pers. ex Fr., Syst. mycol. I: 297. 1821; Epicr. 233. 1838; Monogr. Hym. Suec. I: 442. 1863; Hym. eur. 308. 1874.

SELECTED DESCRIPTIONS AND ILLUSTRATIONS.—Ricken, Blätterp., pl. 67, fig. 1. 1913 (as *Psathyra fibrillosa*). — J. E. Lange, Fl. agar. dan. **4**: 94, pl. 152 D. 1939 (as *Psathyra fibrillosa*). — A. H. Smith *in* Mem. N.Y. bot. Gdn **24**: 233, pl. 64b and 69b. 1972 (as *Psathyrella fibrillosa*).

Carpophora parva vel statura media, terrestria, solitaria. Pileus 15–25 mm latus, e paraboloideo convexus, badiofuscus, hygrophanus, haud roseatus. Velum album, insigne, maturitate etiam appendiculatum. Lamellae griseo-sepiaceae, purpureo-tinctae, late adnatae, acie albae. Stipes 40—75 × 2—4 mm, haud radicans, albus. Sporae 7.7—8.1 × 4.1—4.5 µm, in cumulo purpureo-nigrae, sub micr. badiofuscae. Pleurocystidia 40—55 × 10—14 µm, numerosa, fusiformia vel sublageniformia, pedicellata. Cheilocystidia 27—45 × 11—18 µm. Cellulae spheropedunculatae et clavatae 17.5—30 × 8—12 µm, numerosae. Trama hymenophori colorata.

TYPUS: The Netherlands, prov. Overijssel, Oldenzaal, estate 'Roderveld', 12 Oct. 1976, *E. Kits van Waveren* (L).

CHIEF CHARACTERISTICS. — Carpophores small to medium sized, solitary, terrestrial. Cap 15–25 mm in diam., paraboloid, later more convex, dark reddish brown, hygrophanous, without pink, with white, very distinct and in mature specimens often even appendiculate veil; gills greyish brown with trace of purple, broadly adnate, with white edge; stem 40–75 × 2–4 mm, not rooting, white; spore print purplish black; spores 7.7–8.1 × 4.1–4.5 μm, in water and NH_4OH 10% fairly dark reddish brown; pleurocystidia 40–55 × 10–14 μm, numerous, fusiform to sublageniform, pedicellate; cheilocystidia 27–45 × 11–18 μm, moderately numerous to scattered; spheropedunculate and clavate cells 17.5–30 × 8–12.5 μm, numerous; hymenophoral trama coloured.

MACROSCOPIC CHARACTERS. — Cap 15–25 mm in diam., paraboloid, later more convex, with small and vague or fairly distinct umbo (up to 7 mm in diam.), striate up to 2/3 from margin upwards, dark reddish brown (M. 5 YR 3/2), in marginal area dark brown (M. 7.5 YR 4/4), soon just brown all over, hygrophanous, drying out to pale brown (M. 10 YR 7/4) without pink, at centre at first ochre (M. 7.5 YR 5/4), finally pale ochre (M. 7.5 YR 7/6), dry surface rugulose, slightly micaceous.

Veil white, very distinct, leaving many very small networks and patches of bundled fibrils reaching up to half-way from margin upwards, in some caps even up to umbo often distinctly appendiculate, forming denticles and flocci at margin even in mature specimens, contrasting sharply against brown colour of cap; surface of stem covered along its entire length—except for apex—with loose, small velar fibrils and bundles of fibrils (no scales).

Gills 3–4 mm broad, ventricose, ascending, broadly adnate, greyish brown (M. 10 YR 5/2), browner towards base (M. 10 YR 5/3), both colours mixed with a trace of purple, with white, minutely fimbriate edge.

Stem 40–75 × 1.5–3 (apex) × 2–4 (just above base) mm, thickening towards slightly swollen base (up to 5 mm), straight, not rooting, hollow, white, minutely longitudinally striate, with shiny surface and pruinose apex.

Flesh of cap up to 2 mm thick in centre, dark brown (M. 10 YR 3/3) with some reddish (M. 5 YR 4/2); flesh of stem pale brown, darkening towards base, at base brown (M. 7.5 YR 5/4), with white, thin, superficial layer. Smell none.

Spore print in thin layer dark reddish purple, in thick layer purplish black.

Trama of 'washed' gill, mounted in NH_4OH 10% under binocular lens brown (M. 10 YR 5/4) in a fairly narrow zone along base, remainder of trama pale brown (M. 10 YR 6/3), very pale brown (M. 10 YR 7/3) near and at edge.

MICROSCOPIC CHARACTERS.—Spores 7.7–8.1 × 4.1–4.5 μm (average 8 × 4.5 μm), ellipsoid-amygdaliform, in water and NH_4OH 10% fairly dark reddish brown (M. 2.5 YR 3/6), in KOH 5% dark brownish grey (± M. 10 YR 4/2), not opaque, with small (± 1.5 μm) but distinct, not truncate apical germ pore, small hilar appendix.

Basidia 20–22 × 8–9 μm, 4-spored.

Pleurocystidia 40–55 × 10–14 μm, numerous, very uniform, fusiform to sublageniform with fairly short and usually rather broad pedicel and acute to sub-obtuse apex, thin-walled, colourless, without mucus or crystals.

Cheilocystidia 27–45 × 11–18 μm, moderately numerous to scattered, rather thick-set, fusiform to sublageniform, thin-walled, colourless, without mucus or crystals, intermixed with large numbers (80–90% of total number of marginal cells) of often rather large spheropedunculate and clavate cells, 17.5–30 × 8–12.5 μm. Gill edge sterile.

Caulocystidia (apex of stem) 40–60 × 10–15 μm, fairly numerous, isolated or in small clusters, sublageniform.

Pigmentation of hymenophoral trama under microscope ('washed' gill mounted in

NH_4OH 10%) pale brown from membranal pigment, paler towards edge, very pale near and at edge, neither yellow hyphal septa nor encrustations.

Cuticle of cap cellular, 1–2 cells deep layer of colourless, globose or subglobose, vesiculose cells, 16–40 μm in diam.

Clamps on hyphae of stem and caulocystidia.

HABITAT.—Solitary, terrestrial in grass alongside footpath in mixed coniferous and deciduous wood.

COLLECTION EXAMINED.—THE NETHERLANDS: prov. Overijssel, Oldenzaal, nature reserve 'Het Roderveld', 12 Oct. 1976, *E. K. v. W.* (holotype, L).

In keying out the species described by us above, one arrives with both Lange (*1939*: 94) and Smith (*1972*: 233) at *P. fibrillosa*, their descriptions corresponding sufficiently and well with ours.

With Lange *P. fibrillosa* is a medium sized fungus (cap 20–35 mm in diam., stem ± 80 mm long) of which the cap is loosely-fibrillose towards the edge, no scaliness being mentioned. In contradistinction to Fries's description of *A. fibrillosus* the colour of the cap is called 'watery brownish-grey, umbo of a purer brown' and on plate 152 D this colour is even distinctly reddish brown (M. ± 2.5 YR 5/4). The colour of the gills is called 'dark fuscous' and on plate 152 D it is brown-purplish (M. ± 10 R 6/2, 5/2; 2.5 YR 5/2), whereas with Fries it is purplish black, no brown being mentioned. The colour of the spore print is 'dark bister to sepia' (= some shade of very dark brown with a slight reddish hue) and with Fries black-purple. Lange's plate is sufficiently in accordance with our species as described above.

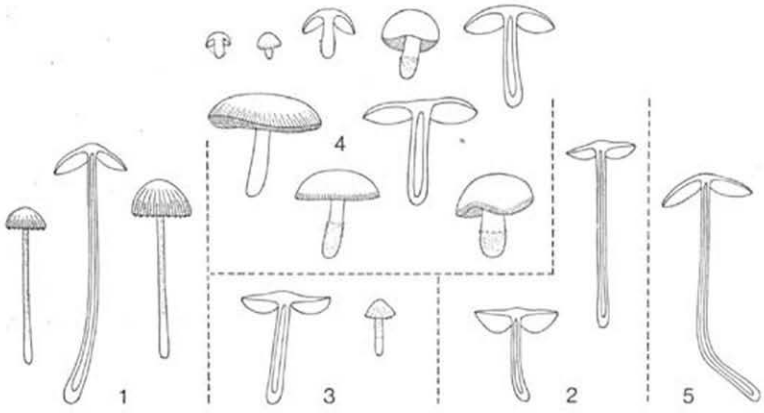


Fig. 1. *Psathyrella friesii*, 12 Oct. 1976. — Habit sketch (×0.5).

Figs. 2–4. *Psathyrella frustulenta*. — 2. 11 Oct. 1976. — 3. 13 Oct. 1976. — 4. 27 March 1977. — Habit sketches (×0.5).

Fig. 5. *Psathyrella obtusata*, 21 Oct. 1976. — Habit sketch (×0.5).

Lange described the marginal cells as somewhat bottle-shaped with a shorter neck, and plate 152 D shows lageniform cystidia. The pleurocystidia, however, were described as sparse and roundish, which—we feel—must have been an erroneous observation as roundish pleurocystidia are unknown in the genus *Psathyrella* and as—if both cheilo- and pleurocystidia are present—the latter always roughly of the same shape as the cheilocystidia.

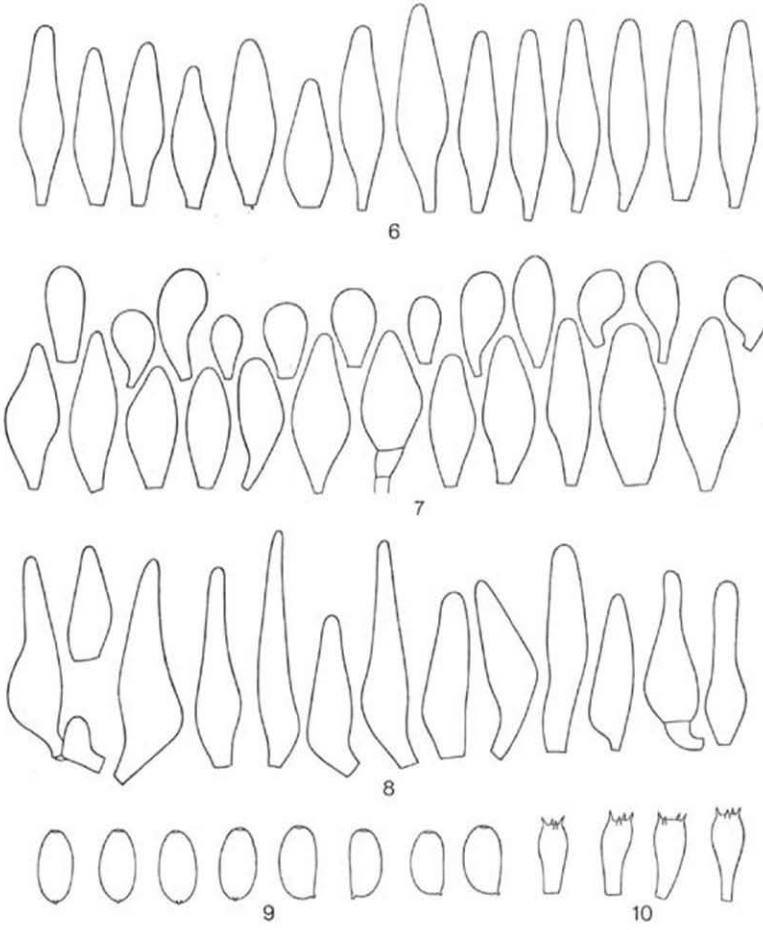
Singer (*1947*: 244), realising that *P. fibrillosa* (Pers. ex Fr.) sensu Lange did not represent *A. fibrillosus* Fr., without giving a description renamed it *Psathyra langei* Sing., but this name was not validly published.

With Smith (*1972*: 233) the cap of *P. fibrillosa* is at first covered with small fascicles of whitish fibrils but soon glabrous, and the stem is at first covered with scattered fibrils in squamules or patches and also soon glabrous. This description, however, is rather an understatement as the photographs of *P. fibrillosa* on plate 64 b and 69 b show a strongly developed and even appendiculate veil in the young specimens, and in mature specimens distinct velar remnants at and even up to some distance from the margin of the cap. This is in full agreement with Fries's descriptions of *A. fibrillosus*, but the colour of the cap is called 'buckthorn brown' to 'cinnamon brown' fading to 'grayish-buff to pallid' against 'lividus' with Fries (*1874*: 308). Smith called the colour of the gills 'pallid buff, becoming dark bister and finally nearly fuscous' against 'purpureo-nigris' with Fries (*1874*: 308). The habit of *P. fibrillosa* as shown on plate 64 b and 69 b corresponds with Lange's description and his plate 152 D (less velar development, however, with Lange) and our own description. With Smith the pleurocystidia are fusoid-ventricose and not vesiculose-clavate (see Ricken below).

For Fries, who already in his Observationes Mycologicae (*1815*: 181) adopted Persoon's *A. fibrillosus* (*1801*: 424), the outstanding character of this species must have been the strongly developed, even scaly velar coating of both cap and stem (e.g. in 1815: 181 cap 'squamis albis fibrillosus stipitis instar vestitus', stem 'totus fere squamulis villoso-fasciculatis albis obsitus'; in 1863: 442 cap 'interdum primitus squamulosus', stem 'undique squamulis fibrilloso-fasciculatis patulis, albis'). The words 'squamoso' and 'squamuloso' being used by Fries for both cap and stem, warrants the conclusion that the species must have been coarsely scaly.

But Fries called the cap very pale greyish to even whitish even in the young stage (e.g. in *1815*: 181 cap 'junior albus, dein sordidus albidus 1. lividus'; in *1863*: 442 cap 'lividus l. albescens') and the colour of the gills grey in the beginning, later purplish black, no brown being mentioned (e.g. in *1815*: 181 gills 'primo cinereo, dein purpurascenti-nigricantes'; in *1863*: 442 gills 'cinereo nigro-purpurascentes'). The colour of the spore print was called black or black-purple.

At one time we believed that—because of the strong development of the veil, described by Fries—he might have been dealing with what we nowadays know as *P. squamosa* (Karst.) Moser. Other reasons for this assumption were that in *P. squamosa* the attachment of the gills also is very broad and that a fungus corresponding with *P. squamosa* figures in none of Fries's publications, whereas it is hard to believe that it did not occur in those days in Sweden (the species is quite common in the Nether-



Figs. 6–10. *Psathyrella friesii*, 12 Oct. 1976. — 6. Pleurocystidiogram (×575). — 7. Cheilocystidiogram (×575). — 8. Caulocystidiogram (×575). — 9. Sporogram (×1210). — 10. Basidiogram (×575).

lands and was described from Finland). But in *P. squamosa* the colour of the gills is distinctly brownish and the colour of the cap also is not in agreement with Fries's descriptions of the colour of the cap in *A. fibrillosus*.

Authors in recent literature either abstained from giving an interpretation of *A. fibrillosus* Fr. or described a species which they named *P. fibrillosa* but in some im-

portant respects distinctly differed from Fries's species. Kühner & Romagnesi's descriptive key (*1953*: 353) for the genus *Psathyrella* (*Drosophila*) does not comprise *P. fibrillosa*, and Dennis, Orton & Hora (*1960*: 186) excluded *P. fibrillosa* 'pending clearer definition'.

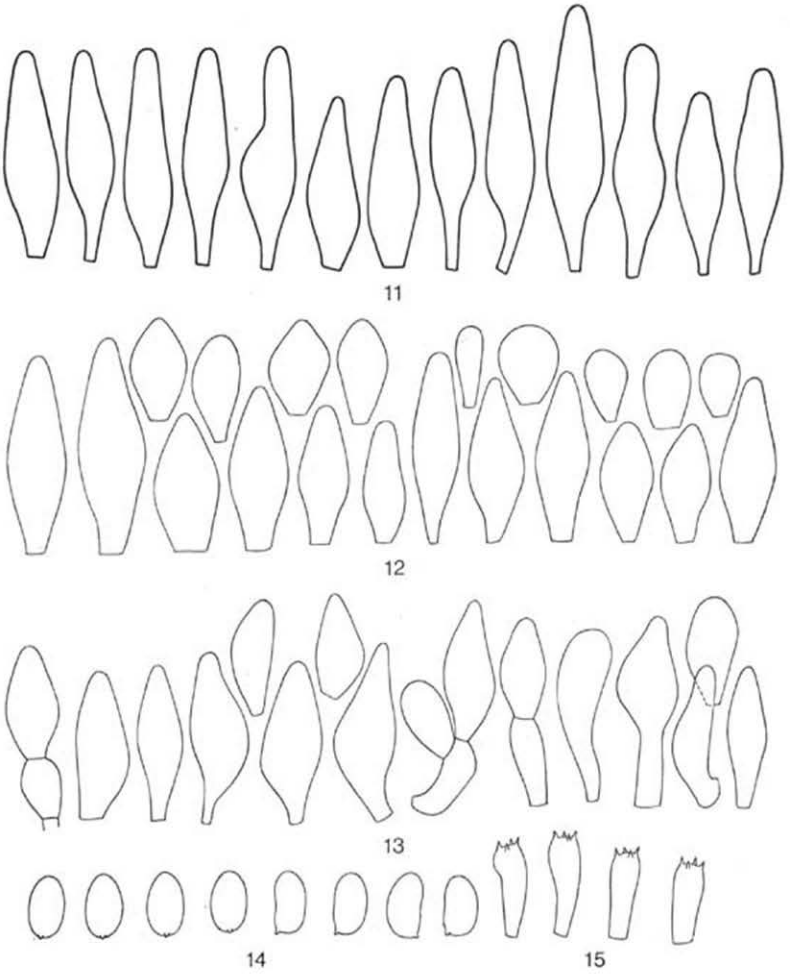
In conclusion, from the above it is clear that for reasons of distinct differences in colour of cap, gills and spore print *A. fibrillosus* Pers. ex Fr. cannot be conspecific with *P. fibrillosa* sensu J. E. Lange and sensu A. H. Smith, the latter species fully corresponding with the species described by us above and therefore as a new species: *P. friesii*.

The description given by Ricken (*1913*: 258) for *Psathyra fibrillosa* agrees with Fries's descriptions in the sizes of cap and stem, in the colour of the cap ('grau', provided 'grau' is taken in the sense of sordid grey and not of sordid brown) and in the description of the veil. But the gills with Ricken are narrowly adnate and on his plate 67[1] the colour of the cap is sordid brown (M. 10 YR 5/4). Moreover it is stated in italics that the cap is furrowed (hence the German name 'gefurchter Faserling') and that the colour of the gills is chocolate-reddish (!). With Ricken the cellular lining of the gill edge does not consist of lageniform cells as with Lange and Smith, but of vesiculose-clavate cells, like in *P. spadiceo-grisea*. Indeed, Ricken states that the presence of a veil in *P. fibrillosa* (on his plate 67[1] shown as concentric zones of small whitish non-appendiculate flocci up to half-way the centre of the cap) is almost the sole difference with *P. spadiceo-grisea*. From these data it is clear that *P. fibrillosa* sensu Ricken is neither conspecific with *A. fibrillosus* Fr., nor with *P. fibrillosa* sensu J. E. Lange and sensu A. H. Smith, alias our new species (see also observations on *P. obtusata*). Moser's description (*1967*: 221) of *P. fibrillosa* is obviously copied from Ricken; unfortunately Moser did not mention the shape of the marginal cells.

The literature contains many descriptions under the epithet fibrillosa of the species here under discussion, but they are either copies or summaries of the Friesian descriptions or not in sufficient agreement with the species as described by Fries.

As a matter of course we felt having to base the above considerations and particularly the colours of cap, gills and spore print in the descriptions of Fries, Lange and Smith on the litteral texts. The process of drying in many species of *Psathyrella*, however, sets in so quickly that the colour of the cap, which at the onset is distinctly dark reddish brown, very often has already turned into some shade of (sordid) brown when the specimens are collected, the dark reddish hue already having disappeared (see Kits van Waveren *1976*: 346). Lange's description of *P. fibrillosa* and his plate 152 D furnish a good example. In his description he called the colour of the cap 'brownish gray, umbo of a purer brown' but on plate 152 D the caps are distinctly reddish. We very much doubt whether the 'buckthorn brown to cinnamon-brown' colour of the cap, fading to 'grayish cinnamon-buff to pallid' as reported by Smith is the true colour of the caps of *P. fibrillosa* sensu Smith in its fresh stage. These colours, however, still differ from and are distinctly browner than the colours mentioned by Fries for *A. fibrillosus*, who in none of his descriptions mentioned any shade of brown. In the really fresh stages the colour of the caps of the species as described by Smith is almost certain to having been darker and more reddish brown.

The descriptions of the colour of the gills, given by Fries, 'purpureo-nigris', distinctly differ from those given by Ricken (chocolate-reddish), Lange (dark fuscous and on plate 152 D even reddish brown), Smith ('pallid buff, dark bister, finally nearly fuscous') and us (greyish brown with a trace of purple).



Figs. 11–15. *Psathyrella frustulenta*, 13 Oct. 1976. — 11. Pleurocystidiogram (×575). — 12. Cheilocystidiogram (×575). — 13. Caulocystidiogram (×575). — 14. Sporogram (×1210). — 15. Basidiogram (×575).

The only author to mention the colour of the spore print is Lange, who called it dark bister to sepia (=very dark brown with a reddish hue). With Fries the colour of the spore print of *A. fibrillosus* is 'atro-purpur' (*1838*, 1874) or black (*1815*). The correct assessment of the colour of the spore print in *Psathyrella*, however, depends on whether the colour is taken from a thin or very thick layer of spores. In our own collection the colour was very dark purple, almost black, when taken from the ridges of the spore print formed between the gills, but distinctly dark reddish purple alongside these ridges. We do not know how and from what part of the spore print Fries took his colours.

PSATHYRELLA FRUSTULENTA (Fr.) A. H. Smith
Figs. 2–4, 11–18

Agaricus frustulentus Fr., Epicr. 209. 1838; Monogr. Hym. Suec. **1**: 442. 1857; Hym. europ. 307, 1874. — *Pannucia frustulenta* (Fr.) P. Karst. *in* Bidr. Känn. Finl. Nat. Folk **32**: 513. 1879. — *Psathyra frustulenta* (Fr.) P. Karst. *in* Medd. soc. fenn. **5**: 18. 1879. — *Drosophila frustulenta* (Fr.) Quél., Enchir. 117. 1886. — *Psathyrella frustulenta* (Fr.) A. H. Smith *in* Contr. Univ. Mich. Herb. **5**: 45. 1941.

TYPE LOCALITY: Sweden.

EXCLUDED.—*Drosophila frustulenta* (Fr.) Quél. sensu Romagn. *in* Bull. Soc. mycol. Fr. **91**: 189. 1975 (=*Psathyrella clivensis* (Berk. & Br.) P. D. Orton.

SELECTED DESCRIPTIONS AND ILLUSTRATIONS.—Ricken Blätterp. 259. 1913. — J. E. Lange, Fl. agar. dan. **4**: 95, pl. 151 D. — Bresadola, Icon. mycol. **18**: pl. 866[2]. 1931 (excluded spore sizes and cystidia). — Moser *in* Gams KryptogFl. 220. 1967. — A. H. Smith *in* Mem. N.Y. bot. Gdn **24**: 217. 1972.

CHIEF CHARACTERISTICS.—Carpophores small to medium sized, terrestrial against small pieces of wood, in woods, solitary; cap 10–30 mm in diam., paraboloid, later convex without or with vague to fairly distinct umbo, reddish brown, hygrophanous, dry cap pale brown without pink; veil strongly developed; gills whitish when young, later conspicuously brown with whitish edge; stem 15–30×2–3.5 mm, not rooting, white; spore print brown; spores 6.3–7.7(–8.1)×3.6–4.5 µm, in water and NH_4OH 10% light brown with distinct germ pore (callus); pleurocystidia 40–70×10–16 µm, very numerous, fusiform; cheilocystidia (15–)22–47(–55)×10–17.5 µm, numerous and intermixed with variable numbers of spheropedunculate cells, 12.5–30×7.5–17.5 µm; hymenophoral trama distinctly coloured.

MACROSCOPIC CHARACTERS.—Cap in young stages (10 mm in diam). paraboloid, later up to 30 mm in diam. and spreading to convex and plane without or with vague to fairly distinct umbo, striate up to 1/4-half-way from margin upwards, dark reddish brown (M. 5 YR 3/2) with marginal area reddish brown (M. 5 YR 4/3, 4/4, 5/4), hygrophanous, drying out to pale greyish brown or pale brown (M. 10 YR 7/4, 6/3, 6/4) and at centre at first ochreous (M. 7.5 YR 6/6, 10 YR 7/6) but in the end very pale ochre; dry surface rugulose, slightly micaceous and without pink.

Veil white, strongly developed, in young specimens cap covered up to even at centre with a dense coating of fibrils, networks, patches and adpressed flocci of fibrils, rendering the surface in some places even white from the veil, which in places may be appendiculate; stem also covered with a thick velar coating; in mature specimens still many very distinct radially arranged velar fibrils and velar networks up to 3–5 mm

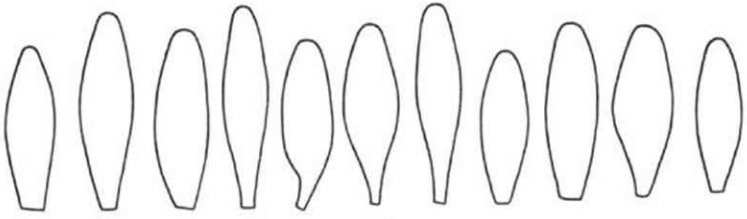
from margin on the cap, and lower 1/3 of stem showing many bundles of fibrils and usually also some flocci which may feign an annular zone.

Gills 3–5(–7) mm broad, in young stages whitish to exceedingly pale brown (M. 10 YR 8/3), in mature stages strikingly brown (M. 5 YR 4/4, 7.5 YR 5/4) in basal half, somewhat paler towards edge, ventricose, ascending, narrowly to fairly broadly adnate, somewhat crowded, with white and minutely fimbriate edge.

Stem 25–50 × 2–3.5(–5) mm, cylindrical but very slightly thickening towards base, straight, not rooting, hollow, minutely longitudinally striate, white, with slightly pruinose apex.

Flesh of cap 2–3 mm thick at centre, dark reddish brown (±M. 7.5 YR 4/2), later dark brown (M. 10 YR 3/3); flesh of stem light brown with thin white superficial layer. Smell none.

Spore print strikingly pale reddish brown (M. 5 YR 5/3).



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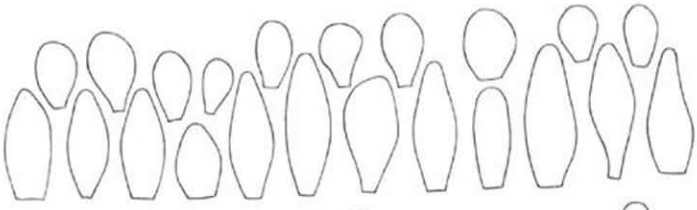

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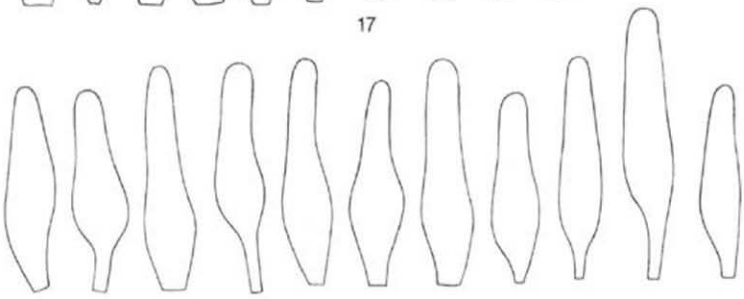

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Figs. 16, 17. *Psathyrella frustulenta*, 11 Oct. 1976. — 16. Pleurocystidiogram (×575). — 17. Cheilocystidiogram (×575).

Fig. 18. *Psathyrella frustulenta*, 27 March 1976. — Pleurocystidiogram (×575).

Trama of 'washed' gill, mounted in NH_4OH 10% under binocular lens, conspicuously coloured but degree and hue variable; either equally golden yellowish brown from base to edge (M. 10 YR 5/4 or paler) or dark yellowish brown (M. 10 YR 5/6) in basal third, yellowish brown (M. 10 YR 5/4) in central part and pale brown (M. 10 YR 6/3, 7/4) towards and at edge (brown colour of gills chiefly due to pigmentation of trama).

MICROSCOPIC CHARACTERS.—Spores 6.3–8.1 × 3.6–4.5 μm (averages 6.9–7.6 × 4–4.4 μm), ellipsoid-amygdaliform and distinctly phaseoliform, in water and NH_4OH 10% strikingly pale brownish yellow with a reddish hue (M. 7.5 YR 6/6), in KOH 5% pale yellowish brown (slightly paler than 10 YR 5/6), not opaque, with indistinct, practically absent germ pore (callus) and small hilar appendix.

Basidia 17.5–29 × 7.5–10 μm, 4-spored.

Pleurocystidia 40–70 × 10–16 μm, very numerous, fusiform to subfusiform with distinct pedicel and subacute to obtuse apex, thin- or very slightly thick-walled, colourless, without mucus or crystals.

Cheilocystidia (15–)22–47(–55) × 7.5–17.5 μm, numerous, fusiform, the vast majority more thick-set and with broader and shorter pedicel than the pleurocystidia, thin-walled, colourless, without mucus or crystals; intermixed with fairly large but locally sometimes smaller numbers of spheropedunculate cells, 12.5–30 × 7.5–17.5 μm, very few with slightly thickened walls. Gill edge sterile.

Caulocystidia (apex of stem) 27–47 × 10–17.5 μm, fairly numerous, isolated or in small clusters; shape and size very variable; similar to cheilocystidia; few spheropedunculate and clavate cels.

Pigmentation of hymenophoral trama under microscope ('washed' gill mounted in NH_4OH 10%) distinctly brown from membranal pigment throughout the entire gill, colour becoming fainter towards edge; quite a number of yellow hyphal septa, very few very small encrustations.

Cuticle of cap cellular, 2–3 cells deep layer of colourless globose or subglobose vesiculose cells, 24–48 μm in diam.

Clamps on hyphae of stem and caulocystidia.

HABITAT.—Solitary, terrestrial against small pieces of wood, in woods.

COLLECTIONS EXAMINED.—THE NETHERLANDS: prov. Overijssel, Oldenzaal, estate 'Roderveld', 11 Oct. 1976, *E. K. v. W.* (L); Delden, estate 'Twickel', area 'Breeriet', 13 Oct. 1976, *E. K. v. W.* (L); prov. Noord-Brabant, Hooghalen, 16 Oct. 1976, *P. B. Jansen* (herb. Jansen); Vlijmen, 27 March 1977, *W. Hanegraaff* (herb. Hanegraaff).

Already on examination of the gills with the binocular lens and microscope this species can easily be recognised by the following striking combination of characters: (i) the golden yellowish brown colour, usually equable from base to edge of the 'washed' gill mounted in NH_4OH 10% and viewed under the binocular lens against a well lit white background, (ii) the small phaseoliform and pale spores, (iii) the absent to scarcely noticeable (callus) germ pore, and (iv) the striking abundance of the pedicellate fusiform pleurocystidia (in *P. clivensis* utriform).

Fries described *A. frustulentus* for the first time in Epicrisis (*1838*: 209), giving a full description in Monographia (*1857*: 442) and a slightly abbreviated one in Hym. europ. (*1874*: 307). The outstanding features of this species as described by him are: (i) the fairly pale rust-red colour of the cap ('aquose ferrugineus'), (ii) the at first white, then pale yellowish brown but finally brown colour of the crowded gills (in

1857: 442 gills 'aquose cinnamomeo fuscescentes', in *1874*: 307 gills 'ex albo aquose cinnamomeus'), (iii) the rather strongly developed veil (in *1857*: 442, cap 'margine l. circa marginem albido-floccosus', stem 'fibrillosus l. flocculis albis adspersus'; in *1874*: 307, cap 'circa marginem albo-floccoso, stem 'flocculoso'), (iv) the dark rust-brown spore print ('fuscoferrugineus') and (v) the habitat in woods (*1857*: 'ad glearum silvaticarum'). Fries at first (*1838*) placed the species in the subgenus *Galera* because of the colour of the spore print; in 1857 Fries stated that the species stands between the Dermini and Pratelli; in 1874 that the species is abnormal because of its dark rust-brown spore print, the watery structure and 'collore hyaline' of the *Psathyras*, and that among the species of the subgenus *Galera* there are none that are related.

Our notes, made immediately after having collected this species on Oct. 13th 1976, correspond in every way with Fries's descriptions: (i) the cap we described as 'reddish brown (M. 5 YR 4/3)', (ii) the gills of the young specimen as 'crowded and whitish to extremely pale brown', those of the mature specimens as 'brown, ± M. 7.5 YR 5/4', (iii) the veil of the young specimen as 'a very dense velar coating from fibrils and networks of fibrils which in places causes the cap to be white and in one place even is appendiculate', (iv) the colour of the spore print as 'brown, M. 5 YR 5/3' (= reddish brown, and (v) the habitat as under *Quercus* in a deciduous wood. In all respects this collection agreed with the Friesian descriptions and so do the other three which later came at our disposal.

The descriptions and interpretations of Fries's species in the literature show considerable uniformity. With Ricken (*1913*: 259), who called *P. frustulenta* a well defined species and whose description of the species agrees with the ones given by Fries, the gills and spore print are cinnamon-brown, the spores are small and almost round (6–7 × 4.5 µm), and the cystidia fusiform. Buch's (*1952*: 268) description is in accordance with Fries's; with him the spores also are small (6–7 × 5(–6) µm). Lange's description (*1939*: 95) also agrees with the Friesian ones; with him the spores are oval and, as depicted on plate 151 D, distinctly phaseoliform (not mentioned in the text), measuring 7 × 4.25 µm, the cheilocystidia sparse and bottle-shaped, no pleurocystidia mentioned. The young specimen depicted on his plate 151 D shows a rather dense velar coating on both cap and stem. With Bresadola (*1931*: pl. 866[2]) the gills are not crowded but 'subdistantes', but otherwise his description agrees with the ones given by Fries. Both Bresadola's description and plate picture the stem as densely flocculose-scaly from velar remnants. With Bresadola, however, the spores are larger, 8–10 × 4.5 µm, and the cystidia are said to be 'clavato-ventricosa, substipitata'. Moser (*1967*: 220) referred to Lange's plate 151 D and from his descriptive key it is clear that he regarded *P. frustulenta* as a species having a copious veil, a medium sized (10–25 mm in diam.) cinnamon to weak coffeebrown cap, pale brown gills and small spores (7–8 × 4–5 µm).

A. H. Smith's recent description of *P. frustulenta* (*1972*: 217) is in accordance with the descriptions mentioned above. In describing the colour of the cap he used several designations for the various shades of cinnamon-brown, stating that some-

times old remoistened caps are 'russet (dark cinnamon brown)', which for us is a strong indication that in really fresh specimens the colour of the caps (as in our own material) must have been reddish brown. With Smith the gills are crowded and when young white or whitish, later they become 'russet' to 'cinnamon brown', and the entire surface of the cap is at first covered by a superficial coating of white fibrils, which become arranged into recurved scales, margin sometimes appendiculate with patches of the broken veil, lower part of stem covered with squamules or patches of white fibrils, which made Smith rank the species with subgenus *Pannucia*! This description of the veil agrees remarkably well with our own findings. Smith did not give the colour of the spore print, but going by his description of the colour of the gills and the cinnamon-ochraceous colour of the spores in KOH under the microscope it must have been brown. With Smith the spores also are small, 7–8.5 × 4.5–5.5 µm, but he did not mention a phaseoliform shape. The pleurocystidia are abundant and 'broadly fusoid-ventricose'. With his description of the macroscopical characters Smith is in complete agreement with Fries's descriptions of this—because of its brown colours—remarkable and in the field striking species, which according to Smith is to be found in woods ('under ferns on conifer needles').

From the data in the literature it is difficult to form an opinion about the true habit of *P. frustulenta* sensu Smith, which—as in our own material—seems to be rather variable. The sizes of the cap, as given in the literature, are fairly uniform, viz. between 10 and 30 mm, exactly our own figures. The figures for the sizes of the stem, however, vary somewhat, viz. from 50 × 1–1.5 mm (Moser) to 30–90 × 2.5–4 mm (Smith), our own figures being 25–50 × 2–3.5(–5) mm. *P. frustulenta* sensu Smith is very closely related to *P. clivensis*, and the habit of the latter species is beautifully demonstrated on Cooke's plate 1183/969.

Romagnesi (*1975*: 189) published a different interpretation of *Agaricus frustulentus* Fr. He stated that on account of the information provided by Orton (*1960*: 369) about *P. clivensis* (Berk. & Br.) P. D. Orton he had concluded that that species is conspecific with his version of *A. frustulentus* Fr., and also that his interpretation of Fries's species differs from the one given by Smith (*1972*: 217). With both conclusions we fully agree. The question then of course rises whether *P. frustulenta* sensu Romagn. (=*P. clivensis*) or whether *P. frustulenta* sensu A. H. Smith represents the true *A. frustulentus* Fr. In trying to solve this question one has to go solely by the macroscopic characters (the microscopic characters of both species are completely different as will be shown later). Of these Romagnesi stated that the sole detail, not being in accord with his interpretation is that Fries called the gills of *A. frustulentus* 'confertis', whereas Romagnesi in his material found them to be 'peu serrées ou espacées'. We fully agree with Romagnesi that the crowdedness of the gills is a minor detail, the crowdedness of the gills in several species of *Psathyrella* varying within one and the same species.

There are, however, we think two major differences between *A. frustulentus* as described by Fries and *Drosophila frustulenta* as described by Romagnesi:

(1) The veil, as described by Romagnesi, must be regarded as rather rudimentary

as it was merely found reduced to a few sparse plushes at the margin of the cap in only one specimen (Romagnesi *1975*: 189), no velar remnants being described for the stem. Later, however, we learned from Prof. Romagnesi (in lit.) that in his original description of his best collection he had described the veil as 'Beau voile marginal blanc pur mouchetant la marge, relativement assez fourni, mais très fugace et vite complètement disparu; les primordiums sont pourvus d'un voile marginal blanc de neige qui ne couvre pas le sommet'. This description, we feel, still does not cover the velar development as it was described by Fries and the strong velar development we noticed in our own collections, in which sometimes semi-mature specimens showed velar flocci even reaching the centre of the cap (in two collections some specimens even showed an annular zone on the stem). Romagnesi's description of the veil is in line with the rudimentary velar development in *P. clivensis* (considered conspecific with *P. frustulenta* sensu Romagn. by Romagnesi) as described by Orton (in the original description of *P. clivensis* by Berkeley & Broome the presence of a veil is not even mentioned).

(2) In our opinion there is a very distinct difference in habitat between *A. frustulentus* Fr. and *Drosophila frustulenta* sensu Romagn. According to Fries *A. frustulentus* grows along gravel roads in woods ('ad glaream viarum silvaticarum') and Smith's specimens and ours also were found in woods. *P. frustulenta* sensu Romagn. on the other hand grows according to the author in the grass and moss of grassland and waste land on chalk soil, usually outside woods, which is precisely the habitat given by Orton for *P. clivensis* ('chalk grassland'). Romagnesi believes there is no real difference between these two habitats, stressing that both come down to open ground. We cannot agree with this statement, believing that it is the substrate in which the carpophores grow that matters, and not whether the place where they grow is open or not.

Having ascertained on the basis of the macroscopic characters (development of the veil and habitat) that *A. frustulentus* Fr. and *P. frustulenta* sensu Romagn. (=*P. clivensis*) very probably are two different species, we can now turn to the microscopic characters. These proved to be totally different for the two species.

Prof. Romagnesi very kindly sent us for examination a full specimen of his collection *719* and fragments of his collections *219*, *980* and *1004* of *P. frustulenta* sensu Romagn. Pleurocystidia (fairly abundant in *Romagnesi 719* and *1004*), basidia and spores were found in all four collections, marginal cells only in *Romagnesi 719* and *1004* (abundant). Orton (*1960*: 369) examined the type specimens of *P. clivensis* and found the characters of the spores and the original description of the macroscopic characters in full agreement with those of a *Psathyrella* found fairly frequently on chalk grassland in Surrey. From the Herbarium Royal Botanic Garden Edinburgh we received on loan the two collections mentioned by Orton (*1960*: 369). The microscopic characters of the four collections of *P. frustulenta* sensu Romagn. and the two of *P. clivensis* turned out to be fully identical and totally different from those of our four collections of *P. frustulenta* sensu A. H. Smith.

The spores of *P. frustulenta* sensu Romagn. measure according to Romagnesi

8.5–10.5×5.7–6.5 µm (our own measurements: 8.1–10.8×5.4–6.3 µm), those of *P. clivensis* according to Orton 9–11(–12)×5.5–6.5(–7) µm (our own measurements: 8.1–10.8×5.4–6.3 µm). The spores of *P. frustulenta* sensu Smith are distinctly smaller (with Smith 7–8.5×4.5–5.5 µm; our own measurements: 6.8–7.2×4.1–4.5 µm) and distinctly phaseoliform, whereas in Romagnesi's material of *P. frustulenta* sensu Romagn. and in Orton's material of *P. clivensis* we only rarely came across a dubiously subphaseoliform spore (accordingly Romagnesi called these spores subphaseoliform and Orton called them 'rarely slightly phaseoliform'). The spores depicted by Romagnesi have a distinctly bulging adaxial face.

The pleurocystidia in Romagnesi's collections of *P. frustulenta* sensu Romagn. are distinctly utriform and in *Romagnesi 719* many cystidia are even capitate; their shape however varies a great deal (see Figs. 27, 28, 29) and they are only moderately numerous. Orton described the shape of the pleurocystidia in *P. clivensis* as rather obtusely lageniform or fusiform but in the material we examined we found them to be utriform (see Figs. 19, 24) and moderately numerous as in *P. frustulenta* sensu Romagn. In our collections of *P. frustulenta* sensu Smith on the other hand we found the pleurocystidia, as described by Smith, fusiform or fusoid-ventricose (see Figs. 11, 16) and very numerous.

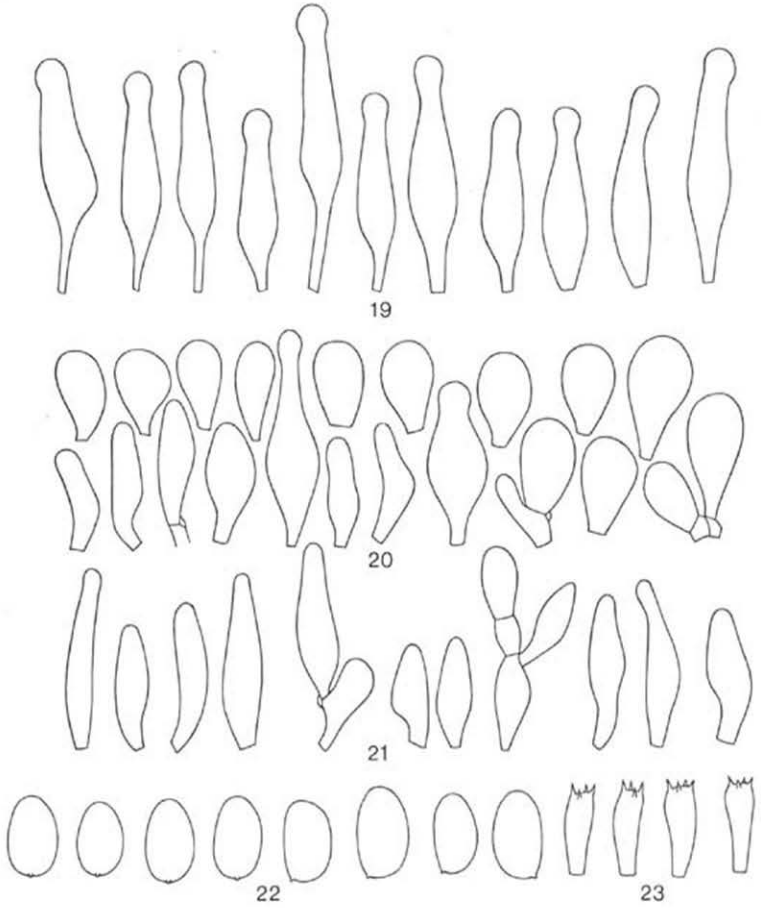
The marginal cells in both collections of *P. clivensis* and in the two collections (*No. 719* and *1004*) of *P. frustulenta* sensu Romagn. in which a gill edge was obtained, consisted almost exclusively of spheropedunculate and clavate cells, intermixed with only very few to scarcely any pleurocystidioid cheilocystidia (Orton even mentioned for the marginal cells only clavate or pyriform cells). On the other hand, in our four collections of *P. frustulenta* sensu Smith these cheilocystidia were numerous, intermixed with fairly large but locally smaller numbers of spheropedunculate cells. The overall picture of the cellular lining of the gill edge of *P. frustulenta* sensu Smith and *P. frustulenta* sensu Romagn. are thus very different.

In conclusion we believe that because of its strongly developed veil and habitat (woods) *P. frustulenta* sensu Smith fully answers Fries's original descriptions of *A. frustulentus*, and therewith represents that species. *P. frustulenta* sensu Romagn., although in all other macroscopic features greatly resembling Fries's species differs from it by its much lesser development of the (rudimentary) veil and by habitat. Comparison of the two taxa showed that very distinct microscopic differences also exist (spore size and shape, shape and number of pleurocystidia, pattern of cellular lining of gill edge). The macroscopic and microscopic characters of *P. frustulenta* sensu Romagn. turned out to be identical with those of *P. clivensis*, with which species *P. frustulenta* sensu Romagn. is conspecific, as already pointed out by Romagnesi (*1975*: 191).

On account of the description in the 'Flore analytique' (Kühn. & Romagn. *1953*: 363) of *P. empyreumatica* (Berk. & Br.) Kühn. & Romagn. we fully agree with Romagnesi (*1975*: 191) that the species described under that name, ranked in a section of subgenus *Psathyra* with little veil, growing in grassland and having spores measuring 8.5–10.2×5.2–6 µm, is also conspecific with *P. clivensis*. The description in the

'Flore' does not mention the colour of the spore print (it must have been brown as the spores are stated to be remarkably pale under the microscope) and the shape of the pleurocystidia. The original *Agaricus empyreumaticus* Berk. & Br. is a different species again (see Orton *1960*: 371).

As we had suspected from the description Orton (*1960*: 369) gave of his *P. cortinarioides*, our examination of the type material revealed this species to be identical



Figs. 19–23. *Psathyrella clivensis*, 10 Nov. 1958. — 19. Pleurocystidiogram (×575). — 20. Cheilocystidiogram (×575). — 21. Caulocystidiogram (×575). — 22. Sporogram (×1210). — 23. Basidiogram (×575).

with *P. frustulenta* sensu Smith. Macroscopically (crowdedness and colour of the gills) the exsiccata were fully identical with the dried specimens of our four collections of *P. frustulenta* sensu Smith and microscopically they also fully answered that species. Orton did not mention the absence of a germ pore and the abundance of the pleurocystidia but his figure 359 depicts phaseoliform spores without a germ pore and the pleurocystidia turned out to be strikingly abundant. Unfortunately Orton did not mention the important colour of the spore print, but going by the pale brown colour of the spores under the microscope it must have been brown. Contrary to Orton who stated not having seen clamps, we found on examination of the superficial layer of the apex of the stem numerous clamps (also mentioned by Smith) both on the hyphae and moderately numerous caulocystidia. On account of these findings we believe *P. cortinarioides* to be conspecific with *P. frustulenta* sensu Fr., A. H. Smith and the material described by us above.

PSATHYRELLA CLIVENSIS (Berk. & Br.) P. D. Orton—Figs. 19–26

Agaricus clivensis Berk. & Br. *in* Ann. & Mag. Nat. Hist. III **7**: 376. 1861. — *Psilocybe clivensis* (Berk. & Br.) Massee, Brit. Fung. Fl. **1**: 378. 1892. — *Psathyrella clivensis* (Berk. & Br.) P. D. Orton *in* Trans. Br. mycol. Soc. **43**: 369. 1960.

MISAPPLIED NAMES.—*Drosophila empyreumatica* (Berk. & Br.) Kühn. & Romagn. sensu Kühn. & Romagn., Fl. anal.: 363. 1953. — *Drosophila frustulenta* (Fr.) Quél. sensu Romagn. *in* Bull. trimest. Soc. mycol. Fr. **91**: 189. 1975.

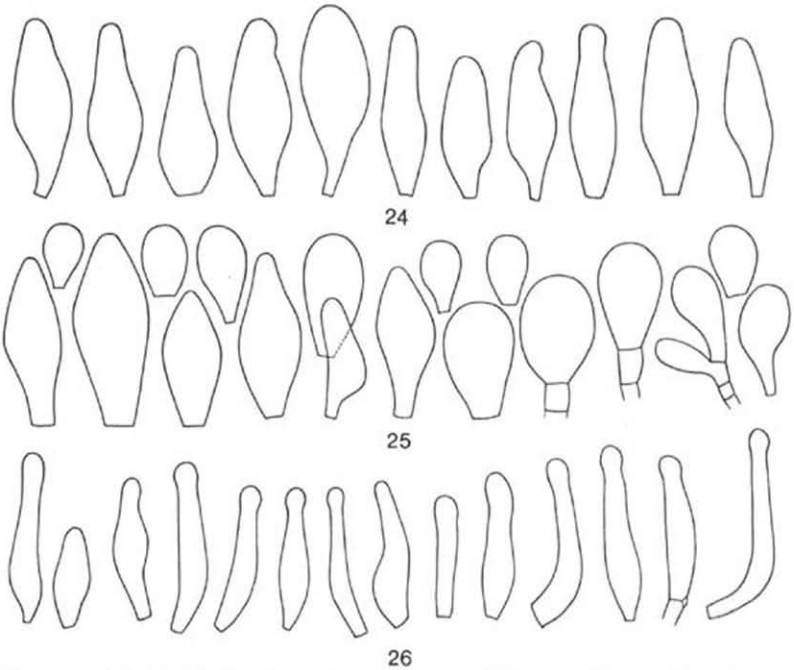
EXCLUDED.—*Psathyrella clivensis* sensu A. H. Smith *in* Mem. N.Y. bot. Gdn **24**: 318 (=?).

SELECTED DESCRIPTIONS AND ILLUSTRATIONS.—Cooke, Ill. Brit. Fungi **7**: pl. 1183/969. 1888–1890; Orton *in* Trans. Br. mycol. Soc. **43**: 369. 1960; Romagnesi *in* Bull. trimest. Soc. mycol. Fr. **91**: 189. 1975 (as *Drosophila frustulenta*); Kühner & Romagnesi, Fl. anal.: 363. 1953 (as *Drosophila empyreumatica*).

CHIEF CHARACTERISTICS.[1]—Carpophores small to medium sized, terrestrial in chalk grassland, solitary; cap 12–30 mm in diam., broadly hemispherical then convex, umber or dark date brown, hygrophanous, dry cap pale ochraceous or whitish, without pink; veil rudimentary; gills whitish when young, later pale umber, with white edge; stem 25–40 × 1.5–3 mm, not rooting, white; spore print clay-umber; spores 8.1–9.9 (–10.8) × 5.4–6.3 µm, in water and NH_4OH 10% pale brownish yellow, with very indistinct germ pore (callus); pleurocystidia 37–60(–75) × 10–17.5 µm, moderately numerous; cheilocystidia 30–50 × 9–20 µm, very scarce, gill edge almost exclusively covered with spheropedunculate and clavate cells, 17.5–32 × 7.5–22 µm; hymenophoral trama distinctly coloured.

MACROSCOPIC CHARACTERS.[1]—Cap 12–30 mm in diam., convex or conico-convex then expanded-convex, sometimes slightly umbonate, often broadly hemispherical, not or slightly striate, rather smooth and shiny when moist, amber or date brown,

[1] Macroscopic characters have been copied from Orton's description. The characters of the trama of the gills and microscopic characters are based on our examination of the two collections mentioned by Orton.



Figs. 24–26. *Psathyrella clivensis*, 23 June 1956. — 24. Pleurocystidiogram (×575). — 25. Cheilocystidiogram (×575). — 26. Caulocystidiogram (×575).

hygrophanous, drying to whitish, pale ochraceous or pale tan often with darker centre; dry surface matt and more or less atomate, sometimes cracking in places.

Veil white, rudimentary, margin of cap only at first with a few very fugacious fibrils. Gills whitish or pale clay then pale clay-umber or coffee colour, sometimes finally with slight violaceous tinge, adnate often with tooth, more or less ventricose, subcrowded.

Stem 25–40 × 1.5–3 mm, equal or slightly thickened at base, white or whitish then discolouring pale dirty brownish from base up, hollow, scattered white silky striate, with apex white pruinose and base white tomentose.

Flesh of cap rather thick at centre, concolorous, drying whitish, often horny date brown over gills; in stem hyaline-whitish. Smell none.

Spore print clay-umber.

Trama of 'washed' gill mounted in NH_4OH 10% under binocular lens conspicuously coloured, yellowish brown (M. 10 YR 5/6) in basal 1/2 or 2/3, gradually paler towards edge and at edge pale brown (M. 10 YR 7/4).

MICROSCOPIC CHARACTERS.[2]—Spores 8.1–9.9(–10.8) × 5.4–6.3 µm (averages 9.2–9.3 × 5.6–5.7 µm), ellipsoid-amygdaliform, rarely subphaseoliform, in water and

[2] See note 1 on p. 297.

NH_4OH 10% pale brownish yellow with a reddish hue (M. 7.5 YR 6/6), in KOH 5% pale yellowish brown (M. 10 YR 5/6), not opaque, with indistinct, practically absent germ pore (callus) and very small hilar appendix.

Basidia 20–30 × 7.5–10 μm, 4-spored.

Pleurocystidia 37.5–60(–75) × 10–17.5 μm, moderately numerous, utriform (but shape variable), thin-walled, colourless, without mucus or crystals.

Cheilocystidia 30–50 × 9–20 μm, very scarce (sometimes even seemingly absent), subutriform or fusiform with obtuse apex or sometimes sublageniform, thin-walled, colourless, without mucus or crystals. Spheropedunculate and clavate cells 17.5–32 × 7.5–22 μm, in very great numbers, practically exclusively forming the cellular lining of the gill edge. Gill edge sterile.

Caulocystidia (apex of stem) 30–45 × 7.5–11 μm, moderately numerous, isolated or in small clusters, shape and size very variable.

Pigmentation of hymenophoral trama under microscope ('washed' gill mounted in NH_4OH 10%) very distinctly brown from membranal pigment, strongest at base, gradually less towards edge, few yellow hyphal septa and very few very small encrustations.

Cuticle of cap cellular, 2–3 cells deep layer of colourless globose or subglobose, vesiculose cells, 16–32 μm in diam.

Clamps on hyphae of stem and caulocystidia.

HABITAT.—Solitary in chalk grassland.

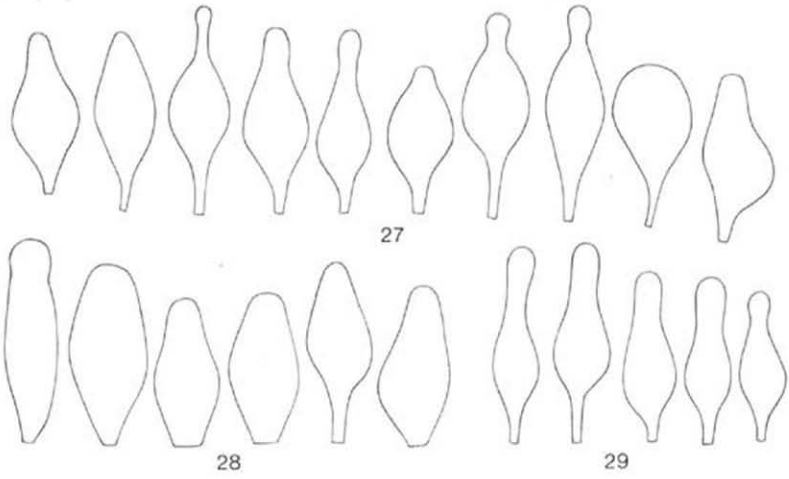
COLLECTIONS EXAMINED.—GREAT BRITAIN: Surrey, Juniper Hill, Mickleham, 23 June 1956, *P. D. Orton 939* (E); Surrey, Epsom Downs, 10 Nov. 1958, *P. D. Orton 1699* (E).

For a lengthy discussion on this species in relation to *P. frustulenta* see p. 293. Romagnesi's description of *P. frustulenta* fully corresponds with the above description, and accordingly Romagnesi regards his *P. frustulenta* conspecific with *P. clivensis*. We have taken the description of the macroscopic characters from Orton as with *P. clivensis* we are dealing with a species, first described from Great Britain and as it was Orton who rediscovered and redescribed the species in 1960.

Smith (*1972*: 318) gave under the epithet *P. clivensis* a description of an apparently different species found only once. His description mentions a few characters, that are not in accordance with Orton's description, with Romagnesi's description of his *P. frustulenta*, and with our observations on Orton's collections. With Smith the spores present a very distinct germ pore (Smith's fig. 623), they are said to be 'obscurely bean-shaped' (but all spores depicted in profile show a very distinct bulging adaxial face), the pleurocystidia are by no means utriform but are called 'fusoid-ventricose, apex subacute to obtuse' and they are depicted as lageniform, the cheilocystidia are abundant and the habitat was 'on humus near a beaver pond'.

PSATHYRELLA OBTUSATA (Pers. ex Fr.) A. H. Smith—Figs. 30–34

Agaricus obtusus Pers., Syn. Fung.: 428, 1801. — *Agaricus obtusatus* Pers. ex Fr., Syst. mycol. **1**: 293. 1821; Epicr.: 232. 1838; Monogr. Hym. Suec. **1**: 441. 1857; Hym. europ.: 306. 1874. — *Psilocybe obtusata* (Pers. ex Fr.) Kummer, Führ. Pilzk.: 71. 1871. — *Psathyra obtusata* (Pers. ex Fr.). Gillet, Hym. France: 591. 1874. — *Psathyra obtusata* (Pers.) P. Karst. *in* Medd. soc. fenn. **9**: 47. 1882 ('obtusa'). — *Drosophila obtusata* (Pers. ex Fr.) Quél., Fl. mycol.: 59. 1888. — *Psathyra spadiceo-grisea* var. *obtusata* (Pers. ex Fr.) Quél., Enchir. Fung.: 117. 1886. — Type locality: Sweden.



Figs. 27–29. *Psathyrella frustulenta* sensu Romagn. — Pleurocystidiograms (×575). — 27. 19 April 1959. — 28. 18 Aug. 1968. — 29. 12 May 1968.

Psathyra rufescens Petch *in* Ann. Roy. bot. Gdn Peradeniya **9**: 126. 1924?

MISAPPLIED NAMES.—*Psathyra obtusata* sensu Ricken, Blätterp.: 261. 1913 (=*Psathyrella* spec.). — *Drosophila obtusata* sensu Romagn. *in* Rev. Mycol. **2**: 246. 1937 (=*Psathyrella* spec.).

SELECTED DESCRIPTIONS AND ILLUSTRATIONS.—Schaeff., Fung. Bav. Icon., pl. 60 figs. 1–3. 1762. — Cooke, Ill. Brit. Fungi, pl. 615/593. 1884–1886. — J. E. Lange, Fl. agar. dan. **4**: 98, pl. 152 A. 1939. — Wakefield & Dennis, Common Brit. Fungi: 201, pl. 79, fig. 2. 1950. — Kühn. & Romagn., Fl. anal.: 363. 1953. — Hongo *in* Mem. Fac. Lib. Arts Educ. Shiga Univ. **11**: 40. 1961. — A. H. Smith *in* Mem. N.Y. bot. Gdn **24**: 385. 1972. — Romagnesi *in* Bull. Soc. mycol. Fr. **91**: 197. 1975.

CHIEF CHARACTERISTICS.—Carpophores small to medium sized, solitary, terrestrial. Cap 20–25 mm in diam., convex without umbo, strikingly brown, hygrophanous, dry very pale brown without pink, with white, rudimentary veil; gills strikingly pinkish brown, with white edge; stem 60–75×2–3 mm, not rooting, white; spore print brown with purplish hue; spores 7.2–8.1×4.5–5 µm, with germ pore, in water and NH_4OH 10% yellowish brown with a trace of reddish, subphaseoliform; pleurocystidia 35–50×9–15 µm, very numerous, fusiform; marginal cells almost exclusively consisting of fairly large (20–30×12.5–20 µm) spheropedunculate and clavate cells, intermixed with very few spheropedunculate cells equipped with a short subcylindrical neck; hymenophoral trama coloured.

MACROSCOPIC CHARACTERS.—Cap 20–25 mm in diam., conico-convex without umbo, striate up to 2/3 from margin upwards, central half strikingly brown (between M. 7.5 YR 4/4 and 5/4), peripheral half much lighter (M. 10 YR 6/4) but with darker striation (M. 7.5 YR 5/4), hygrophanous, drying out to very pale brown (M. 10 YR 8/4) without pink, dry surface rugulose, distinctly micaceous.

Veil white, distinct but scanty; velar fibrils and minute fibrillous networks on surface of cap only in one mm broad zone along margin; surface of lower 2/3 of stem covered with quite a few velar fibrils.

Gills 3–4 mm broad, strikingly pinkish brown, colour of weak chocolate (M. 5 YR 5/3–6/3), moderately ventricose, rather broadly adnate, with white edge.

Stem 60–75 × 2–3 mm, slightly thickening towards base, somewhat undulating, not rooting, hollow, white with smooth surface and pruinose apex.

Flesh of cap 2 mm thick at centre, concolorous (M. 10 YR 4/3 with a trace of reddish), flesh of stem very pale brown with thin white superficial layer. Smell none.

Spore print brown with a purplish hue.

Trama of 'washed' gill, mounted in NH_4OH 10% under binocular lens, in basal half greyish with only a trace of brown (M. ±10 YR 7/2), brown (M. 10 YR 5/3) only in a very narrow strip at the very base, in peripheral half almost colourless (brown colour of gills chiefly due to colour of spores).

MICROSCOPIC CHARACTERS.—Spores 7.2–8.1 × 4.5–5 μm (averages 7.4 × 4.6 μm), ellipsoid-amygdaliform and subphaseoliform, in water and NH_4OH 10% yellowish brown (M. 7.5 YR 5/6) with a trace of reddish (darker than in *P. frustulenta*), not opaque, with small (±1 μm) and moderately distinct, not truncate apical germ pore and small hilar appendix.

Basidia 17.5–22 × (9–)10 μm, 4-spored.

Pleurocystidia 35–50 × 9–15 μm, very numerous, fusiform with short and fairly broad pedicel and acute to subacute apex, thin-walled, colourless, without mucus or crystals.

Spheropedunculate and clavate cells 20–30 × 12.5–20 μm, very numerous and densely packed, vesiculose, thin-walled, without mucus or crystals, intermixed with very few spheropedunculate cells equipped with a short subcylindrical neck (cheilocystidia), 30–37 × 12.5–16 μm. Gill edge sterile.

Caulocystidia (apex of stem) mostly in large clusters and very numerous, shape and size very variable, similar to both types of marginal cells, globose, subglobose and clavate cells (20–47 × 15–25 μm) and globose cells equipped with a short subcylindrical neck (22–40 × 10–15 μm), also quite a few elliptical and subcylindrical cells.

Pigmentation of hymenophoral trama under microscope ('washed' gill mounted in NH_4OH 10%) distinctly brown from membranal pigment at base of gill, colour getting much fainter towards edge, very faint in peripheral half, a fair number of yellowish hyphal septa and very few very small encrustations in basal half.

Cuticle of cap cellular, 2–4 cells deep layer of colourless globose or subglobose vesiculose cells, 24–48 μm in diam.

Clamps on hyphae of stem and caulocystidia.

HABITAT.—Solitary, terrestrial under *Fagus* and *Quercus*.

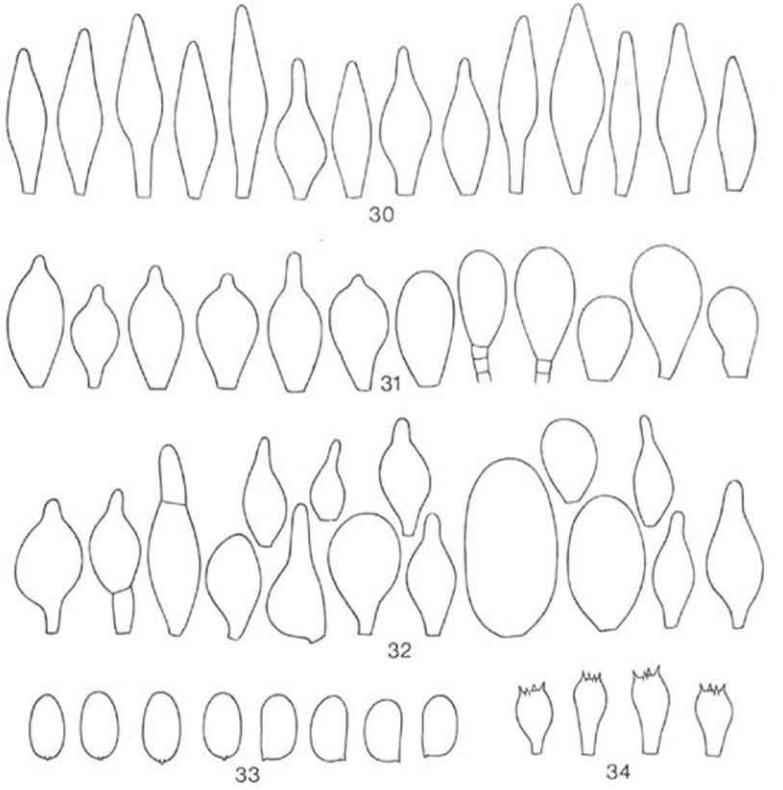
COLLECTION EXAMINED.—THE NETHERLANDS: prov. Noord-Holland, Overveen, estate 'Elswout', 21 Oct. 1976, *E.K.v. W.* (L).

The three most recent and full descriptions of *P. obtusata* are those by J. E. Lange (*1939*: 98), A. H. Smith (*1972*: 385), and Romagnesi (*1975*: 197).

Romagnesi (*1975*: 197) pointed out that A. H. Smith described a *P. obtusatus* with small spores (6–7 × 3.5–4 μm) and a 'drab grey colour' of the gills, and correctly stated that therefore that fungus is very much different from the European species. Romagnesi's statement, however, pertains to the 1941 description by Smith which—also in other respects—differs from the description given by Romagnesi (*1975*: 197)

for *P. obtusatus* and from Smith's 1972 description of that species, in which the spores are said to measure 7–9×4–4.5 µm and the colour of the gills is said to be pallid brown, becoming reddish brown to purplish brown, which is completely in line with the descriptions given by Lange, Romagnesi, and us.

In Smith's 1972 description the colour of the dry cap, the width of the gills and—most important of all—the colour of the spore print are lacking. Romagnesi's description is complete except for the fact that the abundance of the pleurocystidia (one of the characteristic features of the species) is not mentioned. Otherwise both descriptions are in full accordance and they agree with Lange's description (*1939*: 98). All three authors referred the species to Fries's descriptions of *A. obtusatus*.



Figs. 30–34. *Psathyrella obtusata*, 21 Oct. 1976. — 30. Pleurocystidiogram (×575). — 31. Cheilocystidiogram (×575). — 32. Caulocystidiogram (×575). — 33. Sporogram (×1210). — 34. Basidiogram (×575).

As a matter of course the question arises whether indeed the species described by Lange, Smith, Romagnesi (and many more authors), and us, is conspecific with *A. obtusatus* as described by Fries. The two outstanding macroscopic characteristics of *A. obtusatus* as described by Fries are the brown colour of the cap (in *1821*: 'dilute badio'; in *1838* and *1874*: 'umbrinus'; in *1857*: 'spadiceo l. umbrino-fuscus') and the brown colour of the gills (in *1821*: 'umbrinis'; in *1838* and *1874*: 'pallido umbrinis'; in *1857*: 'cinereo-fuscae dein umbrinae'). It is a great pity that Fries did not give the colour of the spore print in *A. obtusatus*, which must have been some shade of brown. Among the small and medium sized species of *Psathyrella* those with distinctly brown gills are striking in the field. In the colour of cap and gills and in all other macroscopic features the descriptions by Fries on the one hand, and by Lange, Smith, and Romagnesi on the other hand are in complete agreement except, however, for the veil.

Whereas Fries emphasizes the absence of a veil in this species, Smith states that the surface of the cap is at first covered with scattered fibrils, but soon glabrous, and that the lower portion of the stem is sparsely covered with whitish fibrils. Romagnesi reports the presence of a 'voile particl léger, en forme de cortine blanche, assez nette sur les jeunes, mais totalement évanescente'. Lange neither mentions nor depicts (plate 152 D) the presence of a veil. From these descriptions it is obvious that the veil in *P. obtusata* is rudimentary and very evanescent. Smith, having been able to examine material from no less than 26 collections, and Romagnesi no doubt having come across the species frequently as he calls it very common, they both must have been able to study the species in all its stages. Fries, on the other hand, although he did see the species himself, calls it 'rarissime', so that it is quite likely that he only very rarely examined material of *A. obtusatus*. This may well account for the fact that he never noticed traces of a veil.

In conclusion we feel with Smith, that the absence of a veil, mentioned in the Friesian descriptions of *A. obtusatus* should not stand in the way of regarding Fries's species as conspecific with P. obtusata as described by Lange, Smith, Romagnesi, and us. This view is supported by the great resemblance between the carpophores depicted on Schaeffer's plate 60, figs. 1–3 (*1762*; cited by Fries!) and on Lange's plate 152 D, both plates depicting, also in the opinion of Romagnesi, *P. obtusata* very well.

Psathyrella obtusata as described by Ricken (*1913*: 261) has the same macroscopic characters as *P. obtusata* as described by Fries, Lange, Smith, and Romagnesi, but the spores are said to be elliptical and not phaseoliform, and the cellular lining of the gill edge with Ricken consists of lancet- to flasklike cells. With Lange, Smith, Romagnesi, and us this cellular lining consists almost exclusively of spheropedunculate and clavate cells, intermixed with an occasional globose cell, bearing a short subcylindrical neck. Therefore the interpretation of *P. obtusata* (Fr.) sensu Ricken remains obscure.

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THE GENUS MELANOTUS PAT.

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(With 80 Text-figures)

The genus *Melanotus* is revised. Its delimitation is discussed. A key is given to 21 accepted species. Of these synonyms, habitat, distribution, and illustrations are given. The new species *Melanotus citrisporus*, *M. protractus*, *M. distinctus*, *M. vorax*, and *M. communis* are described. *Melanotus hepatochrous* and *M. flavolivens* are described anew. A list of host plants is added.

Due to their small size and rare occurrence the Melanoti are agarics whose identification and taxonomy still raise considerable problems. No wonder no key or detailed modern descriptions of many of the taxa have ever been published.

The genus *Melanotus* (Singer, *1975*: 543) is characterized by small carpophores, eccentric or lateral short tipe (but occasionally the stipe is centric or even lacking), absence of veil remnants, brown spore print (often with purplish tint), ovate sublentiform or limoniform smooth spores with either thin- or thick-walled complex brown or opaque spore membrane, distinct apical germ pore, usually fusoid hyaline cheilocystidia, absent pleurocystidia, and a cutis of interwoven cylindrical hyphae with clamp connections and encrusting pigment.

All known species of *Melanotus* grow saprophytically on decomposing organic material (see list of host plants).

Concerning the area of distribution, the majority of species are restricted to regions close to the Equator but some taxa also occur in more temperate zones. The northernmost record of *M. phillipsii* is from Sweden. In the southern hemisphere *M. proteus* occurs in Kenya and also in the Cape Province. *Melanotus hepatochrous* seems to be a rather common fungus in the forests of Tasmania and finally *M. patagonicus* was collected in the Patagonian *Nothofagus* forests, which are covered by snow in winter at least temporarily. Many of the species described hitherto are known only from the type collection and therefore our knowledge about their ecology is at best poor. Due to their habit and habitat most of the classical species of *Melanotus* are published under *Crepidotus* or *Claudopus*. However, microscopical examination immediately reveals that *Melanotus* has no taxonomical relationship to these genera. Despite a number of macroscopical similarities the microscopical characters of *Pyrrhoglossum* and *Pleuroflammula* are so distinct that no species of these genera can be mistaken for *Melanotus*. The delimitation towards eccentric or estipitate species of *Phaeomarasmius* or *Tubaria*, however, can be difficult since their brown spores sometimes possess an oblique germ pore. In such cases generic identification is possible only in well documented collections.

The taxonomic limit raising the most problems is undoubtedly that of *Psilocybe* (*Deconica*). Where must the separating line be drawn between *Psilocybe* and *Melanotus*? Or is the eccentric, reduced or even absent stipe a criterion of sufficient importance to warrant splitting off *Melanotus* from *Psilocybe?* (Singer, *1976*: 543; Romagnesi, *1977*). From the microscopical point of view (spores, basidia, cystidia, cuticle) there are no differences at all between the two genera. Based on our personal field observations the insertion of the stipe can vary from eccentric to sublateral or lateral in a single population in the same locality and on the same host. The pileal position is often a direct response to the microtopography found at the point where the carpophores happen to be attached to the substrate. Under these circumstances it is possible that this 'generic character' is of much less value than is usually assumed. Experiments under pure culture conditions could help to resolve this question.

In this study the taxonomic concept of *Melanotus* follows Singer (*1975*). For the time being it does not matter that the 21 species accepted in several cases are not at all closely related. In my opinion the genus *Melanotus* in its present composition represents a heterogeneous conglomerate of fungi which share similar morphological characters as a result of ecological adaptation.

In preparing this monography on *Melanotus* the assistance and advice of several herbaria (BAFC, BO, E, F, FH, K, LPS, NY, PC, and S) is acknowledged. I am also grateful to Prof. E. J. H. Corner (Cambridge) who loaned part of his SE.-Asian collections of agarics.

If not otherwise stated the magnifications of the figures are: carpophores (nat. size), spores (× 2000), basidia and cystidia (× 1000), and cuticle (× 500).

MELANOTUS Patouillard

Melanotus Patouillard, Essai tax.: 175. 1900. — Type species: *Crepidotus ? bambusinus* Pat. *in* J. Bot. **5**(18): 309. 1891 ≡ *Melanotus bambusinus* (Pat.) Pat., Essai tax.: 175. 1900.

KEY TO THE SPECIES OF MELANOTUS

EUROPE

Melanotus phillipsii (see key to African species)

AFRICA

1a. Spores (5–)6–7.5×4–5 µm, thick-walled; cheilocystidia 14–28×3.5–5.5 µm, lanceolate to fusiform with elongate neck; pileus –10 mm, pale brown; lamellae fuscous; stipe eccentric, lateral or absent. On wood (*Cupressus*).
South Africa (type), Kenya . . . . . 1. *M. proteus*, p. 308

b. Spores more slender, thin-walled (membranes rarely thick-walled) 2

2a. Spores 5.5–7(–8)×3–4(–5) µm; cheilocystidia 20–35×3–7 µm, ventricose-fusoid, occasionally with subcapitate apex; pileus –15 mm, pale brown; lamellae cinnamon to fuscous; stipe eccentric to lateral, chestnut brown. On decomposing twigs. Kenya
2. *M. gelineus*, p. 308

b. Spores 5–6 × 2.5–3 µm; cheilocystidia 16–40 × 3–5 µm, fusoid with elongated neck; pileus –15 mm, pale brown or cinnamon; lamellae concolorous; stipe eccentric to lateral. On dead grasses (*Agrostis*, *Carex*) and herbaceous stems (*Scrophularia*). Morocco
3. *M. phillipsii*, p. 309

NORTH AMERICA / SOUTH AMERICA

1a. Spores thin-walled, 6–8(–9) × (4–)4.5–6 µm, broadly ovate; pileus –12 mm, brown to pale brown; lamellae pale ochraceous; stipe eccentric; cheilocystidia 20–45 × 4–6 µm, fusoid with elongate neck. On decomposing or dead leaves of *Chusquea*. Argentina, Chile . . . . . 4. *M. bruchii*, p. 310
b. Spores conspicuously thick-walled 2
2a. Spores larger than 7 × 5 µm 3
b. Spores smaller 4
3a. Spores 8–11 × 5.7–7.7 µm, ellipsoid to phaseoliform; pileus –10 mm, brown; stipe eccentric to lateral, white; cheilocystidia ampullaceous. On wood. Chile
5. *M. cassiaecolor* sensu Singer, p. 311
b. Spores 7–8 × 5.5 µm; pileus –10 mm, pale brown; lamellae pale yellow-brown; stipe absent; cheilocystidia ?. On husk of *Cocos*. Grenada . . . 6. *M. subcuneiformis*, p. 311
4a. Stipe absent or rudimentary; spores 5.5–7.5 × 4–5 µm; cheilocystidia ?; pileus –15(–30) mm, ochraceous to pale red-brown; lamellae brown with purplish tint. On decomposing leaves and twigs, and rotten wood; known host plants: *Musa*, *Alpinia*, *Psychotria*. Brazil (type), Trinidad, Guadeloupe, Jamaica, Cuba . . . . . 7. *M. alpiniae*, p. 311
b. Stipe more or less well developed, often subcentric 5
5a. Pileus –5 mm, isabelline; lamellae yellowish; stipe whitish; spores 5–6 × 3.5–4 µm; cheilocystidia ?. On decomposing herbaceous stems. Jamaica . . 8. *M. eccentricus*, p. 313
b. Pileus brown to ochre-brown; lamellae and stipe more or less concolorous with pileus 6
6a. Spores 4.5–5.5 × 3–3.5 µm; pileus –10 mm; cheilocystidia 20–30 × 3–6 µm, fusoid with elongate tapering neck. On bark of *Polylepis*. Argentina . . . . 9. *M. polylepidis*, p. 313
b. Spores 6–7(–7.5) × 4–5 µm; pileus –18 mm; cheilocystidia –30 × –12 µm, polymorphous varying from clavate to vesiculose. On rotting wood. Argentina 10. *M. patagonicus*, p. 314

AUSTRALASIA

1a. Spores longer than 10 µm 2
b. Spores smaller than 10 µm 3
2a. Spores 10–13 × 9–12 µm, limoniform to lentiform; pileus –6 mm, cream to pale brown; lamellae grey-brown with lilac tinge; stipe rudimentary or absent; cheilocystidia 20–35 × 5–10 µm, fusoid. On decomposing leaves of *Astelia*. New Zealand
11. *M. citrisporus*, p. 315
b. Spores 10.5–12.5 × 6.5–7.5 µm, ellipsoid; pileus –16 mm, brown; lamellae pale brown to rust brown, without lilac tinge; stipe absent or rudimentary; cheilocystidia 20–35 × 8–18 µm, clavate-capitate. On decomposing leaves of *Musa*. Papua New Guinea
12. *M. protractus*, p. 315
3a. Stipe absent, pileus laterally or subdorsally attached to substratum (see also *M. flavolivens*, *M. hepatochrous*) 4
b. Stipe present, at least in young carpophores 7
4a. Pileus 5–10 mm, conchiform to reniform 5
b. Pileus 20–30 mm, linguiform to spathulate 6
5a. Pileus and lamellae 'atrosanguineus'; spores 5.5–7 × 3.5–4.5 µm, thick-walled; cheilocystidia ?. On rotting wood. Hongkong . . . . . 13. *M. haematites*, p. 317
b. Pileus white; lamellae brown; spores 5.5–6.5 × 3.5–4.5 µm, thick-walled; cheilocystidia?. On decomposing fern-rhachis. Malaya . . . . . 14. *M. ridleyi*, p. 317

6a. Pileus –50 mm, whitish; lamellae brown-purple; spores 6–7×4–4.5 µm, thick-walled; cheilocystidia ?. On rotting wood. Ceylon . . . . . 15. *M. phaeophyllus*, p. 319
b. Pileus –20 mm, pale brown; lamellae brown, without lilac tinge; spores 6–7×4–5 µm, thin-walled; cheilocystidia 20–35×8–11 µm, fusoid with capitate apex; clamp connections absent. On rotting wood. Papua New Guinea . . . . . 16. *M. distinctus*, p. 319
7a. Spores 6.5–8.5(–9)×4–5.5(–6) µm, thin-walled; cheilocystidia 15–30×5–10 µm, fusoid with elongate tapering neck. On decomposing leaves of *Phormium*, *Cortaderia*, and ferns. New Zealand . . . . . 17. *M. vorax*, p. 319,
b. Spores smaller 8
8a. Pileus –30 mm, dark brown, red-brown, or liver brown; lamellae yellowish brown, cinnamon, or deep brown; stipe often rudimentary in old specimens; spores 5.5–7.5×3.5–5 µm; cheilocystidia 20–30×3–6 µm, lanceolate to fusoid with elongate neck. On rotting wood. Tasmania (type), Victoria (Australia), New Zealand 18. *M. hepatochrous*, p. 321
b. Pileus whitish, pale brown or fawn-yellowish 9
9a. Lamellae grey, grey-beige or yellowish beige, without distinct purple tinge; pileus –12 mm; stipe eccentric, more or less concolorous with pileus; spores (5–)6–7×4–4.5 µm; cheilocystidia 15–25×3–5 µm, subfusoid to cylindrical. On decomposing organic detritus, also on decomposing leaves of *Cocos*. The Bonin Isl., New Caledonia, the Solomon Isl. . . . . 19. *M. flavo-livens*, p. 323
b. Lamellae brown with distinct purple or lilac tinge; spores usually thin-walled . . 10
10a. Pileus –30 mm; stipe eccentric to lateral; spores 5–7×3.5–4.5 µm; cheilocystidia 15–25×5–10 µm, clavate to fusoid-capitate, occasionally with mucronate apex. On rotting branches in rain forest. Papua New Guinea . . . . . 20. *M. communis*, p. 324
b. Pileus –15 mm, often laterally attached to substratum in old specimens; stipe eccentric when young; spores 6–7×4–5 µm; cheilocystidia ?. On *Bambusa*. Vietnam 21. *M. bambusinus*, p. 325

1. MELANOTUS PROTEUS (Kalchbr. apud Thüm.) Sing.—Fig. 1

Agaricus proteus Kalchbr. apud Thüm. *in* Flora **59**: 424. 1876 (basionym). — *Claudopus proteus* (Kalchbr.) Sacc., Syll. Fung. **5**: 734. 1877. — *Melanotus proteus* (Kalchbr. apud Thüm.) Sing. *in* Lloydia **9**: 130. 1946. — *Crepidotus proteus* (Kalchbr. apud Thüm.) Pilát *in* Trans. Brit. mycol. Soc. **33**: 231. 1950.

ILLUSTRATIONS.—Pilát (*1950*: 231); Pegler & Rayner (*1969*: 391); Reid (*1975*: 104).
HABITAT.—On humid lumber (type) and on wood of *Cupressus*. South Africa, Kenya (Pegler & Rayner, *1969*: 391), Ceylon? (Cesati, *1879*: 2).
MATERIAL EXAMINED.—SOUTH AFRICA: Somerset East, Jan. 1876, *McOwan & Tuck* (holotype, K).

2. MELANOTUS GELINEUS Pegler—Figs. 2–4

Melanotus gelineus Pegler *in* Kew Bull., Add. Ser. **6**: 477.1977.

ILLUSTRATIONS.—Pegler (*1977*: 477).
HABITAT.—On dead fallen twigs. Kenya.
MATERIAL EXAMINED.—KENYA: Nyanza, Kericho district, Kigumu River, 25 March 1968, *D. N. Pegler 237* (holotype, K).

The microscopical characters of this species suggest those found on *M. phillipsii*, which also occurs in the NW. corner of Africa (Morocco). Both taxa share the

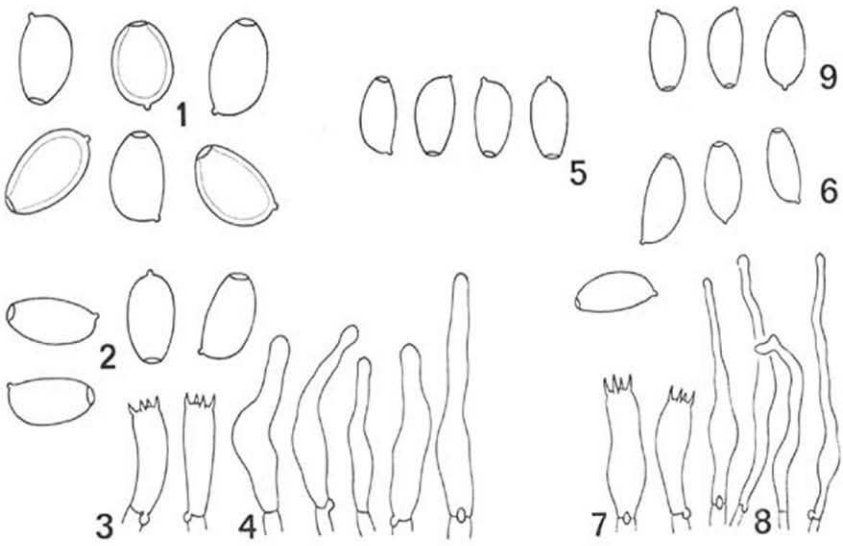


Fig. 1. *Melanotus proteus* (from type), spores.
Figs. 2–4. *Melanotus gelineus* (from type). — 2. Spores. — 3. Basidia. — 4. Cheilocystidia.
Figs. 5–9. *Melanotus phillipsii*. — 5. Spores (from type of *M. phillipsii*). — 6–8. From Fungi Exs. Suec. 2054. — 6. Spores. — 7. Basidia. — 8. Cheilocystidia. — 9. Spores (from type of *Naucoria scutellina*).
For magnifications see page 306.

slender ellipsoid spores that are rather uncommon in the genus *Melanotus*. Spore size and spore shape, however, distinctly separate the two species.

3. MELANOTUS PHILLIPSII (Berk. & Br.) Sing.—Figs. 5–9

Agaricus (*Crepidotus*) *phillipsii* Berk. & Br. *in* Ann. Mag. nat. Hist. **5**: 21. 1878 (basionym). — *Pleuroflammula phillipsii* (Berk. & Br.) Sing. *in* Sydowia **5**: 473. 1951. — *Geophila* (*Psilocybe*) *phillipsii* (Berk. & Br.) Kühn. & Romagn., Flore anal.: 339. 1953. — *Melanotus phillipsii* (Berk. & Br.) Sing. *in* Beih. Sydowia **7**: 84. 1973.

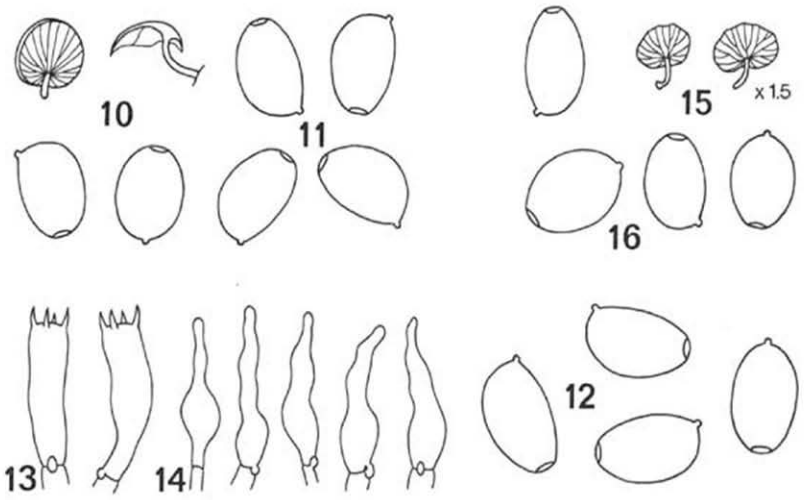
Naucoria scutellina Quél. *in* Bull. Soc. bot. Fr. **25**: 287. 1878.

Pleurotus roseolus Quél. sensu Lange *in* Dansk bot. Ark. **6** (5): 30. 1930.

ILLUSTRATIONS.—Quél. (*1878*: 287, pls. 3, 5); Cooke (1886, IV, pl. 515 C); Pilát, *1948*: 46; Malençon & Bertault (*1970*: 337).

HABITAT.—On decomposing leaves and culms of 'grasses' (*Agrostis*, *Carex*) and herbaceous stems (*Scrophularia*). England (type), Sweden, Denmark (Lange, *1930*: 30), France (Quél., l.c.; Romagnesi, *1937*: 137), Germany (Moser, pers. comm.), Switzerland, C. S. S. R. (Pilát, *1948*: 40), Morocco (Malençon & Bertault, l.c.).

MATERIAL EXAMINED.—ENGLAND: Shrewsbury, Oct. 1876 (holotype, K). SWEDEN: Bohuslän, Rödbo parish, Ellisbo, 17 July 1943, *Nathorst-Windahl* (Fungi exsicc. suec. 2054, '*Crepidotus*', S). FRANCE: Hérimoncourt, July–Aug. 1878, *Pillod* (holotype of *N. scutellina* Quél., herb. Bresadola, S).



Figs. 10–16. *Melanotus bruchii*. — 10, 11. From type of *M. bruchii*. — 10. Carpophores. — 11. Spores. — 12–14. From *Horak 75/297*. — 12. Spores. — 13. Basidia. — 14. Cheilocystidia. — 15, 16. From type of *M. gayi*. — 15. Carpophores (× 1.5). — 16. Spores.

To our surprise type material or at least an authentic collection of *Naucoria scutellina* Quél. was found in the Bresadola Herbarium in Stockholm, Sweden. Since Bresadola added the remark 'Quélet misit', there can be no doubt about the authenticity of this fungus, which is conspecific with *M. phillipsii*, also published in 1878 (priority?).

4. **Melanotus bruchii** (Spegazzini) Horak, *comb. nov.*—Figs. 10–16

Crepidotus bruchii Speg. *in* Boln Acad. nac. Ci. Córdoba **29**: 128. 1926 (basionym.) — *Pleuroflammula bruchii* (Speg.) Sing. *in* Lilloa **22**: 251. '1949' [1951].

Crepidotus gayi Pilát in Trans. Br. mycol. Soc. **33**: 237. 1950. — *Melanotus gayi* (Pilát) Sing. *in* Beih. Nova Hedw. **29**: 258. 1969.

ILLUSTRATIONS.—Pilát (*1950*: 237, *gayi*).

HABITAT.—On rotting branches of broad-leaved trees (type) or decomposing leaves of *Chusquea* spec. Argentina (Tucuman, Cordoba (type), Neuquén), Chile.

MATERIAL EXAMINED.—ARGENTINA: Cordoba, Alta Cracia, 3 Feb. 1925, *Bruch 112* (holotype, LPS 13465). CHILE: Rancagua, April 1818, Bertero (=*M. psychotriae* sensu Sing., herb. Steudel, FH); Valdivia, 1839, *Gay* (holotype of *Crepidotus gayi* Pilát, PC); Valdivia, Fundo San Martin, 10 April 1975, *Horak 75/297* (ZT).

According to the microscopical data found on the type material of *Crepidotus bruchii* Speg. this fungus clearly belongs to *Melanotus* and not *Pleuroflammula* (Singer,

1949: 521). The characters observed on the four above mentioned collections agree in all details. *Melanotus bruchii* Speg. is distinguished by its large thin-walled spores and its lateral to eccentric short stipe.

5. MELANOTUS CASSIAECOLOR (Berk.) Singer sensu Singer

Melanotus cassiaecolor (Berk.) Sing. sensu Sing. *in* Beih. Nova Hedw. **29**: 257. 1969.

According to Singer's description (spores 8–11 × 5.7–7.7 μm) this Chilean collection does certainly not represent *Melanotus cassiaecolor* Berk. (= *M. hepatochrous* Berk.). The characters reported do not fit any of the taxa hitherto known to belong to *Melanotus*. Unfortunately no material was obtained on loan from SGO. Hence we can neither confirm nor refute the impression that this fungus is a representative of *Phaeomarasmius*.

6. MELANOTUS SUBCUNEIFORMIS (Murrill) Singer—Fig. 17

Crepidotus subcuneiformis Murrill *in* Mycologia **5**: 29. 1913 (basionym). — *Melanotus subcuneiformis* (Murrill) Sing. *in* Lilloa **13**: 87. 1947.

HABITAT.—On decaying coconut husk. Grenada (West Indies).
MATERIAL EXAMINED.—GRENADA: Grenada, Sept. 1905, *Broadway* (holotype, NY).

This small and pale brown *Melanotus* is characterized by rather large ovate to sublenticular and thick-walled spores. Macroscopically the species resembles the two other taxa so far reported from the islands in the Mexican Gulf. However, the size of the spores distinctly separate *M. subcuneiformis* from *M. alpiniae* and *M. eccentricus* (see also Hesler & Smith, *1965*: 146).

7. MELANOTUS ALPINIAE (Berk.) Pilát—Figs. 18–27

Agaricus (*Crepidotus*) *alpiniae* Berk. *in* Hooker, J. Bot. Lond., **8**: 133. 1856 (basionym). — *Melanotus alpiniae* (Berk.) Pilát *in* Trans. Br. mycol. Soc. **33**: 216.1950.
Agaricus (*Crepidotus*) *musaecola* Berk. & Curt. *in* J. Linn. Soc. (Bot.) **10**: 291. 1868. — *Crepidotus musaecola* (Berk. & Curt.) Sacc., Syll. Fung. **5**: 883. 1887 (as '*musicola*'). — *Melanotus musaecola* (Berk. & Curt.) Murrill *in* Mycologia **10**: 16. 1918 (as '*musicola*'). — *Melanotus musaecola* (Berk. & Curt.) Sing. *in* Lloydia **9**: 130. 1946.
Claudopus subvariabilis Speg. *in* Boln Acad. nac. Ci. Cordoba **11**: 411. 1889. — *Melanotus subvariabilis* (Speg.) Sing. *in* Lilloa **22**: 511. '1949' [1951].
Crepidotus psychotriae Pat. *in* Bull. Soc. mycol. Fr. **18**: 173. 1902. — *Melanotus psychotriae* (Pat.) Sing. *in* Lloydia **9**: 130. 1946.
Crepidotus fumosifolius Murrill *in* Mycologia **5**: 31. 1908. — *Melanotus fumosifolius* (Murrill) Sing. *in* Lilloa **13**: 87. 1947.

ILLUSTRATIONS.—Pilát (*1950*: 216, *alpiniae*; *1950*: 225, *musaecola*); Dennis (*1970*: 71).
HABITAT.—On decomposing leaves, twigs and wood. Known host plants: *Musa*, *Psychotria*, *Alpinia*. Brazil (type), Guadeloupe, Jamaica, Cuba, Trinidad (Dennis, *1970*: 71).

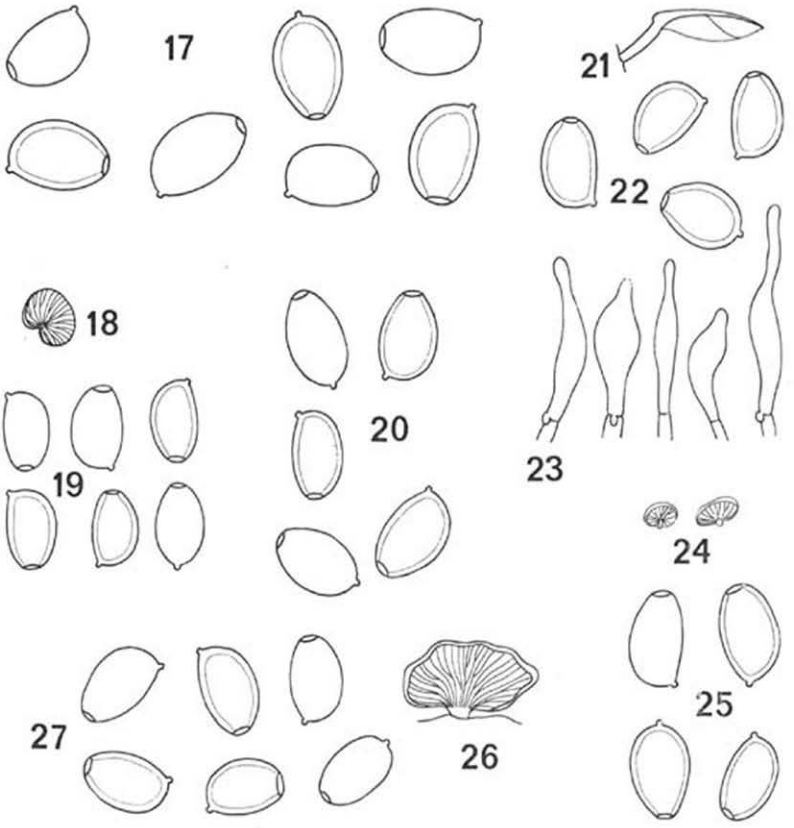


Fig. 17. *Melanotus subcuneiformis* (from type), spores.
Fig. 18–27. *Melanotus alpiniae*. — 18, 19. From type of *M. alpiniae*. — 18. Carpophores. — 19. Spores. — 20. Spores (from type of *Agaricus musaecola*. — 21–23. From type of *Claudopus subvariabilis*. — 21. Carpophore. — 22. Spores. — 23. Cheilocystidia. — 24, 25. From type of *Crepidotus psychotriae*. — 24. Carpophores. — 25. Spores. — 26, 27. From type of *Crepidotus fumosifolius*. — 26. Carpophores. — 27. Spores.

MATERIAL EXAMINED.—BRAZIL: *Spruce 114* (holotype, K); Apiahy, June 1880, *Puiggiari* (holotype of *Claudopus subvariabilis* Speg., LPS 17033). GUADELOUPE: Bois Bains-Jaunes, *Duss* (holotype of *Crepidotus psychotriae* Pat., FH). JAMAICA: Rose Hill, 30 Oct. 1902, *Earle 292* (holotype of *Crepidotus fumosifolius* Murrill, NY). CUBA: *Wright 86* (holotype of *Agaricus* (*Crepidotus*) *musaecola* Berk. & Curt., K).

Among the above mentioned collections there is unfortunately none from which all the necessary microscopical and macroscopical data could be extracted. Without

exception all type material examined is in poor condition. Despite this careful comparison of the authentic collections resulted in the conclusion that these taxa are conspecific.

Upon revising the type collections Pilát (*1950*: 216) emphasized that *M. musaecola* (Berk. & Curt.) Murrill is a synonym of *M. alpiniae* (Berk.) Pilát. Further Hesler & Smith (*1965*: 147) were doubtful about the synonymy of *M. musaecola* originally found in Cuba and *M. fumosifolius* in Jamaica. The spore size of the two fungi ranges between 5.5–7.5×4–5 µm and if compared with *M. alpiniae* (Berk.) Pilát, *M. subvariabilis* (Speg.) Sing—both from Brazil—and *M. psychotriae* (Pat.) Sing. —from Guadeloupe—a complete identity of characters is observed. Therefore the five taxa are considered to represent only one and the same species.

Nevertheless fresh material is needed to resolve further questions as to the colour of the lamellae on fresh carpophores, insertion of the stipe and the size and shape of the cheilocystidia.

Hesler & Smith (*1965*: 147) also regard *M. flavo-livens* (Berk. & Curt.) Sing. as a synonym of *M. musaecola*. The fungus from the Bonin Isl., however, is characterized by yellowish to fawn colours on the pileus, grey or beige lamellae (without purplish tints) and smaller spores. In our own opinion *M. flavo-livens* represents a well defined separate species whose area of distribution spreads from the Bonin Isl. (Pacific Ocean) southwards to New Caledonia and the Solomon Isl. (see No. 19).

8. MELANOTUS ECCENTRICUS (Murrill) Sing.—Figs. 28, 29

Crepidotus eccentricus Murrill *in* N. Am. Fl. **10**: 155. 1917 (basionym). — *Melanotus eccentricus* (Murrill) Sing. *in* Lilloa **13**: 87. 1947.

HABITAT.—On dead herbaceous stems. Jamaica.

MATERIAL EXAMINED.—JAMAICA: E. of Hope Gardens, 12 Dec. 1908, *Murrill* (holotype, NY).:

Together with the type material in the Herbarium of the New York Botanical Garden (NY) a water colour painting was found; hence the morphology of this small species (—5 mm in diam.) is well known (see Fig. 28). The cylindrical stipe is centric or slightly eccentric and always well developed. This character together with the rather slender spores (3–4 µm, but 4–5 µm according to Hesler & Smith, *1965*: 141!) separate *M. eccentricus* from *M. alpiniae*, which also occurs in Jamaica.

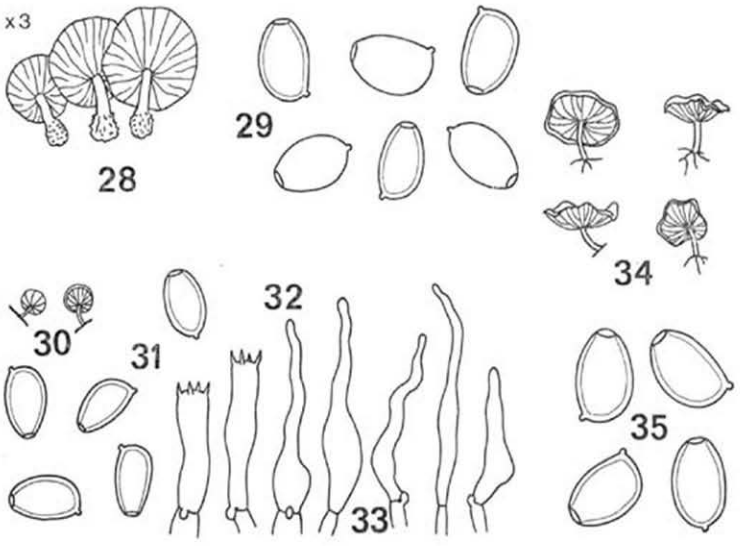
9. MELANOTUS POLYLEPIDIS Singer—Figs. 30–33

Melanotus polylepidis Sing. *in* Beih. Sydowia **7**: 84. 1973.

HABITAT.—On bark of *Polylepis* (Rosaceae). Argentina.

MATERIAL EXAMINED.—ARGENTINA: prov. Jujuy, Lagunas de Yala, 16 Feb. 1966, *R. Singer T 5215* (holotype, F).

HABITAT.—On rotting wood. Argentina.



Figs. 28, 29. *Melanotus eccentricus* (from type). — 28. Carpophores (×3). — 29. Spores.
Figs. 30–33. *Melanotus popylepidis* (from type). — 30. Carpophores. — 31. Spores. — 32. Basidia. — 33. Cheilocystidia.
Figs. 34, 35. *Melanotus patagonicus* (from type). — 34. Carpophores. — 35. Spores.

In this collection the spores, basidia and cheilocystidia are illustrated for the first time. On dried specimens the eccentric tipe is still clearly visible. The morphology of the carpophores and the small thick-walled spores distinguish this *Melanotus* from all others known so far from South America.

10. MELANOTUS PATAGONICUS Singer—Figs. 34–35

Melanotus patagonicus Sing. *in* Beih. Nova Hedw. **29**: 258. 1969.

MATERIAL EXAMINED.—ARGENTINA: prov. Neuquén, Puerto Manzano, 17 March 1963, *R. Singer M 3060* (holotype, BAFC 23963); prov. Neuquén, Puerto Manzano, 18 April 1965, *R. Singer M 5050* (BAFC 23964).

Despite careful preparation it was impossible to recover the cheilocystidia of the type material. Therefore the exact morphology of the cheilocystidia cannot be demonstrated. According to Singer's description there are two types of cystidia on the edge of the lamellae: (a) clavate cells (10–24 × 2.7–4.5 μm) and (b) vesiculose-ventricose cells (18–30 × 9–12 μm).

In the *Nothofagus*-belt of South America three species of *Melanotus* have so far

been observed (*bruchii*, *cassiaecolor* sensu Singer, *patagonicus*). As shown in Fig. 34 the carpophores of *M. patagonicus* are not very *Melanotus*-like since the stipe is predominantly centrically inserted. Among the dried carpophores of the two collections studied not a single one was seen where the stipe is in a lateral position. From the taxonomic point of view this species must be placed directly between *Melanotus* and *Psilocybe*.

11. **Melanotus citrisporus** Horak, *spec. nov.*—Figs. 36–39

Pileo –6 mm lato, semiorbiculari vel conchiformi, pallide brunneo, striato, sicco. Lamellis excentrice concurrentibus, griseobrunneis dein brunneoviolaceis. Stipite –2×–1 mm, cylindrico, laterali, pileo concolori. Sporis 10–13×9–12 μm, limoniformibus, brunneis, poro germinativo instructis, levibus. Cheilocystidiis praesentibus. Sub foliis siccis Asteliae nervosae. Novazelandia. Holotypus PDD 27134.

Pileus –6 mm in diam., dimidiate-hemispherical, conchiform or ear-shaped, cream, beige or pale brown, dry, membranaceous, conspicuously striate-sulcate, glabrous. Lamellae distant, ventricose, broadly attached to lateral stipe, grey-brown turning pale lilac-brown; edge albofimbriate. Stipe –2×–1 mm, cylindrical, rarely rudimentary or absent, lateral to eccentric, concolorous with pileus, dry, glabrous, without veil remnants, solid; rhizoids absent. Odour and taste not distinctive.

Spores 10–13×9–12 μm, limoniform, with distinct truncate germ pore, brown, thin-walled, smooth; apiculus conspicuous. Basidia 25–35×12–15 μm, 4-spored; sterigmata –8 μm long. Cheilocystidia 20–35×5–10 μm, lageniform to fusoid, with broadly rounded or subcapitate neck, hyaline, thin-walled, forming sterile gill edge. Cuticle a cutis of interwoven cylindrical hyphae (5–8 μm in diam.), membranes encrusted with brown (KOH) pigment, not gelatinized. Clamp connections numerous.

HABITAT.—On dry and half-decomposed leaves and culms of *Astelia nervosa* Hook. (Liliaceae). New Zealand.

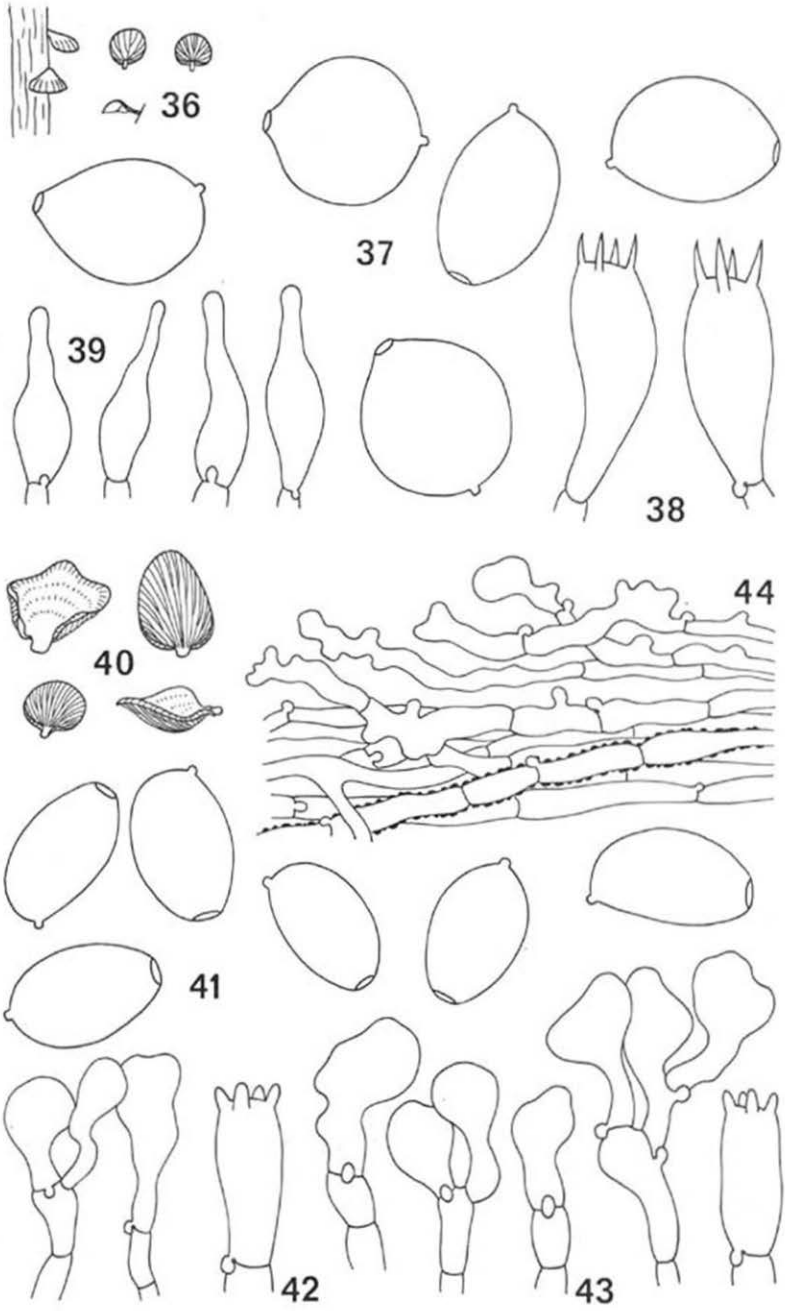
MATERIAL EXAMINED.—NEW ZEALAND: North Island, Mt. Egmont National Park, Stanford Lodge, 12 June 1968, *E. Horak 68/531* (holotype PDD 27134; isotype ZT).

This species represents the first *Melanotus* with limoniform spores which are, moreover, much larger than those of the other known taxa. The ecology of *M. citrisporus* is rather peculiar as well: the carpophores sit on the hanging tips of the long and bent leaves of *Astelia*.

12. **Melanotus protractus** Horak, *spec. nov.*—Fig. 40—44

Pileo –16 mm lato, semiorbiculari vel conchiformi, subsessili, convexo dein irregulariter concavo, ex argillaceo brunneo, sicco. Lamellis lateraliter concurrentibus, argillaceis vel ferrugineis, albofimbriatis. Stipite nullo, margine pilei protracto. Sporis 10.5–12.5×6.5–7.5 μm, ellipsoideis, brunneis, poro germinativo instructis. Cheilocystidiis conspicue capitato-clavatis. Ad folias deiectas Musae. Nova Guinea. Holotypus: ZT, 73/189.

Pileus –16 mm in diam., dimidiate, conchiform or fan-shaped, convex when young, later concave with upturned margin, pale brown to brown, dry, striate,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hygrophanous, thin, minutely fibrillose. Lamellae excentrically or laterally concurrent, densely crowded, ventricose, pale brown turning rust brown; edge albofimbriate. Stipe absent or rudimentary, margin of pileus often directly attached to substratum. Odour and taste not distinctive. Spore print dark brown, without lilac tinge.

Spores 10.5–12.5×6.5–7.5 µm, ellipsoid, brown, thin-walled, smooth; germ pore and apiculus conspicuous. Basidia 20–25×8–11 µm, 4-spored. Cheilocystidia 20–35×8–18 µm, clavate-capitate, occasionally constricted towards base, hyaline, thin-walled, forming sterile gill edge. Cuticle a cutis of subparallel hyphae (4–10 µm in diam.) bearing clavate or irregular-corallioid terminal cells, membranes encrusted with yellow-brown (KOH) pigment, not gelatinized. Clamp connections present.

HABITAT.—On rotting leaves of *Musa* spec. Papua New Guinea.

MATERIAL EXAMINED.—PAPUA NEW GUINEA: Morobe district, Bulolo, Susu, 26 April 1973, *E. Horak 73/189* (holotype, ZT).

This species is well characterized by its large spores and the clavate-capitate cheilocystidia. As far as we know at present *Musa* is inhabited by still another species of Melanotus but this fungus (*M. alpiniae* = '*musaecola*' = '*fumosifolius*') seems to be restricted to localities in Cuba and Jamaica.

13. MELANOTUS HAEMATITES (Berk. & Curt.) Sing.—Fig. 45

Agaricus (*Crepidotus*) *haematites* Berk. & Curt. *in Proc.* Am. Acad. Arts Sci. **4**: 117. 1860 (basionym). — *Melanotus haematites* (Berk. & Curt.) Sing. *in* Lloydia **9**: 130. 1946.

HABITAT.—On dead wood. Hongkong.

MATERIAL EXAMINED.—Hongkong: Hongkong, 1854, U.S. Pacific Exp., 119 (holotype, FH).

Our knowledge of this species is based on the following rather short diagnosis: 'Atro-sanguineus; pileo reniformi postice affixo glabro; lamellis ventricosis latiusculis On dead wood. Hongkong. — Has somewhat the habit of *Panus*.'

According to our observations the ovate-lentiform and thick-walled spores measure 5·5–7×3·5–4·5 µm. The germ pore is distinct. Cheilocystidia and basidia not recovered in the poorly preserved type material. Fresh material is needed to obtain more information about this outstanding black-red coloured species.

14. MELANOTUS RIDLEYI (Massee) Sing.—Fig. 46

Crepidotus ridleyi Massee *in* Kew Bull., Misc. Inf.: 169. 1899 (basionym). — *Melanotus ridleyi* (Massee) Sing. *in* Sydowia **9**: 404. 1955.

Figs. 36–39. *Melanotus citrisporus* (from type). — 36. Carpophores. — 37. Spores. — 38. Basidia. — 39. Cheilocystidia.

Figs. 40–44. *Melanotus protractus* (from type). — 40. Carpophores. — 41. Spores. — 42. Basidia. — 43. Cheilocystidia. — 44. Cuticle.

ILLUSTRATIONS.—Pilát (*1950*: 233).
HABITAT.—On dead fern rhachis. Malaya.
MATERIAL EXAMINED.—MALAYA: Selangor, *Ridley 110* (holotype, K).

According to Massee (*1899*: l.c.) this species is allied to '*Crepidotus turbidulus* Berk.' (= *M. hepatochrous*) from Tasmania. The two taxa, however, are clearly distinguished by the morphology of the carpophores, the size of the spores and their host plants. Up to date only two Melanoti are recorded that grow on ferns: *M. ridleyi* and *M. vorax* (New Zealand).

Comparing the macroscopical and microscopical data observed on the type material of *M. ridleyi* Massee we do not share Pilát's opinion (*1950*: 233) that this species is conspecific with '*M. musaecola* (Berk. & Curt.)' (= *M. alpiniae*). Among other differences the spores of the neotropical '*M. musaecola*' are larger than those of *M. ridleyi*.

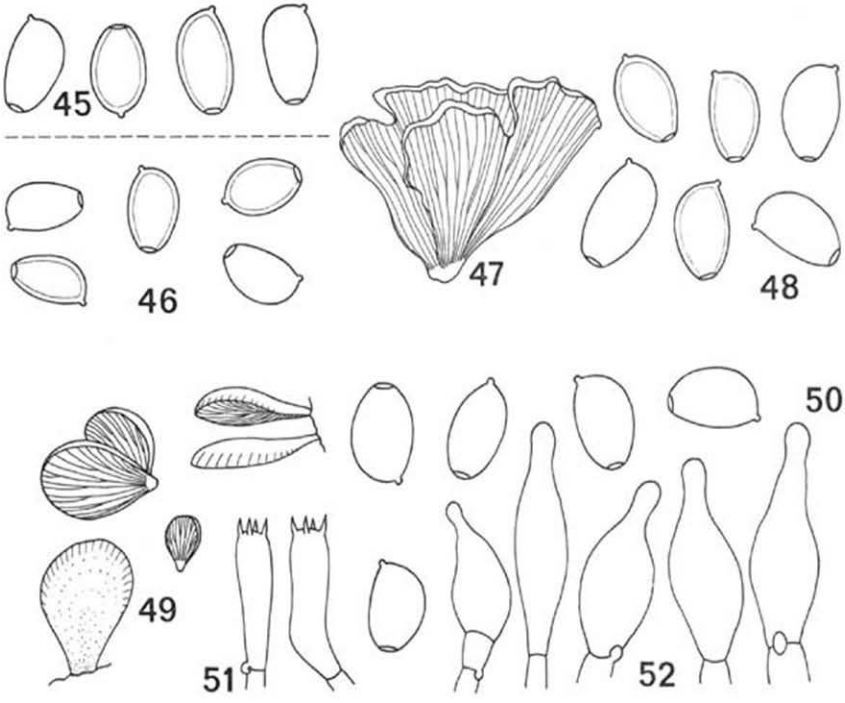


Fig. 45. *Melanotus haematites* (from type), spores.
Fig. 46. *Melanotus ridleyi* (from type), spores.
Fig. 47, 48. *Melanotus phaeophyllus* (from type). — 47. Carpophore. — 48. Spores.
Fig. 49–52. *Melanotus distinctus* (from type). — 49. Carpophores. — 50. Spores. — 51. Basidia — 52. Cheilocystidia.

15. MELANOTUS PHAEOPHYLLUS (Berk. & Br.) Pilát—Figs. 47, 48

Agaricus (Crepidotus) phaeophyllus Berk. & Br. *in* Hook., J. Bot. **6**: 486. 1847 (basionym).—*Melanotus phaeophyllus* (Berk. & Br.) Pilát *in* Trans. Br. mycol. Soc. **33**: 240. 1950.

ILLUSTRATIONS.—Pilát (*1950*: 230).
HABITAT.—On old wood. Ceylon.
MATERIAL EXAMINED.—CEYLON: Hautane Range, June 1844, *No. 36* (holotype, K); Peradeniya, July–Dec., *No. 87* (K).

Among all known species of *Melanotus* this fungus is remarkable due to its large size (—50 mm in diam.) and shape, which suggest *Paxillus panuoides*. The carpophores are broadly attached to the wood as substratum and there is no sign of a stipe even in young specimens.

16. **Melanotus distinctus** Horak, *spec. nov.*—Figs. 49–52

Pileo –20 mm lato, semiorbiculari vel linguiformi, lateraliter substrato affixo, pallide brunneo, sicco. Lamellis lateraliter concurrentibus, brunneis, albofimbriatis. Stipite nullo. Sporis 6–7.5×4–5 μm, ovatis, brunneolis, poro germinativo inconspicuo, levibus. Cheilocystidiis praesentibus.
Ad lignum putridum. Nova Guinea. Holotypus: ZT, 72/655.

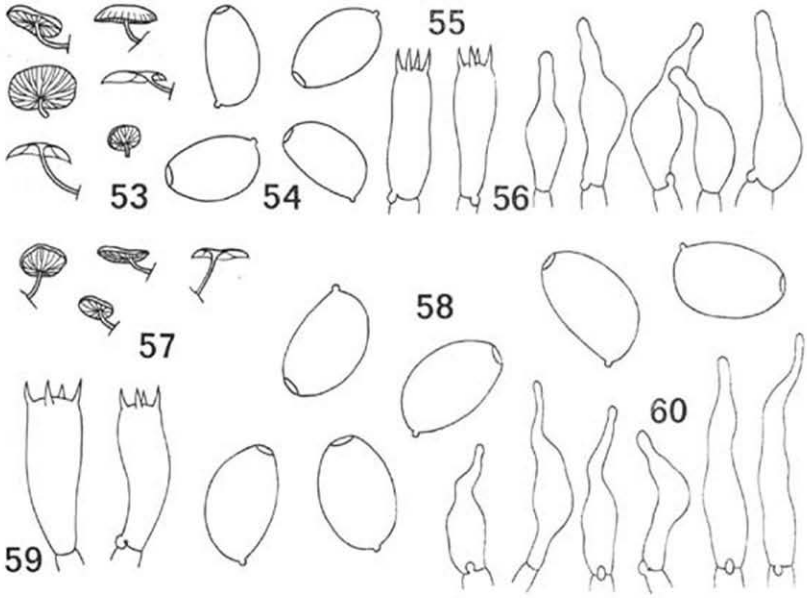
Pileus 6–20 mm in diam., linguiform or conchiform, with margin broadly attached to substrate, pale brown, drying to whitish or pallid, hygrophanous, dry, slightly striate towards margin, glabrous. Lamellae laterally concurrent, ventricose, crowded, brown, without lilac tinge; edge albofimbriate. Stipe absent. Odour and taste not distinctive. Spore print brown, without lilac shade.
Spores 6–7.5×4–5 μm, ovate, pale brown, thin-walled, smooth; germ pore often indistinct. Basidia 18–22×5–6 μm, 4-spored. Cheilocystidia 20–35×8–11 μm, ventricose-fusoid with subcapitate neck, hyaline, thin-walled, forming sterile gill edge. Cuticle a cutis of parallel cylindrical hyphae (3–7 μm in diam.), terminal cells not differentiated, membranes encrusted with brownish (KOH) pigment, not gelatinized. Clamp connections absent from all septa.

HABITAT.—On rotting wood in rain forest. Papua New Guinea.
MATERIAL EXAMINED.—Papua New Guinea: Morobe district, Bulolo, Watut, 21 Nov. 1972, *E. Horak* (holotype, ZT, 72/655).

The most distinguishing characters of this species are the spathulate estipitate carpophores, the thin-walled spores (like *M. bruchii*) and the fusoid-capitate cheilocystidia.

17. **Melanotus vorax** Horak, *spec. nov.*—Figs. 53–60

Pileo –12 mm lato, e convexo applanato, argillaceo vel pallide brunneo, subviscido, striato. Lamellis adnatis ex argillaceo brunneis, albofimbriatis. Stipite –10×–1 mm, cylindrico, excentrico vel sublaterali, pileo concolori. Sporis 6.5–8.5×4–5.5 μm, ovatis, luteibrunneis, levibus, poro germinativo instructis. Cheilocystidiis fusoideis. Ad frustulos plantarum. Novazelandia. Holotypes: PDD 27135.



Figs. 53–60. *Melanotus vorax*. — 53–56. From type of *M. vorax*. — 53. Carpophores. — 54. Spores. — 55. Basidia. — 56. Cheilocystidia. — 57–60. From *Horak 67/126*. — 57. Carpophores. — 58. Spores. — 59. Basidia. — 60. Cheilocystidia.

Pileus –12 mm in diam., hemispherical or convex when young, becoming expanded, centre depressed in old carpophores, cream, argillaceous or pale brown, chocolate brown when moist, dry to subviscid, striate towards margin, membranaceous, glabrous, slightly hygrophanous. Lamellae adnate, occasionally subdecurrent, crowded, whitish or argillaceous turning to pale brown or deep brown, often with pale red-brown tinge, edge albofimbriate. Stipe –10×–1 mm, cylindrical, eccentric or sublaterally inserted, curved, concolorous with pileus or dark brown, apex pruinose, glabrous towards base, solid, dry, often attached to substratum with white mycelium, single in groups. Odour and taste not distinctive. Spore print brown.

Spores 6.5–8.5(–9)×4–5.5(–6) µm, ovate, yellow-brown, smooth, thin-walled, germ pore and apiculus distinct. Basidia 18–22×6–8 µm, 4-spored. Cheilocystidia 15–30×5–10 µm, fusoid with tapering neck, apex rounded, hyaline, thin-walled, forming sterile edge. Cuticle a cutis of interwoven cylindrical hyphae (3–8 µm in diam.), membranes slightly gelatinized, encrusted with brown (KOH) pigment. Clamp connections present.

HABITAT.—On decomposing leaves of *Cortaderia*, *Phormium*, and ferns (*Dicksonia*, *Cyathea*). New Zealand.

MATERIAL EXAMINED.—NEW ZEALAND: South Island, Canterbury, Mt Grey, Kowai River, 30 Dec. 1968, *E. Horak 68/688* (holotype, PDD 27135; isotype, ZT); Mt Grey, Kowai Bush, 22 Sept. 1967, *E. Horak 67/126* (ZT); Mt Grey, Kowai

Bush, 30 Dec. 1968, *E. Horak 68/689* (ZT). — Nelson: Puponga, 18 May 1968, *E. Horak 68/477* (ZT). — North Island: Gisborne, Urewera National Park, Lake Waikareiti, 30 June 1968, *E. Horak 68/623* (ZT); Taranaki, Mt Egmont National Park, Rahiri Lodge, 17 June 1968, *E. Horak 68/563* (ZT).

The description of *M. vorax* is based on 8 collections made at different sites in New Zealand. According to our field observations this fungus is widely distributed on decomposing leaves and stems of grasses, New Zealand flax and ferns. We must emphasize that the spores of carpophores growing on *Phormium tenax* are often larger than those observed on carpophores from other host plants.

18. MELANOTUS HEPATOCHROUS (Berk.) Sing.—Figs. 61–76

Agaricus (*Crepidotus*) *hepatochrous* Berk. *in* Hook., J. Bot. **7**: 574. 1848 (basionym). — *Melanotus hepatochrous* (Berk.) Sing. *in* Sydowia **5**: 472. 1951 (as '*M. haematochrous*' Sing. *in* Sydowia **6**: 348. 1952).

Agaricus (*Crepidotus*) *insidiosus* Berk. *in* Hook., J. Bot. **7**: 574. 1848. — *Melanotus insidiosus* (Berk.) Pegler *in* Austr. J. Bot. **13**: 336. 1964.

Agaricus (*Crepidotus*) *cassiaecolor* Berk. *in* Hook., Fl. Tasm. **2**: 246. 1860. — *Melanotus cassiaecolor* (Berk.) Sing. *in* Sydowia **15**: 70. 1950.

Agaricus (*Crepidotus*) *turbidulus* Berk. apud Saccardo, Syll. Fung. **5**: 889. 1887; **9**: 1891.

Crepidotus subhaustellaris Cleland, Toadstools Mushrooms ... South Australia: 131. 1934.

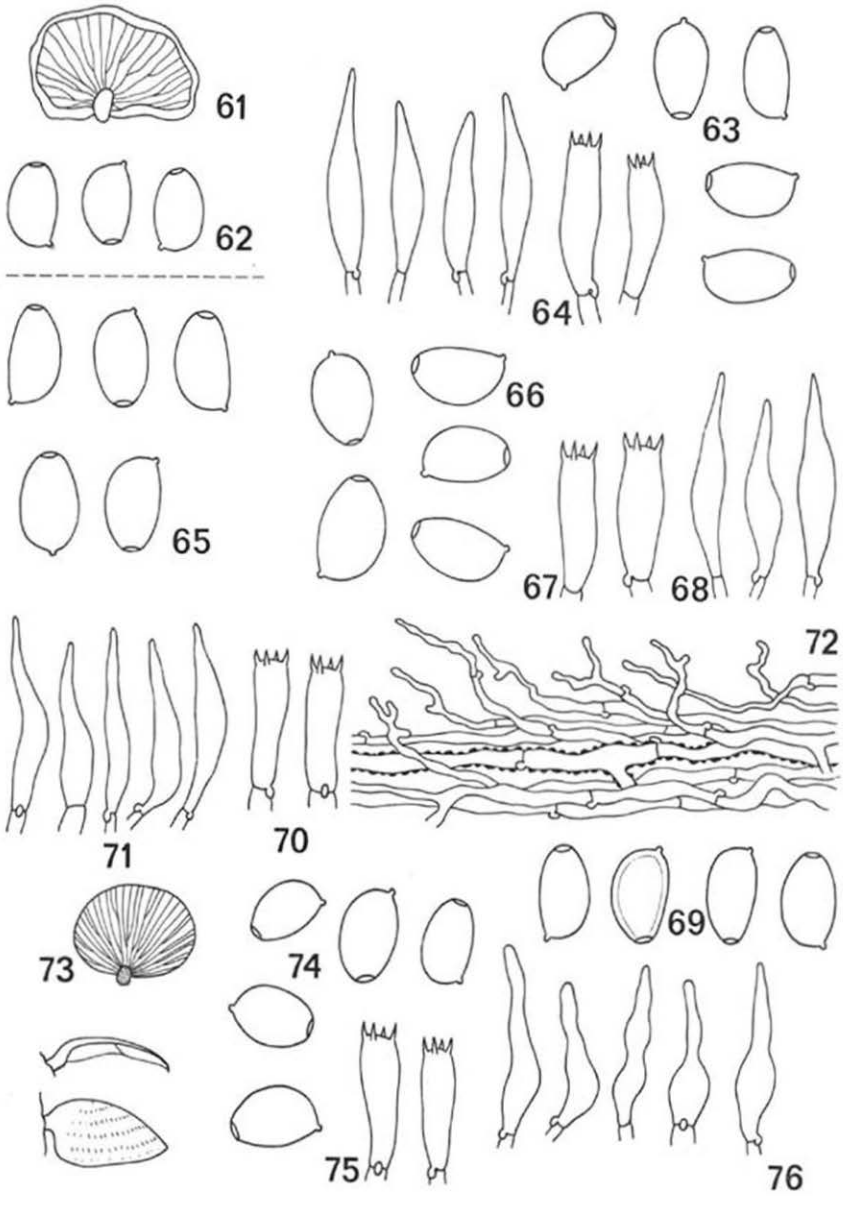
Pileus –30 mm in diam., orbicular, semiorbicular or reniform, also flabelliform, convex to plane, dark brown, reddish brown or brown when moist, fading to pale brown or cinnamon brown, dry, estriate, glabrous or minutely felty. Lamellae concurrent at stipe, broadly adnate, crowded, argillaceous becoming cinnamon brown or dark brown, often with ferrugineous tint; edge albofimbriate. Stipe –4× –2.5 mm, eccentric to lateral, sometimes directly attached to substratum, cylindrical, curved, whitish or concolorous with pileus, dry, glabrous, solid; veil remnants absent. Odour and taste acidulous. Spore print brown to lilac-brown.

Spores 5.5–7.5×3.5–5 μm, ovate to sublentiform, yellowish to pale brown, smooth, thin-walled; germ pore distinct. Basidia 15–22×5–6 μm, 4-spored. Cheilocystidia 20–30×3–6 μm, lanceolate to fusoid with elongate neck, thin-walled, hyaline, forming sterile edge. Pleurocystidia absent. Cuticle a cutis of interwoven cylindrical hyphae (2–8 μm in diam.), terminal cells often branched or forked (like *Marasmiellus*), membranes not gelatinized, encrusted with brownish (KOH) pigment. Clamp connections present.

ILLUSTRATIONS.—Pilát (*1950*: 223, *hepatochrous*; *1950*: 225, *insidiosus*; *1950*: 218, *cassiaecolor*; *1950*: 236, *turbidulus*).

HABITAT.—On rotting bark, wood or leaves (known host plants: *Eucalyptus*, *Xanthorrhoea*, *Podocarpus*). Tasmania (type), South Australia, New Zealand.

MATERIAL EXAMINED.—TASMANIA: Tasmania, *Gunn 756* (holotype of *Agaricus hepatochrous* Berk., K); Penguite, May 1845 (holotype of *Agaricus insidiosus* Berk., K); Tasmania, *Archer* (holotype of *Agaricus cassiaecolor* Berk., K); holotype of *Agaricus turbidulus* Berk. (K). SOUTH AUSTRALIA: Mt Lofty, 20 May 1920, *Cleland* (holotype of *Crepidotus subhaustellaris* Clel., WAITE 12622). NEW ZEALAND: South Island, Westcoast, Ahaura, 14 March 1968, *E. Horak 68/159* (ZT).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The preceding redescription of *M. hepatochrous* is based on its type specimen, on the type specimens and descriptions of the above mentioned synonyms, and on fresh material collected in New Zealand.

Comparison of the original descriptions, the hitherto unpublished drawings and the microscopical data extracted from the type specimens of *M. hepatochrous*, *M. insidiosus*, *M. cassiaecolor*, and *M. turbidulus* (all described from Tasmania) leaves little doubt but that these taxa are conspecific. In addition the microscopical characters of *Crepidotus subhaustellaris* Clel. agree in many respects with those of *M. hepatochrous* so that this fungus is also relegated to the synonyms of the Tasmanian *Melanotus*. The most distinctive characters of *M. hepatochrous* are the thin-walled spores, the lanceolate or fusoid-conical cheilocystidia, the branched tips of the cuticular hyphae, the dark brown or reddish brown pileus and the cinnamon brown lamellae, which do not show an obvious purple tint.

19. MELANOTUS FLAVO-LIVENS (Berk. & Curt.) Sing.—Fig. 77

Agaricus flavo-livens Berk. & Curt. *in* Proc. Am. Acad. Arts Sci. **4**: 117. 1860 (basionym). — *Crepidotus flavo-livens* (Berk. & Curt.) Sacc., Syll. Fung. **5**: 887. 1887. — *Melanotus flavo-livens* Curt.) Sing. *in* Lloydia **9**: 130. 1946.

Pileus –12 mm in diam., orbicular to reniform, convex or plane, pale ochraceous, fawn or pale argillaceous, estriate, cottony or minutely felty, dry. Lamellae concurrent at stipe, broadly adnate, crowded, ventricose, greyish to pale argillaceous or pale ochraceous without distinct purplish tint (fresh carpophores), edge albofimbriate. Stipe 2–5(–10) × 1–1.5 mm, eccentric, sublateral or rudimentary, cylindrical, curved, white or concolorous with pileus, dry, glabrous, without veil remnants, solid, single in groups. Odour and taste not distinctive.

Spores (5–)6–7 × 4–4.5 µm, ovate to sublentiform, smooth, thick-walled, germ pore present. Basidia 15–20 × 5–7 µm, 4-spored. Cheilocystidia 15–25 × 3–5 µm, subfusoid to cylindrical, hyaline, thin-walled, not pigmented, forming sterile gill edge. Pleurocystidia none. Cuticle a cutis of interwoven to subregular cylindrical repent hyphae (4–10 µm in diam.), membranes not gelatinized, encrusted with brown (KOH) pigment. Clamp connections present.

ILLUSTRATIONS.—Pilát (*1950*: 221).

HABITAT.—On dead wood (type) or decomposing plant detritus (*Heliconia*, *Cocos*). Bonin Islands, New Caledonia, Solomon Islands.

MATERIAL EXAMINED.—BONIN ISLANDS: Bonin Islands (holotype, K). NEW CALEDONIA: Yaté, 25 Feb. 1977, *E. Horak 77/168* (ZT); Yaté, 25 Feb. 1977, *E. Horak 77/168* (ZT). SOLOMON ISLANDS: Kolombangara, 27 Aug. 1965, *E. J. H. Corner* (RRS 1113, ZT).

Figs. 61–76. *Melanotus hepatochrous*. — 61, 62. From type of *M. hepatochrous*. — 61. Carpophore. — 62. Spores. — 63, 64. From type of *Agaricus insidiosus*. — 63. Spores. — 64. Basidia and cheilocystidia. — 65. Spores (from type of *Agaricus cassiaecolor*). — 66–68. From type of *Agaricus turbidulus*. — 66. Spores. — 67. Basidia. — 68. Cheilocystidia. — 69–72. From type of *Crepidotus subhaustellaris*. — 69. Spores. — 70. Basidia. — 71. Cheilocystidia. — 72. Cuticle. — 73–76. From *Horak 68/159*. — 73. Carpophores. — 74. Spores. — 75. Basidia. — 76. Cheilocystidia.

The original description of *Agaricus flavo-livens* reads as follows: 'Pileo flabelliformi flavido pulverulento; stipite nullo; lamellis angustis purpureoalbis. On dead wood. Bonin Islands.'

In the preceding description this poor diagnosis is complemented with observations on fresh collections made in New Caledonia and the Solomon Islands.

Examining the type material of *Agaricus flavo-livens* Berk. & Curt. we cannot agree with the opinion of Hesler & Smith (*1965*: 147) that this fungus should be considered a later synonym of *M. musaecola* (= *M. alpiniae*). *Melanotus flavo-livens* is a sound and independent species from the islands in the West Pacific.

20. **Melanotus communis** Horak, *spec. nov.*—Figs. 78–81

Pileo –30 mm lato, rotundato-reniformi vel conchiformi, centro convexo, albidulo vel pallide brunneo, sicco. Lamellis adnexis, ex argillaceo brunneis, lilacino tinctis, albofimbriatis. Stipite –5 × –1.5 mm, cylindrico, excentrico sublateralive, pileo concolori. Sporis 5–7 × 3.5–4.5 µm, ovatis, brunneis, levibus, poro germinativo instructis. Cheilocystidiis clavatis vel fusoideo-mucronatis. Ad ramos putridos in silvis. Nova Guinea. Holotypus: ZT, 71/465.

Pileus –30 mm in diam., reniform or conchiform, with centre convex or umbonate and margin not upturned, varying from whitish to brownish, dry, estriate, not hygrophanous, smooth when young, often radially cracked in old carpophores.

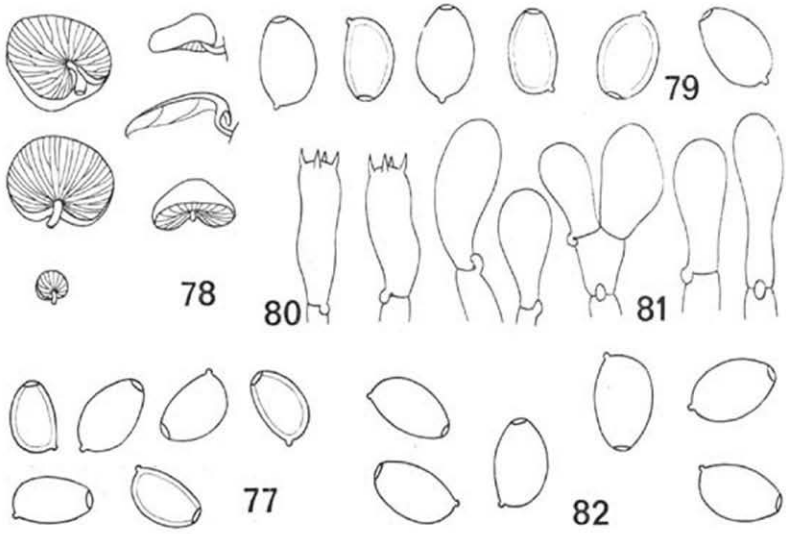

Fig. 77. *Melanotus flavo-livens* (from type), spores.

Figs. 78–81. *Melanotus communis* (from type). — 78. Carpophores. — 79. Spores. — 80. Basidia. — 81. Cheilocystidia.

Fig. 82. *Melanotus bambusinus* (from type), spores.

Lamellae adnexed, densely crowded, ventricose, eccentrically concurrent, argillaceous turning grey-brown or deep brown, often with distinct lilac tints; edge albofimbriate. Stipe –5 × –1.5 mm, cylindrical, curved, eccentric to sublaterally inserted, concolorous with pileus or pallid, pruinose at apex, dry, solid, single in groups. Odour and taste not distinctive. Spore print dark brown, with lilac hue.

Spores 5–7 × 3.5–4.5 µm, ovate, brown, smooth, thin or thick-walled; germ pore and apiculus distinct. Basidia 15–22 × 5–7 µm, 4-spored. Cheilocystidia 15–25 × 5–10 µm, clavate, fusoid-subcapitate or clavate-mucronate, hyaline, thin-walled, forming sterile gill edge. Cuticle a cutis of interwoven cylindrical hyphae (2—8 µm in diam.), membranes not gelatinized, encrusted with brown (KOH) pigment. Clamp connections present.

HABITAT.—On rotting branches in forests. Papua New Guinea.

MATERIAL EXAMINED.—PAPUA NEW GUINEA: Eastern Highlands, Mt Michael, Frigano, Hut Track, 31 Dec. 1971, *E. Horak 71/465* (holotype, ZT); Mt Michael, Frigano, Hut Track, 8 Dec. 1971, *E. Horak 71/397* (ZT); Northern district, Popondetta, Mt Lamington, Kandata, 13 April 1972, *E. Horak 72/380* (ZT); Goroka, Daulo Pass, 12 Jan. 1972. E. *Horak 72/69* (ZT).

This species is very common in the rain forests of Papua New Guinea. It is characterized by thin-walled spores, clavate or fusoid-subcapitate (and often also mucronate) cheilocystidia and rather large whitish to pale brownish carpophores. In fresh material the lamellae show a distinct purple tinge.

21. MELANOTUS BAMBUSINUS (Pat.) Pat.—Fig. 82

Crepidotus ? bambusinus Pat. *in* J. Bot., Paris **5**(18): 309. 1891 (basionym). — *Melanotus bambusinus* (Pat.) Pat., Essai Tax.: 175. 1900.

ILLUSTRATIONS.—Pilát (*1950*: 218).

HABITAT.—On rotting twigs of *Bambusa*. Vietnam.

MATERIAL EXAMINED.—VIETNAM: Tonking, Ke So, 28 July 1890, *Bon 4462* (holotype, PC); Ke So, 24 March 1914 (PC).

Melanotus bambusinus is the type species of *Melanotus*. Unfortunately the type collection and the second collection mentioned above are in fragmentary condition. Only the morphology of the spores is sufficiently well known.

SPECIES INCERTAE SEDIS

CREPIDOTUS TJIBODENSIS. P. Henn *in* Monsunia **1**: 17. 1900

Original diagnosis: 'Pileo submembranaceo-carnosulo, conchiformi vel flabellato, sessili, basi protracto, albo, levi, glabro, 5–15 mm lato longoque, margine tenui; lamellis ad basim radiantibus, inaequilongis, subconfertis, latis ad marginem crispulis, albo-violaceis dein brunnescentibus; sporis olivaceo-brunneis, late ellipsoideis, laevibus, 6–8 × 4–5 µm. Java, Tjibodas: an Zweigen, Juli 1890 (M. Fleischer).'

No type material was traced in the Hennings herbarium in Berlin (B) but according to the good description it is very likely that this species belongs to *Melanotus*.

List of host plants of Melanotus species

Pteridophyta, Filicales:
- Cyatheaceae: *Dicksonia, Cyathea.—M. ridleyi, M. vorax*

Spermatophyta, Gymnospermae:
- Podocarpaceae: *Podocarpus.—M. hepatochrous*
- Cupressaceae: *Cupressus.—M. proteus*

Spermatophyta, Angiospermae:

Monocotyledoneae:
- Gramineae: *Cortaderia.—M. vorax*; *Bambusa.—M. bambusinus*; *Chusquea.—M. bruchii*; *Agrostis.—M. phillipsii*
- Cyperaceae: *Carex.—M. phillipsii*
- Agavaceae: *Phormium.—M. vorax*
- Palmae: *Cocos.—M. subcuneiformis, M. flavo-livens*
- Musaceae: *Musa.—M. protractus, M. alpinia* (*M. musaecola, M. fumosifolius*); *Heliconia.—M. flavo-livens*
- Zingiberaceae: *Alpinia.—M. alpiniae*
- Liliaceae: *Astelia.—M. citrisporus*; *Xanthorrhoea.—M. hepatochrous* (*M. subhaustellaris*)
- Other 'grasses'.—Further host plants: *M. phillipsii, M. eccentricus, M. vorax, M. flavo-livens*; *Zea, Juncus* (see Singer, *1975*: 544)

Dicotyledoneae:
- Myrtaceae: *Eucalyptus.—M. hepatochrous* (*M. subhaustellaris*)
- Rosaceae: *Polylepis.—M. polylepidis*
- Rubiaceae: *Psychotria.—M. alpiniae* (*M. psychotriae*)
- Scrophpulariaceae: *Scrophularia.—M. phillipsii*

On logs, branches, twigs, bark, or leaves of deciduous trees.—*M. alpinia* (*M. fumosifolius, M. subvariabilis*), *M. bruchii, M. communis, M. distinctus, M. flavo-livens, M. gelineus, M. haematites, M. hepatochrous* (*M. cassiaecolor, M. insidiosus, M. turbidulus*), *M. patagonicus, M. phaeophyllus, M. proteus.*

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THE HISTOGENESIS OF BULB AND TRAMA TISSUE OF THE HIGHER BASIDIOMYCETES AND ITS PHYLOGENETIC IMPLICATIONS

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(With two Text-figures, one Table, and Plates 32–37)

At the base of the stipe in Agaricales basal plectenchyma is found which may enlarge to form a bulb. This tissue is not homogeneous. It is characterized by peculiar configurations: free tips of branches, sinuous hyphae, loops, spirals and rings (sometimes enclosing another hypha) and hyphal knots. The hyphal knots present themselves as bundles of hyphae, which may or may not be the centre of cell division, or as agglomerations of cells surrounded by coiled hyphae. The latter structure, present in many species of Agaricales, is found in its perfect form in the trama of the Amanitaceae, which recalls the trama of the Russulaceae. The young pileus trama of many species shows the same characteristics; these also occur in the trunk of *Ramaria*, in young bulbs of Gasteromycetes, and in various veils. The diverse kinds of cell formation in the primordia of Agaricales are treated at some length, the conception meristemoid is defined, and a comparison with the development of some of the true Aphyllophorales is made. The heteromerous trama of the Asterosporales and the trama of the Amanitaceae, characterized by acrophysalides, are considered to be derived from the young trama of other Agaricales. The tissue of the bulbs of the strains 59b and 59c of *Agaricus bisporus* is analyzed. Strain 59b is homologous with the bulb tissue of a normal fruitbody of *Agaricus bisporus*. In agreement with G. Fritsche the conclusion is drawn that 59c is a gigas-form. Watling's carpophoroids of *Psilocybe merdaria* are considered.

The fundamental differences between the development of true Aphyllophorales and that of cantharelloid fungi, Agaricales, and Gasteromycetes are emphasized. As for the evolution within the Asterosporales, it is concluded that the degradation of certain characters in the gasteromycetoid forms (Heim, Malençon) need not contradict the arguments advanced by R. Singer and A. H. Smith.

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INTRODUCTION

This study was undertaken as the result of two previous studies; the first on ontogenetic investigation of the bulbs of the strains '59b' and '59c' of *Agaricus bisporus*, 'the cultivated mushroom', obtained by Fritsche & von Sengbusch (*1963*) as spontaneous mutations in single spore cultures; the second on an investigation into the origin of the atypical trama in *Lactarius* and *Russula* (Reijnders, *1976*).

The first investigation showed that bulbs of the strains 59b and 59c have a characteristic structure. It follows that the next step was to compare these with the tissue of normal bulbs of *Agaricus bisporus* (Lange) Imbach. The investigation was subsequently extended to bulbs of other Agaricaceae, both in the primordial and the more mature states. Some of these structures, in particular the hyphal knots, also occur in the remaining trama of the fruitbody so that it was necessary to observe these in a wide variety of species. The comparison was facilitated by the fact that it was possible to examine a large number of microtome sections from previous work (e.g. Reijnders, *1963*). At the same time it also seemed advisable to investigate fresh and living material, especially that of bulbs so that the study was extended to include all the Agaricales; it was not possible to exclude the bulbs of a few Gasteromycetes or the trunk of some Clavariaceae. It will become apparent that in all these examples structures are formed showing marked similarity. In the younger stages of the real Aphyllophorales (Corticiaceae, Stereaceae, Steccherinaceae, and Polyporoideae) these structures do not occur. The development from the point of initiation has not been adequately investigated in the Aphyllophorales but it appears to be entirely stereotypic (see below).

By basal plectenchyma a tissue is indicated that differentiates from the protenchyma as soon as the primordium has been formed. The term protenchyma is used for the generative tissue which makes up all the parts of the carpophore. In the Aphyllophorales (Corner, *1950*) generative hyphae are spoken of. Although this term is also applicable to the Agaricales and the Gasteromycetes, it seems proper to continue to use the terms protenchymatic and protenchyma because here in many cases the generative hyphae form complexes which serve to form certain structures that function as a unit. The basal plectenchyma soon differentiates from the primary protenchyma at the base of the primordium, becoming distinguishable by its special structure. Inflation of the cells takes place forthwith. The basal plectenchyma is probably universal in the Agaricales, though its extent can vary widely. The exten-

sion of the basal plectenchyma is limited in families like the Pleurotaceae, Hygrophoraceae, and Tricholomataceae (approximately in the circumscription of Kühner & Romagnesi, *1953*), that is in such species as show a dominant stipitocarpous type of development.

Previously we discussed the fact that the bulb at the base of the stipe in many species is homologous to the basal plectenchyma (Reijnders, *1974*). This is not quite true, however, because for example in such species as are pileocarpous or hymenocarpous from the beginning a certain amount of undifferentiated protenchyma remains in the bulb so that species with a strongly developed bulb have a large basal plectenchyma completely enveloping the remaining primary protenchyma. In later stages this remaining plectenchyma can for example be found in the volva (namely in those species which are termed bulbangiocarpous, e. g. *Volvariella*). Some remaining basal plectenchyma can also be found in the centre of the cap trama, that is when the stipe is initiated inside the bulb. In that case the upper stipe, characterized by parallel longitudinal hyphae, may have a zone of primary protenchyma which forms a part of the cap trama. Subsequently in many species the cap trama will increase in volume through the formation of cells in a proximal direction by the hyphal bundles of the cap margin. It is thus necessary that both the structure of the cap trama and that of the base of the stipe be studied. Before describing the results considerations should be given to the manner in which the cell formation of the primordium takes place.

In many cases basal plectenchyma is also found in what Corner (*1950*) assembled as clavarioid fungi. In many places in his extensive monograph he depicted the basal plectenchyma (see for example figs. 40, 43, 51, 170, 173, 222, etc.). It is interesting to verify to what degree the sclerotium, as in *Typhula*, can be considered homologous to the basal plectenchyma; this could not be ascertained from the description given by Berthier (*1973*: 45). For this a drawing by Corner (*1950*: fig. 51, *Typhula sclerotioides*) is of importance.

THE INITIATION OF CELLS IN THE PRIMORDIUM.—The initiation of the primordium normally consists of a ball of interwoven hyphae. The first differentiation usually gives rise to the basal plectenchyma and also to the velum (if present). When a bundle of parallel hyphae forms quickly at the upper part of the ball and lengthens the species is referred to as stipitocarpous. Corner (*1950*) gives many fine drawings of such bundles in his monograph (e. g. figs. 7, 34, 39, 40, 42, 43, 65, 74, 170, 173, 200).

When cell formation in the bundle is followed immediately by cell inflation, that is if the zone of inflation is situated at the proximal end of the bundle, Corner (*1929*: 282) terms this 'direct development'. When there is some alteration in the time factor in the 'growing point' he terms the development 'indirect'. It is not quite true that there is merely an alteration in the time factor because, as will be shown below, inflation also occurs in tissues not formed by such a 'growing point'. In our opinion it is not correct to state in this connection that the direct method always

takes place in 'clavarioid' fungi, the tissue in the trunk of *Ramaria* comparing more closely to a basal plectenchyma.

In the Agaricales the cells are formed by the cooperation of the protenchyma, which remains plectenchymatic, and the bundles. For this reason we do not agree with Corner that the development of the Agaricales and the Gasteromycetes should be regarded as the sum of alterations in individual hyphae. We referred to this earlier (Reijnders, *1963*: 277). In this the development of the Gasteromycetes and Agaricales differs from true Aphyllophorales.

An apical sheaf like that above is found in the Agaricales: *Cantharellula umbonata*, *Clitocybe clavipes*, etc. When the balls of primordial hyphae have become serried a longitudinal orientation arising in the centre or a little way beneath the apex is often visible. In that case a remnant of the original plectenchyma remains in the upper part of the primordium, where typical plectenchymal structures (hyphal knots) can be recognized; these will form the centre of the cap trama. In more concentrated forms (Reijnders, *1963*: 221 onwards) hyphae may also be longitudinal from the beginning but at the upper end of the hyphae, that is just beneath the veil, a zone of cell division may be found which deposits cells mostly downwards (*Coprinus*). In principle we speak of a pileo-stipitocarpous development in both cases but we fear that, especially in the first case of a remnant of an original protenchyma, we have often called such a primordium stipitocarpous (especially because of the long shaft). It is difficult to draw distinctions but there are many clear cases in which a large part of the cap trama is made up of originally plectenchymatic protenchyma (e. g. *Marasmius rameali*s).

There are two ways in which cells are initiated in the primordium: ramification of the hyphae and cell division. Ramification takes place in bundles of parallel hyphae as well as in plectenchyma. The bundled hyphae in the cap margin form hyphae inwards that join the hymenophore, and hyphae outwards that strengthen the cap trama or the veil. The first palisade hyphae of the hymenophore often originate in the plectenchyma of the cap trama and grow downwards (Reijnders, *1948*: pl. 7 fig. 28, *Leucocoprinus*). Many hyphae also originate by ramification at the surface of the primordium to strengthen the veil (Reijnders, l.c.: pl. 22 figs. 130–133, *Strobilomyces*).

In addition to this striking phenomenon of cell increase by ramification and individual septation of hyphae so formed there exist many places with coordinated cell division, as though these were meristems. The term meristemoids is proposed for these tissues.[1] Both the apical hyphal bundles in clavarioid fungi and the bundles in the cap margin of the Agaricales are therefore meristemoids in which the cell division (and growth) is coordinated. A zone in the upper part of the stipe in which rapid cell division takes place falls equally into this category (Pls. 36A, B, *Coprinus*

[1] Some authors refer to pseudo-tissues in fungi because these originate from hyphae. Pseudomeristems or parameristems could also be used but meristemoid has not been applied to fungi in the past and indicates clearly what is meant.

macrorhizus (Pers. ex Fr.) Rea). At the same time, however, in other parts of the primordium are to be found layers of cells which are so close to one another and where cell increase is so rapid, that it is also possible to speak of meristemoids. Such a zone often occurs at the periphery of the cap trama; this layer then forms the veil, or a marked part thereof, and concurrently or subsequently the pileipellis (Pl. 35C, *Psathyrella candolleana* (Fr.) Maire; Pl. 35D, *Coprinus macrocephalus* Berk.; Pl. 35B, *Cortinarius limonius* (Fr. ex Fr.) Fr.). In the lower part of the cap trama or just above the hymenophore or belonging to this area there is normally a layer of radial, parallel hyphae growing partly downwards and then strongly ramifying. Just above this layer a dense tissue with marked cell formation is present. In the trama of the lamellae ramification in divergent hyphae (in most cases the structure of the young lamellae is divergent) is dominant, but the subhymenium can again be a layer with a cellular structure in which divisions take place to form those elements of the hymenium which push themselves between the previously formed palisade tissue (intercalary growth). In that case because of the richly coordinated cell divisions occuring in that layer it would also be correct to speak of a meristemoid.

The basal plectenchyma and the bulb tissue are not homogeneous; this also applies to other plectenchymatic tissue in primordia and tissue in mature fruitbodies. In microtome sections of those parts where the tissue is compact there are not infrequently visible sectioned groups of round elements (that at first might be regarded as cells but that could also be hyphae), surrounded by curved, coiled or spiral hyphae. In between these a framework of less numerous hyphae which pass straight through are sometimes discernible. In looser parts (compact tissue also becomes looser in later stages) we often find places where the hyphae adhere to one another in entangled bundles; other places show many short side branches or else the hyphae are divided into many short cells (or hyphal knots); also interposed places where the tissue is looser and the hyphae are more separate are present. Particular attention will be paid to these hyphal knots in the description of the histological structure of the above mentioned material. In addition many free hyphal ends and typical structures like loops and rings are also encountered.

To conclude this introduction another phenomenon should be mentioned. In previous work (Reijnders, *1963*: 269, 276) we noted the structural consistency of the primordia and the proportional growth of all the parts in relation to one another and referred to cell inflation. This does not initiate everywhere at the same time but in very young primordia proceeds in such a manner that the globular shape may be preserved and all the parts remain in their same positions. Later the so-called period of rapid elongation takes place.

The formation of new cells has the same consistency as the cell inflation. Just enough cells are formed by hyphal branching and by cell division in meristemoid tissue to give rise to a well proportioned fruitbody.

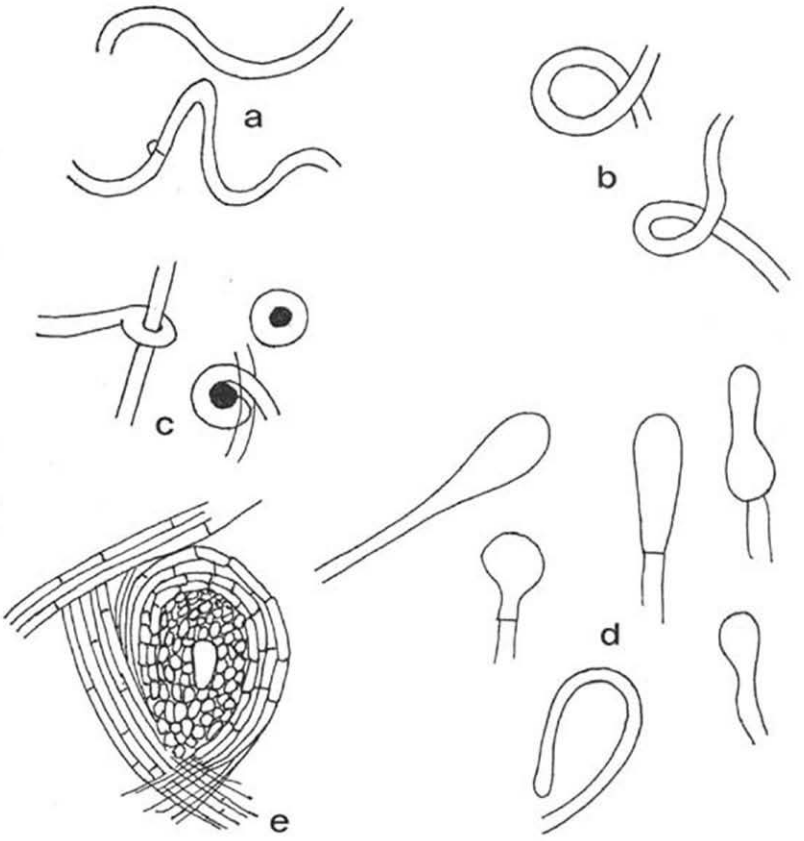


Fig. 1. Hyphal configurations in plectenchymatic tissues in Agaricales. — a. Sinuous hyphae. — b. Loops. — c. Spiral hypha enclosing an other hypha, and rings. — d. Free ends of branches, with or without inflated terminal cells. — e. Coiled hyphae, surrounding a group of isodiametric cells, with the inflated tip in the centre.

OBSERVATIONS

THE ELEMENTS.—Authors disagree about the use of the term plectenchyma. Some apply this term to all tissues or pseudo-tissues which are formed by hyphae. The one speaks of prosoplectenchyma when the tissue clearly consists of interwoven hyphae, and of paraplectenchyma or pseudo-parenchyma when the tissue appears to consist of cells. Other authors restrict the term plectenchyma to the first case, where the tissue clearly consists of interwoven hyphae, and use pseudoparenchyma

for the second type, in which the tissue appears to consist of cells; it is to this interpretation that we will confirm. (Yet others reserve the term plectenchyma for a more specialized structure, viz. when the elements adhere to one another through an intercalary substance and are difficult to separate; but this application of the term is very rare.)

We ourselves apply the term plectenchyma to any fungal tissue in which the characteristics of hyphae are recognizable. Such plectenchyma is seldom homogeneous in either mature fruitbodies or in primordia. In places the tissue is denser and looser. We termed the places where the hyphae adhere in bundles hyphal knots. Occasionally only hyphal bundles can be seen in such places but in many cases the hyphae appear to be divided into short cells. This phenomenon will be dealt with below (see chapter on hyphal knots and meristemoids). At first it must be considered whether it is in fact a question of a deceptive structure. All our observations had to be made with only two dimensional sections so that what appears to be a cell may in fact be a hyphal cross section. As a result in dense tissue many 'cells' may appear to be adjacent to one another. These circles are usually empty, making them more easily recognizable. Where the hyphae cross the section obliquely the hyphal walls may be visible as short ellipses. There is another optical illusion when hyphal bundles cross one another in the section and once more apparent 'cells' are seen. The section is often thick enough (10 μm on the average) to make this possible. We have often wondered to what extent such optical illusions are responsible for the conclusion that they are short cells. There are places in the hyphal knots, however, where so many adjacent cells are visible that optical illusion could not be the explanation. The hyphae following the direction of the section for some distance (i. e. are recognizable as hyphae) should be closely examined to find out whether they have many septa. Rows of cells are indeed often to be seen in these hyphae. Furthermore counting these longer length of hyphae around the knots makes it possible to calculate the number of sections one can expect to see. Also often perceptible are bunches of grape-like figures: one or more longer hyphae surrounded by rows of cells, or hyphae of a bundle locally divided into cells but it should not be assumed that another bundle passes through the first one. Comparison of the tissue of the primordia of *Russula* and *Lactarius* with that of other Agaricales may reveal the same structure of hyphal knots: coiled hyphae around large groups of cells. In the above genera, however, we are definitely dealing with cells; they are seen again as spherocysts in the mature tissue. Extensive comparison of both mature material and microtome sections of primordia led to the conclusion that cell division is often more marked in the hyphal knots than in the looser parts of the tissue in which the cells of the hyphae are longer. The significance of this phenomenon will be referred to below.

Some structures always present in the plectenchyma, especially when this is denser, are the very sinuous or undulating hyphae (Pls. 32G, 36 F, and Fig. 1a) and also the loops (Pl. 32G, and Fig. 1b). Where a loop encircles another hypha if the loop is viewed laterally (Pls. 33A, B, 34B, 36C, G, and Fig. 1c), in section an apparent ring or spiral may be seen. This configuration is frequently seen in dense tissues,

Table I

		hyphal knots			meristemoid	free tips	inflated intercalary elementa	sinuous hyphae	loops spirals rings	system of straight hyphae	photo's
		merely an agglomeration of hyphae	with cell formation	coiled hyphae mostly around cells							
Cantharellus cibarius	m		p.tr. ±	p.tr. ±		p.tr.++					
Cantharellus tubaeformis	m	st.,p.tr.									
Paxillus involutus	m		b.pl.,p.tr.								
Chroogomphus rutilus	m		b.pl.,p.tr.								Pl. 33F
Gomphidius roseus	m,v		veil, ?								
Suillus aeruginascens	m,+v		p.tr., veil			p.tr.++,inf.			+		Pl. 33C
Suillus luteus	m,v		veil								
Xerocomus subtomentosus	m		b.pl.,p.tr.								
Boletus edulis	f	?				p.tr.,bulb,inf.		+	+		Pl. 36C
Boletus satanas	f		bulb,sh.b.	bulb		+		+	+		Pl. 36E
Gyroporus cyanescens	m		b.pl.,p.tr.	±		+		+	+	+	Pl. 33D, E
Pleurotus dryinus	m,v		veil	veil				veil	veil		Pl. 35A
Panellus serotinus	m		tr. ±	tr. ±				+	+		
Hygrophorus hypothejus	m,+v		b.pl.								Pl. 34A
Hygrophorus chrysaspis	m		b.pl.,p.tr.±								
Hygrophorus dichrous	m		b.pl.,p.tr.	b.pl.,p.tr.							
Armillaria luteovirens	m,v	– (veil)	– (veil)	– (veil)							
Armillariella mellea	m,v				m.l. veil						
Cathathelasma imperiale	f	b.pl. ±						+	+		
Galera marginata	m,v	veil ±									
Galera paludosa	m,v	– (veil)									
Alnicola melinoides	m,v	veil ±									
Kühneromyces mutabilis	m,v		veil ±								

Inocybe geophylla	f	b.pl.	b.pl.,s.c.h.				b.pl.	+	++		
Inocybe asterospora	m		b.pl.,p.tr., veil	b.pl.,p.tr.		+ t.c.			++		
Cortinarius calochrous	m		bulb			bulb					
Cortinarius praestans	f	b.pl.						+	++		
Cortinarius traganus	f		b.pl.			+		+	+		
Cortinarius limonius	m,v		veil		m.l. veil not serried			veil			Pl. 35B
Cortinarius acutus	m,v	– (veil)									
Dermocybe uliginosa	m,v		veil		m.l. veil not serried						
Leucocortinarius bulbiger	m		bulb	±					+	bulb	
Agrocybe aegerita	m,v	veil									
Conocybe hebelomatoides	m			p.tr.,bulb		bulb, acroph.	p.tr.				
Naematoloma udum	m,v	veil ±									
Naematoloma ericaeum	m,v	– (veil)									
Naematoloma radicosum	m,v	veil									
Psathyrella candolleana	m,v				m.l. veil						Pl. 35C
Psathyrella hydrophila	m,v				m.l. veil	+					
Psathyrella nolitangere	m,v				m.l. veil						
Psathyrella velutina	m,v				m.l. veil ±						
Coprinus fimetarius	m,v				m.l. veil						
Coprinus macrocephalus	m,v				m.l. veil						Pl. 35D
Coprinus macrorhizus	m,+v				m.l. veil						Pl. 36A,B
Coprinus radians	m,v				m.l. veil						
Coprinus auricomus	m,v		b.pl.		m.l. veil						
Cystoderma carcharias	m,v				m.l. veil not serried						
Phaeolepiota aurea	m,v				m.l.not well developed						
Lepiota aspera	f	bulb	±			++, inf.	+	+	++		
Lepiota mastoidea	f		bulb, sh.b.			++			+		

Table I (continued)

		hyphal knots			meristemoid	free tips	inflated intercalary elements	simuous hyphae	loops spirals rings	system of straight hyphae	photo's
		merely an agglomeration of hyphae	with cell formation	coiled hyphae mostly around cells							
Macrolepiota rhacodes	f	bulb				++	+	+	+		
Macrolepiota procera	f	bulb	±			++, t.c.	+	+	+		
Leucocoprinus cepaestipes	m,v		± veil					veil			
Leucocoprinus denudatus	m,v	veil	±								
Leucoagaricus naucinus	m		bulb, veil		m.l. veil not serried	++					
Agaricus bisporus	f,m	+	bulb, sh.b.			++, inf.	+	+	++	+	Pl. 32G,H
Agaricus bisporus strain 59b	f,m	+	±	++, s.c.h.		++, inf.		+	++	+	Pl. 32A,B,C,E
Agaricus bisporus strain 59c	f,m	+	+	+, s.c.h.		++, inf.		+	+	+	Pl. 32D,F;33A,B
Agaricus osecanus	f		bulb			++, t.c.	+	±	+	+	Pl. 36H
Volvariella speciosa var. gloiocephala	f,m					acroph.	+				
Volvariella bombycina	m		bulb,p.tr., volva	+		+	+		+	+	Pl. 35E
Volvariella surrecta	m		bulb	bulb,volva						+	
Volvariella pusilla	m										
Pluteus atricapillus	f,m		b.pl.,p.tr.	+		+, t.c.		+	+		
Pluteus salicinus	f		bulb			+					
Limacella guttata	f,m		bulb	++, s.c.h.		bulb, p.tr., acroph.			+	+	Pl. 34B
Amanita solitaria	m		bulb,p.tr.	++, s.c.h.		bulb, p.tr., acroph.				+	Pl. 34C

Amanita rubescens	m		bulb, p.tr.	++, s.c.h.		bulb, p.tr., acroph.				+	Pl. 34D
Lycoperdon pyriforme	f	+	young bulb, ±			++		+	+		Pl. 36F,G
Chamonixia caespitosa	m		columella	++		++, inf.				+	Pl. 34E
Scleroderma aurantium	m		young bulb, veil								Pl. 34F;35F
Geastrum triplex	m		young bulb, veil								
Ramaria aurea	f	+	±			++	+	+	++		Pl. 36D
Ramaria formosa	f	+	+, sh.b.	±		++, inf.		+	++		
Ramaria mairei	f	+	±	±		++, inf.		+	++		

The following indications have been used:

acroph. = acrophysalides
b.pl. = present in basal plectenchyma
bulb = present in bulb
f. = freehand section of mature material
inf. = inflated
m. = microtome section
m.l. = matrix layer
p.tr. = pileus trama
s.c.h. = sometimes central hypha
sh.b. = short branches
st. = present in stem
t.c. = terminal cell
v. = the veil has mainly been examined
veil = present in veil
\+ = present in either basal plectenchyma, bulb or pileus trama or in both, not specified
++ = numerous
± = present, not numerous
– = definitely missing

Nomenclature according to Singer (1975).

in both primordia and maturer froms. An actual ring in the hypha can be formed by anastomosis of the loop (Pls. 32A, 33B, and Fig. 1c). Tips of hyphal branches are found nearly everywhere. These free tips of the penetrating hyphae are characteristic of the basal plectenchyma and the young cap trama, whereas they are seen much less or not at all in mature tissues. Where they are seen they are regarded as a peculiarity of the tissue (Amanitaceae). Occasionally the tip of the branch consists of a terminal cell; the tips are often club-shaped (Pls. 32D, E, H, 33D, 36E, H, and Fig. 1d). Besides inflated terminal cells there are also in many cases intercalary elements in the hyphae which have suddenly become much broader. A further complication in these tissues, which may occur in the most varied tissues (but by no means always), is formed by a system of straight hyphae forming a type of framework through the undulating hyphae; these straight hyphae may be somewhat wider.

We have summarized our results on 73 species in Table I; this was the only way to avoid very lengthy descriptions, with many repetitions. The nature of our comparisons in many species was such that sometimes little attention was paid to certain parts. An empty space, therefore, may mean that these structures were not studied but not necessarily that they were absent. In a number of species we studied only the veil.

HYPHAL KNOTS AND MERISTEMOIDS.—In simple form a hyphal knot is a bundle of hyphae which continue to adhere to one another during the expansion of the tissue, while the rest becomes looser.

The knots usually consist of many short cells, so that it can be assumed that cell division is more marked here than in the surrounding tissue. How did these agglomerations of hyphae initiate? Could they have been formed by interweaving of the growing hyphae? Frequently there appear twisted hyphae in the hyphal knots, e. g. in the veil (Pl. 35A, *Pleurotus dryinus* (Pers. ex Fr.) Kummer; Pl. 35F, *Scleroderma aurantium* L. ex Pers., exoperidium; *Gomphidius roseus* (Fr.) Karst.; *Suillus aeruginascens* (Secr.) Snell, etc.) or in the lipsanenchyma. In many cases the latter tissue is strengthened by hyphae growing out of the edge of the cap or the stipe (even out of the edge of the gills). In cases where the mature fruitbody has a luxuriant ring the lipsanenchyma shows marked growth, e.g. *Agaricus* sp., *Macrolepiota* sp., *Limacella*, etc. Cell formation must then take place in the lipsanenchyma; this may be concentrated in hyphal knots. Sometimes, however, it is evident that the cells continue to divide in the whole lipsanenchyma.

In most cases the hyphal knots are initiated by the loosening of an originally compact tissue. In a very young primordium the tissue can be very dense. In these interwoven hyphae, active cell formation commonly takes place. Such tissues are subsequently pushed apart, either because they are stretched or because some cells inflate. Cell division continues in the hyphal knots and these alternate with places where hyphae have much longer cells (Pl. 33F, basal plectenchyma of *Chroogomphus rutilus* (Schaeff. ex Fr.) Lundell). The hyphal knots may also occur in places where cell formation is even more serried so that it is not incorrect to speak of a meriste-

moid. For example the matrix layers, found in the cap are forced apart by the lengthening hyphae. In this manner the hyphal knots present in the veil are formed (Pl. 35B, *Cortinarius*, veil on the cap). In a very young primordium of *Agaricus bisporus*, for example, a closed tissue completely made up of cells is present; later hyphal knots can be distinguished.

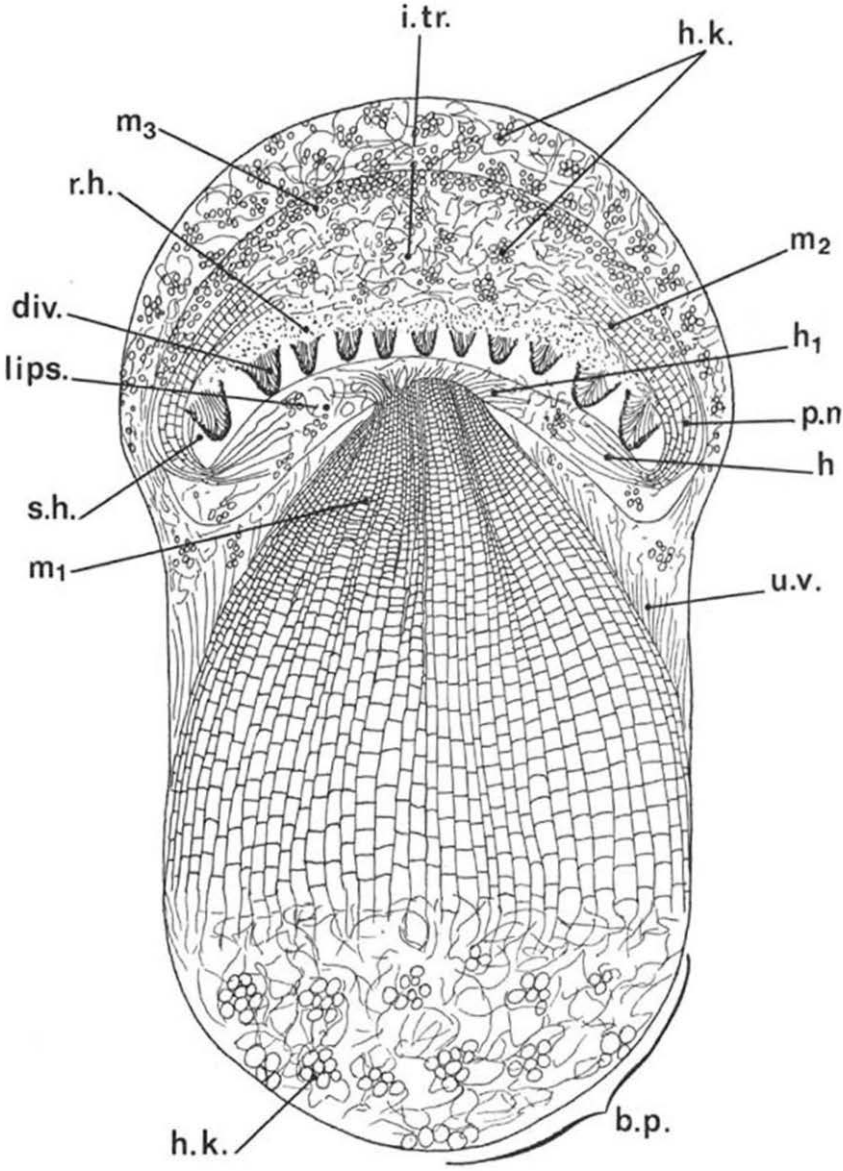
In the hyphal knots there are commonly twisted or spiral-like hyphae which wind themselves between the other hyphae. In many cases such coiled hyphae are to be found around the knot as well as around the bundles of hyphae. A very characteristic configuration may then be seen: the bundle of twisted hyphae around a group of cells (Fig. 1e). As shown in Table I, this typical structure in the original primordial tissue (basal plectenchyma and pileus trama) is to be found in various species throughout the system. It is especially well developed in the strains 59b and 59c of *Agaricus bisporus*, more particularly in genera like *Amanita* and *Limacella*. Here the bundles of curled hyphae and the alternating cell complexes are just as clearly marked as in the trama of *Russula* (Reijnders, *1963*: pl. 8 figs. 4–6). Compare these figures to those of Plates 32B, 34C and D.

Whether a central hypha can be distinguished in the centre of the cell group of such complexes or not is important. In *Russula* and *Lactarius* the development of these complexes starts as primary rosettes around an induction hypha (Reijnders, *1976*). In these genera the cell groups sometimes appear to arrange themselves around the hyphal tips (l.c.: pls. 13E, 14A). In general, however, cell formation takes place along the whole hypha. In other species as well it appeared that sometimes, but by no means always, a club-shaped tip of a hypha is visible in the centre of a cell group of such a hyphal knot. (No new names are applied to these twisted complexes because it was assumed that they develop from simpler hyphal knots or are connected to them in some way.) For example this was the case in *Agaricus bisporus* strain 59b (Pl. 32E), *Limacella guttata* (Pl. 34B), *Gyroporus cyanescens* (Pl. 33E). In *Amanita rubescens* this peculiarity turned up so often that mere chance was unlikely. Here the tissue of the trama of the young stipe and cap has a system of long, broadened, club-shaped, usually somewhat curved hyphae. These are the tips regularly found in the centre of cell groups which are surrounded by bundles of coiled hyphae. (The later formed acrophysalides are short and pear-shaped in *Amanita rubescens*.) These observations are nevertheless too few to warrant that this is caused by induction.

It is, of course, quite possible that the hyphae in all the hyphal knots have an induction effect on one another that advances cell division. Here again there is insufficient evidence.

We have already described meristemoids as a close tissue in which coordinated cell division takes place. Such parts may be found in various places in the primordium. At some points it would appear that they consist wholly of cells with no thin hyphae included (Pl. 35D, *Coprinus macrocephalus*, matrix layer of the veil; Pl. 36B, *C. macrorhizus*, the same type of stipe). This would also be true in tissues formed by such meristemoids, i.e. here the 'hyphes connectives' of Fayod, the undifferentiated generative hyphae, would be absent. Probably this is not entirely true.

These meristemoids closely resemble the meristems of the Phanerogams; sometimes


i.tr.
h.k.
m3
r.h.
m2
div.
h1
lips.
p.n
h
s.h.
m1
u.v.
h.k.
b.p.

they are referred to as such. This is not correct because the meristemoids initiate from hyphae which together form a simple tissue; cell division, therefore, can only take place in one direction and the cell walls between the cells of different hyphae are double.

Many phases between individual hyphae and a neatly closed meristemoid can be distinguished. At the proximal end, behind the hyphal bundle of the cap edge, there may be a closed meristemoid but individual hyphae undergoing much cell division may also be found there.

The presence of a meristemoid would appear to be a progressive characteristic. The neatly arranged adjacent cells resembling a tissue of higher plants are often seen in the stipe or cap of more highly developed groups; in many instances such a texture occurs where there is considerable inflation (e.g. Pl. 36B, *Coprinus macrorhizus*; compare also Reijnders, *1963*: pl. 21 figs. 3–5, *Marasmius*; pl. 26 fig. 5, pl. 27 figs. 2, 3, *Mycena*; pl. 39 figs. 1–4, *Conocybe*, etc.). The veil of connected cells (Pl. 35D, *Coprinus macrocephalus*) and the spherocyst veil are usually also formed by a meristemoid as a specially evolved form of the veil.

It is difficult to say whether, and if so to what extent, these cells formed by the meristemoid undergo secondary septation, but as they soon differentiate by inflation this is highly unlikely.

The different types of cell formation which can occur in a primordium of an agaric are illustrated in a schematic diagram (Fig. 2).

HYPHAL KNOTS IN VEILS

It is desirable to establish whether hyphal knots occur in parts of the carpophore other than the bulbus and the trama. Hyphal knots were found in certain veils. It is important to distinguish between innate and emanated veils among the veils of the Agaricales (Reijnders, *1963*: 224–227). An innate veil is initiated when the differentiation of the cap and the stipe of a young primordium is embedded rather than superficial. If this is the case some protenchyma (the first undifferentiated tissue of the primordium) remains at the periphery. Occasionally some changes had taken place earlier at the periphery but hyphae were never added. An emanated veil is formed by the growth of hyphae out of the surface of the young primordium. Frequently it is difficult to demarcate the two types of veils precisely because the two processes, differentiation of cap and stipe surface and the outgrowth of hyphae, may begin at almost exactly the same time (Reijnders, *1963*: 227–230).

An innate veil which shows little further growth will, of course, soon begin to

Fig. 2. Scheme of cell formation in an advanced primordium of an agaric (as shown in a slightly tangential section).

ABBREVIATIONS USED. — b. p., basal plectenchyma; div., divergent trama of the young folds of the lamellae; h_1, hyphae that grow from the stipe into the lipsanenchyma; h_2, hyphae growing from the pileus margin into the lipsanen chyma; h. k., hyphal knots; i. tr., initial pileus trama; lips., lipsanenchyma; m_1, meristemoid of the stipe tissue; m_2, meristemoid of the pileus margin; m_3, matrix layer of the veil; p. m., sheaf of parallel hyphae in the pileus margin; r. h., radiating hyphae over the hymenophore (belonging to it); s. h., subhymenium and palisade of the hymenium; u. v., hyphae growing from the stipe into the universal veil.

tear as the primordium enlarges, and the knots will be absent, like for example, in *Galera paludosa* (Fr.) Kühn.; or will be rare, like in *Galera marginata* (Batsch ex Fr.) Kühn., *Hypholoma udum* (Pers. ex Fr.) Kühn., and *H. ericaceum* (Pers. ex Fr.) Kühn.

The parts showing the most marked growth would have to be investigated to reveal any hyphal knots. This may also be true in an innate veil because where there is concentrated development the veil is strengthened by a number of hyphae growing out from the surface.

Some good examples of hyphal knots were found in the universal veil of *Cortinarius limonius* (Fr. ex Fr.) Fr. (Pl. 35B) and to a lesser extent in that of *C. uliginosus* (Berk.) Moser. In the extending velum *sui generis* it is not just a question of the strengthening of the innate veil; there are also good examples, e.g. in young stages of *Pleurotus dryinus* (Pers. ex Fr.) Kummer (Pl. 35A) in which an emanated universal veil is present, and in *Suillus luteus* (L. ex Fr.) S. F. Gray. In the last species examination showed that the veil is made up of hyphae from the upper cap layer which grow downward and meet hyphae which grow out of the stipe surface (between the elements of the hymenium). In this veil a good deal of cell formation resembling hyphal knots exists. The hyphae in such rapidly growing veils are often grouped in convoluted bundles. Here again the hyphal knots are not always well demarcated; the hyphal bundles show some areas with short cells where cell formation seems to take place. Hyphal knots are also present in the young volva of *Volvariella* (e.g. *Volvariella bombycina* (Schaeff. ex Fr.) Sing., Pl. 35E). This is not surprising because the volva in the bulbangiocarpous species is only a part of the bulb.

The spherocysts veil may be derived from the above type of veils with localized cell formation. The spherocysts usually arise from a sort of matrix layer at the surface of the primordium, where much cell division takes place. Through the repeated formation of numerous septa in the same elements rows of cells are often formed which differentiate to progressively form spherocysts towards the outside (Pl. 35D, *Coprinus macrocephalus* Berk.; Pl. 35C, *Psathyrella candolleana* (Fr.) Maire). In the zone of transition to the veil in the uppermost layer of the cap trama there are for instance many complexes of small round cells which do not all adhere to one another (Pl. 35B). In the veil above these cells there are more separated hyphal knots arising from the groups of small cells of the cap trama. A layer of closely serried cells where much cell division occurs, i.e. a matrix layer of the spherocysts veil, could originate from the kind of feature found in *Cortinatius limonius* (Fr. ex Fr.) Fr.

Hyphal knots may also be found in certain parts of the peridium of the Gasteromycetes. Peridia are generally very heterogeneous in origin; they need not be homologous to the veils of the Agaricaceae (Reijnders, *1963*: 363–364), which are themselves not homologous. On the other hand there is no need to doubt the homology of the exoperidia of, for example, *Scleroderma* or *Geastrum*; these consist of outwardly growing and entwining hyphae; as established, the original bulbus of the Agaricales may be compared to that of the Gasteromycetes (i.e. homologous). In the exoperidium of the above mentioned genera were found clear examples of hyphal knots; these occur again among twisted hyphae, loops, and hyphal bundles (Pl. 35F, *Scleroderma*, and *Geastrum triplex* Jungh.).

CORRESPONDING STRUCTURES

Can structures which correspond to those found in the plectenchyma of bulbus and trama also occur outside the carpophore, e.g. in the mycelium? Heim (*1967*: 177) illustrated a number of configurations of hyphae in the mycelium from cultures of *Psilocybe fagicola* Heim & Cailleux. Here there are obvious similarities to those structures found in the plectenchyma: spirals, curled hyphae, groups of approximately isodiametric cells at the ends of twisted hyphae, etc., but these structures do not always occur in the same places, as they do in the hyphal knots.

The similar initiation of sclerotia is of more importance. Townsend & Willetts (*1954*) differentiate among three developmental patterns of sclerotium formation. In *Rhizoctonia solani* a compact mass of cells is formed by localized branching and repeated septation in adjacent cells. In *Botrytis* these processes are accompanied by repeated dichotomous branching of hyphae over a restricted area. *Sclerotinia gladioli* represents a third strand type in which numerous lateral branches originate from a few parallel hyphae. Many cell divisions are initiated in the area by septation; through adhesion of the hyphae and through these processes a compact body is finally formed.

Adhesion in order to form bundles (locally by lateral hyphae) and the abundant cell division in adjacent hyphae are also typical of hyphal knots but the twisting and curling of the hyphae frequently encountered earlier appear less common in the initial stages of sclerotia. In the sclerotia moreover many cells are formed, so that a combination of the structures producing this phenomenon is understandable.

Like in some types of sclerotia corresponding structures in the developmental stages of papulaspores (Weresub & Le Clair, *1971*) are present.

A COMPARISON OF THE TISSUE FOUND IN THE BASAL PLECTENCHYMA AND THE BULB IN AGARICALES WITH THE TRAMA OF ASTEROSPORALES AND AMANITACEAE

Over such a large range as the trunk of *Ramaria*, the trama of *Cantharellus cibarius* Fr., the basal plectenchyma and the bulb of numerous Agaricales, and some younger stages of Gasteromycetes, were found a number of structures characteristic of these plectenchymatic tissues. These include free ends of hyphal side branches and hyphal knots, balls of adhering and interwoven hyphae not infrequently divided into short cells and eventually forming a close mass of spherocysts, commonly surrounded by coiled hyphae. From these structures the derivation of the different construction of the trama of the Asterosporales on the one hand and the Amanitaceae on the other hand should be shown. This ought to make it possible to solve a problem which has intrigued mycologists, especially systematic mycologists, for some time.

The heteromerous trama of the Russulaceae consists not only of spherocysts and connective hyphae but also of vascular hyphae. It was previously thought that these spherocysts were absent in the trama of the Agaricales, except in a few species

of *Amanita* in which subglobular cells can make up a large part of the trama but these cells proved to be really more or less pear-shaped and not quite round. In young fruitbodies and in *Russula* primordia hyphal knots in the trama were found consisting of short cells surrounded by curled hyphae. These structures are illustrated in our study of the development of some *Russula* species (Reijnders, *1963*: pl. 8 figs. 4–6). Moreover the same structures are visible in the trama of *Limacella guttata* (Fr.) Konr. & Maubl. (Pl. 34B), *Amanita solitaria* (Bull. ex Fr.)Mérat (Pl. 34C), *Amanita rubescens* (Pers. ex Fr.) S. F. Gray (Pl. 34D), etc. These structures do not differ from those which were repeatedly discerned in the bulb and sometimes in the cap trama of other Agaricales, though in a less perfect from. As a rule the homology of all these trama structures can be accepted.

In 1963 we were not yet aware that the complexes of spherocysts in *Russula*, like in *Lactarius*, develop around a central hypha indicating induction. Recently (Reijnders, *1976*) we investigated the origin of this heteromerous trama in some detail and found that such induction can also occur in those Asterosporales which have a gasteroid habitus (*Arcangeliella*, *Elasmomyces*). In the latter case the clumps of spherocysts were simpler and looked more like the ordinary type of hyphal knots, surrounded by coiled hyphae. Thus far we have been unable to prove with certainty any form of induction started by a central hypha. Apart from this phenomenon the structures are exactly alike, so that it is possible to speak of a homology. In *Lactarius* the spherocyst masses arrange themselves around the longitudinal, central hyphae, with the result that they are parallel to the axis of the primordium. Primary rosettes are formed which in cross section are seen to consist of a central hypha surrounded by a row of spherocysts; these are deposited by a hypha coiled spirally around the central hypha. In *Russula* more of these spherocyst cylinders, which form around a central hypha, often merge in larger complexes. The central hyphae degenerate rapidly.

The trama structure of the Amanitaceae is unusual in that short laterals form which finally become so numerous that they take up the major part of the trama. The peculiarities of these elements were discovered by Bonorden as early as 1858 (Reijnders, *1963*: 6). Bas (*1975*: 54) proposed that they be termed acrophysalides. These elements are not found only in the trama of the Amanitaceae; even there they are not always the same in shape. In *Amanita vittadinii* (Mor.) Vitt. they consist of a chain of markedly inflated cells (Reijnders, *1963*: pl. 54 fig. 1); in *Amanita rubescens* on the other hand they are short, pear-shaped elements (Reijnders, l.c.: pl. 55 fig. 6); in *Limacella guttata* (Fr.) Konr. & Maubl. they vary in shape (Reijnders, l.c.: 119, pl. 52 fig. 1). Similar elements are found in the bulb; in *Amanita rubescens* the bulb is mostly taken up by such pear-shaped, much inflated cells while there are still only a few in the developing fruitbody, their number decreasing upwards. In *Amanita rubescens* there are in addition other widened hyphae with free ends. It is clear that the acrophysalides of the stipe and cap trama in the Amanitaceae must be regarded as homologous to the similar elements in the bulb, and that these in turn are homologous to the free ends of hyphal ramifications in the bulbs of other species of Agaricales which may also have a club-shaped terminal cell (e.g. Pl. 36E, F, H).

It is thus apparent that the Amanitaceae have hyphal knots in the trama involved in the initiation of cells. They are clearest in a somewhat older primordium or in a young fruitbody because in a young primordium the tissue is often too compact, though the differentiation into hyphal knots and intercalary hyphae probably took place earlier. The cells of the hyphal knots grow out and lengthen so that in a more developed stage they will form hyphae; these in turn, produce side branches which form acrophysalides. This process does not differ from processes normal in other Agaricales.

The conclusion is warranted that the apparently atypical trama of the Asterosporales, like that of the Amanitaceae, may be traced back to the normal tissue at the base of the stipe (and also often in the trama) of other Agaricales and that the atypical character of these structures arose only from an accentuation of certain processes which are in principle normal (except possibly in the induction of one particular hypha) for the Agaricales in general and even for the clavarioid fungi and the Gasteromycetes.

ANOMALIES

(1) Histological analysis of the strains '59b' and '59c' of *Agaricus bisporus*. Fritsche & von Sengbusch (*1963*) obtained different forms of fruitbodies from single spore cultures and indicated these as 59a, 59b, and 59c. Form 59b was obtained from 59a, and 59c appeared spontaneously in 59b. All three forms (possibly mutants) deviate from the normal type of fruitbody in that they lack a stipe or cap and do not form lamellae. The fruitbodies are bulb-shaped and show some differences worth mentioning. Form 59a has a cavity in the lamellar position of normal specimens and is puff-ball shaped. Form 59b differs from 59a because of its smooth surface and the possibility that it will show a slight external stipe resulting from the narrowing of the undersurface. Strain 59c produces huge, irregular tubers which can weigh up to 825–1800 gram and usually have an irregular surface. Transitional forms of 59b and 59c may be obtained in pure culture; a reversion to the 59b form is often seen in culture. On one occasion a new form appeared in a culture of 59c: a gigantic tuber tapering apically to a much smaller stipe supporting a rudimentary cap (Fritsche, *1968*: fig. 9).

From the above phenomena and bearing in mind the separation of the bulb from the rest of the mushroom (Reijnders, *1974*), a morphologist will assume that here it is a question of hypertrophied bulbs initiated because the rest of the fruitbody was unable to develop. *Agaricus bisporus* (Lange) Imbach is hymenocarpous (Reijnders, *1963*: 202), i.e. the first differentiation of the fruitbody in the tuber is formed by the palisade hyphae of the hymenophore, which grow downwards in a ring perpendicular to the axis of the primordium, but we do not wish to suggest that at this stage there is no differentiation at all in the bulb itself.

To analyse the tissues of forms 59b and 59c we were able to use fresh material supplied by the 'Proefstation voor de Champignoncultuur', for which we would

like to thank Dr. G. Fritsche. We concentrated especially on a comparison of microtome sections of the fixed material of young fruitbodies of 59b and 59c with similarly prepared sections of normal primordia. Material was fixed with Bouin's fluid as usual and stained with Mayer's haemalum. Finally we studied the bulb tissue of mature specimens of some species of the genus *Agaricus*. The formation of the plectenchyma in the bulbs had the same appearance as in all the other species. This comparative investigation seemed to be needed because at first about either the presence or the function of the hyphal knots was uncertain.

Plate 32A shows the tissue of a young stage, a small bulb with a diameter of 950 µm. In many places the hyphae appear to form a ring around the transverse section of another hypha. Spirally coiled up hyphae are present as well as a system of straight hyphae, also groups of isodiametric cells. There are also numerous hyphae ending freely. We photographed coiled hyphae and round cells in a fairly advanced stage (diam. 1.8 mm, Pl. 32B). Occasionally these groups of isodiametric cells appear to be arranged around a central terminal end of a wider hypha (Pl. 32E, a more advanced stage of 59b: length *c.* 5.8 mm, width 3.2 mm).

The above structures may be found in bulbs of strain 59b. To supplement the data we made a microtome section of a bulb of strain 59c with a diameter of a few centimeters. As these bulbs become much larger than those of 59b the measurements of the elements of this tissue can be compared with those of the more advanced stage of 59b above. In that case the structures seem to be the same in 59c but the diameter of the elements is larger. This applies to a high degree to the free hyphal ends, which have a width of up to 19 µm (usually *c.* 10 µm) in the 59b stage, and may even be 49 µm wide in the 59c stage; 20–40 µm being more normal. There also exists a difference in the diameters of the short cells: in 59b 6–11 µm (average *c.* 8 µm), in 59c (6.5–)8–15 µm. The width of the straight hyphae (6–8 µm) is much the same as the former 5–15 µm (usually *c.* 7 µm). On comparison with a smaller stage of the normal *Agaricus bisporus* (width *c.* 1.4 cm) smaller measurements were found: free hyphal ends 5–8 µm, round cells 3–6.5 µm (average *c.* 5 µm), straight hyphae 3–8 µm (average *c.* 5 µm). The unusual width of 59c will be considered below. Further the measurements of a young, living specimen of *Agaricus bisporus* (cap width *c.* 1 cm) do not compare to those of relatively small bulbs of 59c: free hyphal ends up to 16 µm, hyphae 6.5–10 µm. Cross sections of the lower part of this living bulb show a plectenchyma with markedly coiled hyphae having undulations and loops. It is noticeable that some cells in the chain of a hypha are much broader than the rest (up to 16 µm). Free hyphal ends are numerous, as are knots of coiled hyphae with short ramifying branches (fewer short cells).

Comparison of this material, fixed or unfixed, led to the deduction that the bulbs of 59b and 59c are identical with those of normal specimens of *Agaricus bisporus* and with the Agaricales in general. This may well be used to support the idea that the bulbs of 59b and 59c are actually hypertrophic bulbs in which further development and differentiation into a fruitbody are not genetically possible. There is only one morphological difference between 59b and 59c on the one hand and the normal

bulb of *Agaricus bisporus* on the other. In the first two we find a more differentiated rind of thinner, periclinal, loosely woven hyphae (diam. 2–3 μm) packed more closely together at the periphery (Pl. 32c). This layer is absent in normal primordia, which are surrounded by a universal veil only slightly differentiated from the lower or adjacent trama; the looser lipsanenchyma is left out of consideration.

Fritsche (*1972*) also investigated the cytology of strain 59c. She came to the conclusion that 59c has more nuclei in the cells than 59b; furthermore that the nuclei of 59c are statistically larger than those of 59b. Superficially the primordia of 59b have the normal form of primordia; the measurements may also be compared to those of *Agaricus bisporus*; the mature fruitbodies are, however, slightly smaller than normal fruitbodies. By contrast strain 59c is a gigas form (Sinnott, *1960*: 438). Gigas forms often depend on the number of chromosomes (polyploidy). Polyploidy is very common in Phanerogams and also occurs in fungi (see, e.g. Esser & Kuenen, *1965*: 326–330). We conclude that the bulbs of 59c are hypertrophied bulbs of the normal *Agaricus bisporus* formed by a delay in the development of the normal fruitbodies and that they are probably examples of polyploidy. The fruitbody forms of strains 59b and 59c are like those which Singer (*1975*: 18–19) termed carpophoroids. It would be useful to investigate whether in other cases of such monstrosities there is also a very marked development of the bulb.

(2) Watling's aberrant forms of *Psilocybe merdaria*. Ascertainment of whether forms 59b and 59c should be classed among the carpophoroids depends on what is understood by carpophoroids. According to the definition used by Singer (*1949*: 25), the carpophoroids are completely sterile bodies which formed in place of those bearing basidia. In agreement with this, forms 59b and 59c belong in the carpophoroids. The gasteromycete-like forms of *Psilocybe merdaria* described by Watling (*1971*) have superficial cavities along whose walls a hymenium is formed. Besides these gasteromycete-like types Watling obtained a whole series of monstrosities where especially the cyphelloid and the pleurotoid, *Melanotus*-like forms (with lateral stipes) occur.

It is unfortunate that because descriptions have been macroscopic rather than histological we know so little about the hyphal development inside these structures. We believe that the teratoid forms of *Psilocybe merdaria* are not homologous to the fruitbodies of 59b and 59c, which actually represent bulbs. Here it would be fitting to go into the causes of the initiation of *Psilocybe* abnormalities.

At first sight it is surprising that gasteroid and cyphelloid forms should develop together, though their growth patterns are seemingly contradictory. The gasteroid form appears to be very concentrated; strongly developing parts are scarcely present. In pleurotoid and cyphelloid forms the growing margin of the cap plays a more important role, the development of these forms falling under the diffuse type (Reijnders, *1963*). If the phenomenon is an atavism part of the monstrosities would indicate a gasteromycetic origin and the other part a relationship to, e.g., *Pleurotus* (Polyporaceae sensu Singer). It is not really necessary to go that far. Sporulation

continues in the bovist-like bodies of *Psilocybe merdaria*. Watling's descriptions make it clear that in many of these teratoid forms the hymenophore does not develop normally (there is also a *Weraroa* type). In the cyphelloid type abnormal lamellae are also formed. Both in this type and in the gasteroids the stipe is poorly developed; at least it is never long and robust; in gasteroid forms the stipe is often comparable to a columella.

In our book on the development of fruitbodies in Agaricales (Reijnders, *1963*) we attempted to emphasize the significance of the order of succession of which the parts of the fruitbody developed in the primordium. The hyphae that are to form the hymenophore appear first among undifferentiated generative tissue, which we termed protenchyma, in a hymenocarpous primordium. Like most of the closely investigated species of *Stropharia Agaricus bisporus* is hymenocarpous but in *Psilocybe* this structure does not appear (or is less apparent) before the stipe rudiments. (We referred to *Psilocybe merdaria* as isocarpous.) The studies made by Urayama, Hagimoto, Konishi, and Gruen have indicated that substances produced in the lamellae can influence the growth of the stipe. This is related to the inflation of the stipe cells, though the longitudinal arrangement of the stipe cells might also be influenced; this orientation of the hyphae shows that a stipe is being formed. In strains 59b and 59c of *Agaricus bisporus* no hymenophore is formed, and later no stipe. In *Psilocybe merdaria* the deficiency in the developmental mechanism of the hymenophore could thus cause abnormal stipe formation. If the stipe remains small and short the fruitbody inside the bivelangiocarpous primordium stays covered and a gasteroid form results. It is thus conceivable that cyphelloid aberrations are also initiated when the fruitbody does open but that the rudimentary stipe is unable to support the body. Cyphelloids with different attachments may develop via pleurotoids (Reijnders, *1963*: 252–256).

Observations on the development of the Aphyllophorales

Few studies have been published on the development of the Aphyllophorales. The histological differentiation of this group is, as far as is known, more marked than in the Agaricales. Corner's distinction of hyphal types in the Polyporaceae etc. and that of Maas Geesteranus (*1962*) in spine fungi promoted investigation of the origin of these elements. Studies like those of Kennedy & Larcade (*1971*) on the development of *Bjerkandera adusta* lead to the conclusion that innumerable details of the origin of the fruitbodies are still unknown.

When the youngest stages of certain common species of Aphyllophorales are described it is to ascertain whether they have a basal plectenchyma and also to see how they grow. It was possible to collect young forms of *Hyphodontia quercinum* (Fr.) J. Erikss., *Stereum sanguinolentum* (Fr.) Fr., *Irpex lacteus* Fr., *Coriolus versicolor* (L. ex Fr.) Quél., *Hirschioporus abietinus* (Dicks. ex Fr.) Donk, *Gloeophyllum abietinum* (Bull. ex Fr.) Karst., and *Gloeophyllum odoratum* (Wulf. ex Fr.) Imazeki. Since in the

absence of a rapidly increasing elongation there is no demarcation of stages it is not really correct to speak here of primordia.

HYPHODONTIA QUERCINUM (Fr.) J. Erikss.—We made median sections through effused fruitbodies of 3–5.5 mm in diam. lying on the rind. The fruitbodies are made up of two layers; one layer has entangled or horizontal hyphae which advance over the substrate, and the other layer has erect hyphae on which parallel bundles can develop which are to form the teeth. The first layer incorporates much substrate and may be 200 μm wide, while the second layer may be 300–650 μm wide. Only one kind of hypha exists (diameter up to 1.0–1.5 μm) which has the same appearance as the mycelial hyphae on the cork layer, i.e. the generative hyphae. These are oriented parallel to one another at the margin of the young fruitbody. They often extrude through a fissure in the bark, where they are still much intertwined.

STEREUM SANGUINOLENTUM (Fr.) Fr.—The youngest stage of this species forms a small cushion with an arched upper surface which may be about 1850 μm broad and 650 μm high (Pl. 37A). The structure rests on the substrate but is only basally and centrally attached, at which point a zone of much intertwined hyphae (1.5–2 μm in diam.) is present. From this point the hyphae extend in all directions and form a dome. The central height is about 400 μm. At the edge of the dome the hyphae are mostly parallel but not close together (Pl. 37B); they grow outwards. The extending hyphae are also generative hyphae. Between the outwardly growing hyphae more coloured hyphae are also visible; these are initially much broader than the generative hyphae; they widen towards the periphery (diameter up to 5 μm) and often show club-shaped extremities. These hyphae are probably vascular hyphae which may eventually end in a cystidium. Skeletal hyphae are either absent or not clear at this stage; they become visible at a more advanced stage (3.5 μm in diam.). They are thin but thicker-walled than the generative hyphae (diameter *c.* 2.5 μm).

IRPEX LACTEUS Fr.—The young stage (Pl. 37C), of which we made median sections, also presses against the substrate and is only attached at the centre (width 2150 μm, height 820 μm). The hyphae extrude through a lenticel and are much entangled at their bases. From this point deeply coloured, thin hyphae extend outwards, being thus generative hyphae (Pl. 37C). More towards the periphery the colouring lessens, giving rise to faintly coloured, wider hyphae (diameter up to 3 μm) with thicker walls. These are skeletal hyphae. The typical form and colouring of the generative hyphae can be seen most distinctly at the periphery and the edge of the dome. However, there seem to be a number of gradations between the generative and skeletal hyphae. The generative hyphae lose their coloured contents and if they also thicken it becomes difficult to distinguish them from the skeletals. The extremities of the skeletals often extend above the surface and the terminal, somewhat wider cell contains abundant protoplasm and in many cases has not yet developed a thick wall. At the edge of the structure entangled hyphae are found again; these extend outwards and are more or less parallel, but they do not form an

obvious meristemoid. As in *Hyphodontia*, the teeth are formed at regular intervals by hyphal bundles in which the hyphae do not adhere closely until a later stage (Pl. 37E). The skeletals and the intermediate forms can be distinguished immediately in the teeth.

CORIOLUS VERSICOLOR (L. ex Fr.) Quél.—The youngest stages form a cushion about 672 μm wide and 570 μm high. Beneath this cushion there may be a stipe or mat (about 400 μm long and 200 μm broad) made up of the same hyphae as the cushion; they are entangled or somewhat longitudinally orientated. At the very base of the cushion-shaped structure the hyphae are still entwined over an area of about 100 μm, after which they extend evenly towards the periphery, there being no differentiated margin. There are two kinds of hyphae; somewhat irregular hyphae with clamp connections and dark granular contents (diameter 1.5–2 μm), and straighter, paler and usually wider hyphae (up to 3 μm). The irregular kind are clearly generative hyphae while the latter are mostly skeletals, especially towards the periphery, where they are thick-walled and their lumen is reduced to a thin line. It is also probable that a great many of the paler hyphae are generatives which have lost their protoplasmic contents, as we also find a lot of pale hyphae in the stipe where they are intertwined so that the arrangement closely resembles that in *Irpex*. An older stage is about 2.2 mm wide. At that stage the pores form and a transverse section shows teeth about 240 μm long in which the trama consists of almost parallel generative hyphae. Palisade cells (about 13 μm long) are already present in the hymenium. At the margin the hyphae are almost parallel but lie free from one another and do not form a real meristemoid.

HIRSCHIOPORUS ABIETINUS (Dicks. ex Fr.) Donk.—For this species the young stages investigated did not differ much in structure. When the diameter is about 1750 μm and the height about 380 μm the hyphae are entwined over a small distance at the base, where this is centrally attached to the substrate (e.g. 64 μm high). The hyphae radiate further, producing a slightly arched cushion. At the margin there are nearly parallel hyphae that are partly separate from one another. The tubes have already been formed at this phase and the walls (dissepiments) are distinguishable in longitudinal section as nearly parallel teeth. The generative hyphae, recognizable by their dark colour and granular protoplasm, are about 1.5 μm wide and especially numerous at the base The skeletal hyphae, found mostly at the periphery, have a thick wall that does not stain with haematoxylin, and often coloured cell contents (diameter *c.* 2.5 μm). Here some colourless hyphae must also be regarded as generative hyphae that have lost their protoplasmic contents. The palisade cells of the hymenium soon form and are initially 15–20 μm long.

GLOEOPHYLLUM ABIETINUM (Bull. ex Fr.) P. Karst.—In this species the young fruitbodies are dorsally attached right from their early formation. Our specimen extended 5.5 mm forward; a median section was taken through the base. Here the hyphae are intertwined over a short distance (*c.* 220 μm), after which they grow

forward and then both upwards and downwards to produce an almost fan-shaped body (Pl. 37F). Three types of hyphae can be distinguished: (i) pale, septated, thin-walled hyphae with a granular protoplasm (diameter 1.5–2.5 μm). These generative hyphae are common in the entangled part at the base, but they may also be found elsewhere; (ii) strongly pigmented hyphae with dark, rather thin walls (diameter 1–2 μm) and few or no septa; the hyphae are abundant and are probably intermediate forms giving rise to iii; (iii) skeletal hyphae with a thick wall and no septa (diameter 1.8–3.8 μm). Rings, to be found in the trama, originate by the bending of some of the hyphae (especially type ii); the hyphae then lie more or less obliquely in the trama. The extremities of some of these hyphae widen and are brightly coloured (diameter 6.5 μm). Five rings were visible at the 5.5 mm stage. Club- or bottle-shaped ends develop on the lower surface (the hymenium). On the upper surface the hyphae sometimes become erect and form bundles; they are also partly intertwined, giving a floccose-hairy (pilose) surface texture.

GLOEOPHYLLUM ODORATUM (Wulf. ex Fr.) Imazeki.—The young stages of *Gloeophyllum odoratum* consist of a small cushion, arched on the upper surface and flat below. These cushions often rest on one another because it would seem that at a certain point new fruitbodies may be formed on the upper surface. We investigated such bodies, which were, for example, 9 mm wide and 4.3 mm high, or 13.3 mm wide and 5.5 mm high.

The median section shows that the frequently dark coloured hyphae (diameter 1.3–2 μm) are entangled at the point of attachment to the substrate. In many cases these parts (250–670 μm) are not sharply defined because the basal part of the young fungus incorporates much of the substrate. Many skeletal hyphae are found in this zone and even more where the hyphae radiate towards the periphery. They have a thick, often encrusted wall and no septa (diameter 1.5–4 μm). Between the skeletals are paler, thin-walled generative hyphae (diameter 1.3–3 μm). There are also paler hyphae where the wall is distinguishable as a dark line (i.e. intermediates?).

Even at this young stage rings in the trame are found that are approximately parallel to the arched upper surface (Pl. 37G). The direction of growth of the hyphae is different in the rings and the hyphae lie closer together. Many widened hyphal extremities are seen in the rings (diameter 3–4 μm). Occasionally the hyphae deviate so far from their original direction of growth that the part of them in the rings is perpendicular to it. Above the rings the hyphae are much looser (i.e. farther apart). At the edge of the cushion the structure is the same as elsewhere at the periphery: there is no meristemoid.

CONCLUSIONS.—Comparison of the initial developments of these seven species of Aphyllophorales reveals a remarkable uniformity. *Hyphodontia* is excluded; this really forms a cover of two layers, the lower of which consists of entangled hyphae in the young stages, which are usually attached by the centre of the base to the substrate. All the others have a basal zone with intertwined primordial hyphae and a zone

where the hyphae radiate towards the periphery. The basal zone is usually somewhat limited. There is no obvious growing-limb, at least not in these young stages; a real meristemoid has not (yet) developed. Where a diffuse developmental type in the Agaricales is discerned the fruitbodies of this type are still formed initially by a bundle of adhering, coordinated hyphae (Reijnders, *1963*: 221) which later widens at its extremity. This may be only a gradational difference. There is another difference in the development of Aphyllophorales in comparison with the Agaricales: the quite different nature of part of the hyphae. Skeletal hyphae cannot be distinguished in the Agaricales but cell inflation is very marked and especially important during the growth of the fruitbody.

Referring to the origin of the skeletals Lentz (*1971*: 100) wrote: 'In orthodox instances, development is not by transformation of a generative to a skeletal unit, but by apical outgrowth of the skeletal element from the generative.' Although we cannot provide any actual proof these assumptions seem rather dogmatic. The numerous intermediates between the two types of hyphae which are seemingly present in some species (*Irpex*, *Gloeophyllum*, *Osmoporus*) and which have also been found in other species indicate that there may exist at least one other type of hypha which because of its thickened wall is sometimes difficult to distinguish from a skeletal hypha (see also Corner, *1950*: fig. 13, *Pterula*).

CONCLUSIONS AND PHYLOGENY

The basal plectenchyma in the Agaricales, just like the bulb which in effect is an expansion of this tissue, is characterized by a special structure which can also be found in the trama of a primordial cap and not seldom in mature specimens. This cap trama is initially part of the bulb tissue formed by the primary protenchyma.

The characteristics of this structure are:

(1) Undulating, interlocking hyphae and loops.
(2) Spirals and sometimes rings closed around other hyphae.
(3) Inflated, intercalary elements.
(4) Many free extremities of ramifications, often with clavate or widened terminal cells (P. 36H, *Agaricus*), so that they may resemble acrophysalides.
(5) Hyphal knots consisting of at least one bundle of adhering hyphae or usually coiled hyphae, which are often locally divided into short cells, occasionally forming short branches.

In many instances around these groups of short or round cells there are other hyphae; the tissue then appears like groups of coiled hyphae with a centre of apparent spherocysts. These groupings may occasionally be found between straight hyphae of a different nature, but this need not necessarily be so. We find such a structure in the most diverse species (Reijnders, *1963*: pl. 8 figs. 4–6, *Russula emetica*; Reijnders, *1976*: pl. 13E, *Lactarius mammosus*; pl. 15D, *Russula ochroleuca*; pl. 16C, *Russula fragilis*; pl. 17E, *Arcangeliella*). In our investigations for this study we also came across many instances of it (Pl. 34E, *Chamonixia caespitosa* Rolland; Pl. 33D, *Gyroporus*

cyanescens (Bull. ex Fr.) Quél.; Pl. 34A, *Hygrophorus hypothejus* (Fr.) Fr.; Pl. 32E, *Agaricus bisporus* (Lange) Imbach, strain 59b; Pl. 34B, *Limacella guttata* (Fr). Konr. & Maubl.; Pl. 34C, *Amanita solitaria* (Bull. ex Fr.) Mérat, etc.). Thus it appears that this structure is a common one. We must also assume that in matrix layers with a marked formation of closely grouped cells the coiled hyphae are present but less clear. They probably play a part in the formation of cells and perhaps in their nutrition.

In contrast to the above, the hyphal knots sometimes lie in looser tissue (Pl. 33C, *Suillus aeruginascens* (Secr.) Snell; Pl. 34F, young bulb of *Scleroderma aurantium* L. ex Pers. In this last case it is probably a question of remnants of hyphal knots that were originally closer together (compare also Pl. 35B, *Cortinarius limonius* (Fr. ex Fr.) Fr., veil; Pl. 33F, *Chroogomphus rutilus* (Schaeff. ex Fr.) Lundell & Nannf., inflation of the hyphae and separation of the knots). When in due course no more new cells are being formed and the old cells are inflated, even fewer of the hyphal knots remain (Pl. 32F, *Agaricus bisporus* strain 59c).

The structures with coiled hyphae led to a comparison of the trama of the Agaricales in general with that of the Asterosporales. The spherocyst formation in *Arcangeliella* (Reijnders, *1976*: pl. 17E) and *Elasmomyces* appears to be identical to the occurrence of short cells in the hyphal knots of the Agaricales. It was only not possible to show the phenomenon of induction in the Agaricales but it has often been found that in the centre of a group of cells surrounded by a coiled hypha a free end of a wide hypha appears like in *Arcangeliella* (l.c.: pl. 17E). Instances of this have been photographed on Plate 33E *Gyroporus cyanescens*, Plate 34B *Limacella guttata*, Plate 32E *Agaricus bisporus* strain 59b. It may be assumed that in this kind of hyphal knot the hyphae have an effect on one another and possibly also on cell formation just like that in a meristemoid in which the cell division is coordinated but this has not been proved and it is possible that no central hypha is present in most hyphal knots (not even when they are very young?).

The structures during development in real Aphyllophorales with those in Agaricales were compared earlier. It is striking that there is no clear growth margin in very young stages. There is no bundle of interlocking hyphae which produce new hyphae by means of regular branching, nor is there a meristemoid. Hyphae grow much more separate; apart from secondary septation the new cells are formed at their tips, but growth is directed by the shape of the whole structure. Young stages (here it is difficult to speak of primordia) show that there is coordination in the growth and regularity in the increase in volume of the whole.

That there is no growth margin of interlocking hyphae is also demonstrated by the phenomenon of haptomorphosis, that is that the edge of the fruitbody can grow around all sorts of obstructions, or that different individual fruitbodies grow together at their edges to produce a single distinct specimen. This is not seen in the Agaricales.

Is there in the Aphyllophorales no meristemoid zone of adjacent hyphae in which the cell division is coordinated? This ought to be investigated in greater detail. Though tissue formation in these groups, or at least in the greater part thereof,

deviates from that in the Agaricales (and Gasteromycetes), this does not apply to the clavarioid and cantharelloid fungi. As far as the trama tissue is concerned these last two groups, which are regarded as related to each other, show striking resemblances to the Agaricales. Investigation of the stalk of certain *Ramaria* species showed that all the structures characteristic of the bulb of the Agaricales were also to be seen here (Pl. 36D, *Ramaria aurea* (Fr.) Quél.). The tissue of the branches in which the hyphae are parallel has, of course, been more closely investigated than that of the stalk. In young stages of *Cantharellus tubaeformis* the hyphae are loosely interwoven but their main direction or orientation is parallel. The tissue is not homogeneous, however; denser patches where the hyphae lie against one another alternate with thinner patches. The denser places often resemble hyphal knots and the cells are sometimes shorter. In *Cantharellus cibarius* such patches are more common in the interwoven cap trama than in the stipe, where the hyphae are approximately parallel. We (Reijnders, *1963*) were unable to study the basal plectenchyma because it had probably been cut off from the specimen.

The fact that the heteromerous trama of the Asterosporales may be regarded as a specialised instance of the trama of the Agaricales (and Gasteromycetes) in general also affects phylogenetic interpretations. Hyphal knots may be centres of intercalary cell formation. Frequently in young primordia of Agaricales groups of cells initiated in hyphal knots are formed. After inflation these knots become not spherocysts but ordinary hyphal cells. In the trama of the Agaricales, which do not belong in the Asterosporales, no spherocysts are found but there are many in the veils. In the veils they can be regarded as derived elements. The inflation that is so marked in the tissues of the Agaricales serves to increase the volume. The same occurs in the spherocysts of *Russula* and *Lactarius*, where the total volume of those elements is eventually much greater than that of the hyphae (Reijnders, *1963*: 272).

Although in the primordia of *Amanita* and *Limacella* structures of groups of small, round cells surrounded by coiled hyphae indeed occur, much of the increase in volume in these genera is also a result of numerous vesicular acrophysalides representing a special case of free-ending ramifications. Kühner, therefore, considered the Amanitaceae and the Russulaceae to be related. This relationship is based on the structure of the trama which in both families is derived from the original structure of the basal plectenchyma: in the one the cells formed by the hyphal knots are dominant, in the other the free hyphal extremities are dominant. In both families a large part of the carpophore is taken up by this tissue, while the part formed by the meristemoid of the cap margin is limited. Even so this resemblance between the Amanitaceae and the Russulaceae does not actually indicate a phylogenetic relationship; other Agaricales show the same structures, the proportions only being a little different. Singer (*1958*) and Smith (*1971*) proposed that the spherocysts originate from the cellular subhymenium of certain Gasteromycetes. Judging by the comparisons made in the present paper it is no longer necessary to find a special explanation for this origin of the so-called heteromerous trama; in the lamellae of

Russula both the spherocysts of the trama and the cells of the subhymenium are present (Reijnders, *1976*: pls. 14E, 15A) but apart from their different sizes they originate in different ways. According to Singer and Smith, spherocysts occur not only in the Asterosporales but also in the trama of several other hypogeal fungi, where they probably develop in the usual manner. This should be investigated more closely.

This study of the structure of the trama and underground parts also leads us to comment on the phylogeny of the Agaricales, Gasteromycetes, and Aphyllophorales. The dividing lines between these three groups—which are not natural taxa but only of practical value—are very vague. There exist Gasteromycetes which are much more closely related to Agaricales than to other Gasteromycetes. As it is known that Gasteromycetes also occasionally develop gymnocarpously, they can only be defined as Higher Basidiomycetes that do not eject their spores. That the demarcation between the Aphyllophorales and the Agaricales is also vague is demonstrated by Singer's (*1975*) inclusion of *Polyporus* in the Agaricales.

Moreover these groups are polyphyletic. For this reason it is pointless to attempt to show that the Agaricales are derived from the Gasteromycetes or vice versa. Much has been written about these interesting relationships, especially about the Asterosporales. We cannot cover the subject fully in this article. Our study of the ontogeny of both groups has led to certain general views which will be given below. Perhaps we shall have an opportunity to reconsider the whole problem in more detail at a later date.

(1) Basidia are complex organs which serve to produce the ballistospores. They would never have originated below ground level so that hypogeals with basidia must have derived from epigeals. If the first had undergone only development underground basidia would never have formed—only other sporulating structures. The question still remains whether fruitbodies with a peridium would have been formed. Though Singer & Smith (*1960*) reasoned that the spore-ejecting basidia of the Agaricales originated (by selection) from the spore forming cells of certain Gasteromycetes the fact that the Gasteromycetes show recognizable basidia, even in their underground forms, remains unexplained.

(2) In underground forms columellae are often present. These can be regarded (by comparison) as stipe rudiments, but a stipe cannot function underground. For what reason, therefore would they have developed?

(3) The underground Asterosporales often have bipolar, even gymnocarpous primordia (Reijnders, *1963*: 210–213). Those forms which developed underground would show a radial construction, bipolarity being of no use, and they would not be gymnocarpous.

(4) Like the stipe beneath the ground the spherocysts in the trama are also non functional. As previously stated, these should definitely be regarded as remnants of preceding development above ground level, their most important task being the enlargement of the carpophore (Reijnders, *1963*: 272, 360).

(5) Agaricales also often undergo a long period of underground development.

There they form bulbs inside of which a whole fruitbody develops, needing only to stretch to reach above ground and disperse the spores. It is less well known that the gymnocarpous primordia of *Russula* also remain hidden beneath ground level for some time. By the time the young growing specimens appear above the ground there are no longer any primordia in the vicinity (Reijnders, *1976*: 67).

At the time of Patouillard (1854–1906) it was thought that the Gasteromycetes were angiocarpous, the Agaricales hemiangiocarpous, and the Aphyllophorales gymnocarpous. It has since become apparent that this is not the case. One can say, however, that these three criteria are often applied to these groups. In the same way it can be said: Gasteromycetes: often completely subterranean; Agaricales: often partly subterranean; Aphyllophorales: usually not subterranean. In many cases it has been found that these subterranean parts are distinguished, initially at least, by a special structure. This structure also influences, to a greater or lesser extent, the trama of the parts above ground, which are not only formed by ramifying bundles of parallel hyphae. It is possible that a subterranean fruitbody might evolve to attain an above ground habit, that is a bulb could change into a stiped mushroom. It appears more probable, however, that an above ground mushroom would change into a subterranean form by growth retardation and reduction of the stipe; this has often been described.

Singer & Smith's (*1960*) most important objection to an evolution in the Asterosporales of agaricoid forms to gasteroid is that the different structures which could be explained by degradation are not correlated, i.e. that the typical *Russula* and *Lactarius* characteristics appear to a different extent and are scattered throughout the underground forms. Among these forms there is a distinction between different levels, new characteristics constantly being added; species of the genera of these levels may or may not have other characteristics. According to Singer & Smith this can be better explained by progressive evolution than by degradation.

We do not wish to exclude the possibility of progressive evolution. We do, however, object to the derivation of one recent form from another recent form. For the greater part the forms from which the recent Asterosporales are derived no longer exist. It is very probable that there was once a type of progressive evolution of agaricoid forms. Gasteroid forms could have appeared at any level of evolution. 'Gasteromycetation' does not seem to have taken up much time in the process of evolution. This is shown not only by the agaricoid forms, which start out with several subterranean characteristics, but also by the gasteroid anomalies of *Psilocybe* (See McKnight *in* Singer, *1975*.; Watling, *1971*). The structural difference is not so great because the main characteristics of the trama of the above and below ground parts can be the same. Only the external form changes, while some parts (meristemoid, formation of spherocysts) undergo reduction.

The fact that more primitive forms retained a gasteroid rather than an agaricoid form might be explained by the occupation of special niches by the gasteroid forms. This was previously discussed by Reijnders (*1971*). The appearance of new, further evolved types must have made the pressure of selection greater on the above ground

forms. More primitive forms may, therefore, still be present in a particular niche, giving the impression that the above ground forms actually developed from the gasteroid forms! The reverse may also occur; the subterranean form will have again adapted to an epigeous habit since the genes necessary for the development of the parts above ground will in many cases still be present. In general, however, 'gasteromycetation', with the degradation of certain characteristics only seems more probable.

Résumé

On trouve à la base du stipe dans les Agaricales le plectenchyme basal, qui peut s'élargir en formant un bulbe. Ce tissu, qui n'est pas homogène, est caractérisé par des structures particulières: des extrémités libres de ramifications, des hyphes sinueuses, des anses, des spirales et des anneaux qui peuvent renfermer une autre hyphe et des agglomérations d'hyphes dites: «nodules». Ces dernières sont en réalité des faisceaux d'hyphes, qui constituent souvent le centre de divisions cellulaires, ou bien elles se présentent sous la forme d'un groupe de cellules unies, entouré d'hyphes enroulées. Cette dernière structure qui se retrouve chez un grand nombre d'espèces d'Agaricales, se manifeste parfaitement dans la trame des Amanitaceae, qui rappelle celles des Russulaceae. La trame du jeune piléus de beaucoup d'espèces accuse souvent les mêmes particularités qui se présentent également dans le tronc des *Ramaria*, dans le jeune bulbe des Gastéromycètes et dans divers voiles.

Les différentes manières de la naissance des cellules dans les primordiums ont été étudiées en détail; la notion: «méristémoïde à hyphes» a été définie.

La trame hétéromère des Astérosporales et la trame des Amanitaceae dérivent de la jeune trame d'autres Agaricales.

Les tissus des bulbes des souches 59b et 59c de l'*Agaricus bisporus* ont été analysés. 59b est homologue au bulbe d'un carpophore normal d'*Agaricus bisporus*. En accord avec G. Fritsche, l'auteur est arrivé à la conclusion que 59c représente en outre «un type gigas». Les carpophoroïdes (formes aberrantes) de *Psilocybe merdaria* (décrites par Watling) ont été discutés.

Les différences fondamentales entre le développement des vrais Aphyllophorales, d'une part, et celui des Chanterelles des Agaricales et des Gastéromycètes, de l'autre, ont été considérées.

En ce qui concerne l'évolution au sein des Astérosporales, l'auteur raisonne qu'une dégradation de quelques caractères dans les formes gastéroïdes (Heim, Malençon) ne contrarie pas nécessairement les arguments qui ont été avancés par R. Singer et A. H. Smith. Une descendance de formes hypogées à partir de formes épigées est plus vraisemblable que l'inverse.

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EXPLANATION OF PLATES 32–37

ABBREVIATIONS USED IN PLATES. — m. s., microtome section; f. s., freehand section of mature material.

PLATE 32

Figs. A–H. *Agaricus bisporus*. Fig. A. strain 59b, m s.: young bulb, initiation of hyphal knots, spiral hyphae (s), rings, ×320; Fig. B. strain 59b, m. s.: more advanced stage, coiled hyphae, ×128; Fig. C. strain 59b, m. s.: cortex layer, ×128; Fig. D. strain 59c, m. s.: inflated tips (t), ×80; Fig. E. strain 59b, m. s.: inflated tip in the centre of a cell group surrounded by coiled hyphae (t), ×200; Fig. F. strain 59c, m. s.: rather advanced stage, hyphal knot (hk), cell division (c), dolipores, ×80; Fig. G. m. s.: rather advanced stage, sinuous hyphae (sh), loops, ×200; Fig. H. f. s.: tips of short branches (t), ×200.

PLATE 33

Figs. A, B. *Agaricus bisporus*. Fig. A. strain 59c, f. s.: spiral growth of hypha, enclosing another hypha (s), ×200; Fig. B. strain 59c, f. s.: ring (r) enclosing a hypha, ×200.

Fig. C. *Suillus aeruginascens*, m. s.: pileus trama of young stage with hyphal knots, ×200.

Figs. D, E. *Gyroporus cyanescens*. Fig. D., m. s.: young bulb, hyphal tip (t), coiled hyphae, straight hyphae (sh), ×200; Fig. E., m. s.: pileus trama of a young stage, hyphal knots, a knot surrounding an inflated tip (t), ×200.

Fig. F. *Chroogomphus rutilus*, m. s.: stipe of a young stage, hyphal knots with cells which are due to inflation (i), ×200.

PLATE 34

Fig. A. *Hygrophorus hypothejus*, m. s.: stipe of a young stage, basal plectenchyma with coiled hyphae (ch), hyphal knots (hk) and layer of inflating hyphae (i), ×200.

Fig. B. *Limacella guttata*, m. s.: bulbus of a rather young stage, spiral growth around a hypha (s), coiled hyphae, ×200.

Fig. C. *Amanita solitaria*, m. s.: upper part of the stipe of a rather advanced stage, large acrophysalides, coiled hyphae around hyphal knots, ×200.

Fig. D. *Amanita rubescens*, m. s.: somewhat advanced stage, upper part of the bulb (stem), hyphal knots, coiled hyphae (ch) and straight hyphae (sh), ×200.

Fig. E. *Chamonixia caespitosa*, m. s.: young bulb with hyphal knots (hk), ×200.

Fig. F. *Scleroderma aurantium*, m. s.: young bulb, initiation of hyphal knots (hk), ×200.

PLATE 35

Fig. A. *Pleurotus dryinus*, m. s.: veil of a young stage with hyphal knots, ×200.

Fig. B. *Cortinarius limonius*, m. s.: veil with hyphal knots (hk) of a rather young stage and matrix layer, ×200.

Fig. C. *Psathyrella candolleana*, m. s.: veil with matrix layer (ml), ×200.

Fig. D. *Coprinus macrocephalus*, m. s.: veil with matrix layer (ml), ×200.

Fig. E. *Volvariella bombycina*, m. s.: hyphal knots (hk) in the volva of a young stage, ×200.

Fig. F. *Scleroderma aurantium*, m. s.: hyphal knots (hk) in the exoperidium, ×200.

PLATE 36

Figs. A, B. *Coprinus macrorhizus*. Fig. A., m. s.: very young stage with differentiation into three zones: basal plectenchyma (bp), young cells of the stipe, and meristemoid (m), ×80;

Fig. B., m. s.: older primordium with intertwined hyphae of pileus trama (tr), surrounded by veil meristemoid (m) and stipe tissue (st), ×80.

Fig. C. *Boletus edulis*, f. s.: mature bulb, twisting hypha (s) enclosing other hypha (h), ×200.

Fig. D. *Ramaria aurea*, f. s.: mature trunk, hyphal knot (hk), ×200.

Fig. E. *Boletus satanas*, f. s.: club shaped extremity of hypha, ×200.

Figs. F, G. *Lycoperdon pyriforme*. Fig. F., f. s.: sinuous hypha (sh), tips (t), ×200; Fig. G., f. s.: spiral growth of hypha (s) enclosing another hypha, ×200.

Fig. H. *Agaricus osecanus* f. s.: short-celled tips (t), ×200.

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Figs. A, B. *Stereum sanguinolentum*. Fig. A., m. s.: young stage, intertwined generative hyphae (gh), ×32; Fig. B., m. s.: the same stage, margin, ×80.

Figs. C–E. *Irpex lacteus*. Fig. C., m. s.: young stage, width 2150 μm, ×32; Fig. D., m. s.: basis of the same young button with intertwined generative hyphae (gh), ×80; Fig. E., m. s.: development of teeth in the same button, ×200.

Fig. F. *Gloeophyllum abietinum*, m. s.: base of a young stage, intertwined generative hyphae (gh), ×20.

Fig. G. *Gloeophyllum odoratum*, m. s.: zonation of the trama, ×80.

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DIE STRUKTUREN DER BASIDIOSPORENWAND UND DES APIKULUS, UND DEREN BEZIEHUNG ZUR EXOGENISATION DER SPORE

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(Mit 4 Abbildungen und Tafeln 38–48)

Es ist möglich, aus den bisherigen Beobachtungen ein Grundschema der Sporenwand zu entwickeln und die bekannten Strukturen als davon abgeleitet zu verstehen. Die Sporenwand ist aus zwei im Elektronen-mikroskop verschieden aussehenden Substanzklassen aufgebaut, einem elektronenopaken und einem transparenten Material. Die beiden Substanzklassen sind mehr oder weniger vermengt oder entmischt und bilden auf diese Weise zwei Klassen von Tegumenten, das Eusporium und das Myxosporium. Die Tegumente unterliegen modifizierenden Faktoren wie Differenzierung und Reduktion. Die Exogenisation führt von der Endospore zur unechten Exospore und weiter zur echten Exospore. Als unechte Exospore wird eine morphologische Endospore, aber funktionelle Exospore bezeichnet. Die Apophysenwand ist am Aufbau der Sporenwand beteiligt. Deren Außenschicht wird zum Sporothecium, die Innenschicht wird, wenn sie verschleimt, Bestandteil des Myxosporiums, oder, wenn sie nicht verschleimt, des Eusporiums. Totale Reduktion der Sporenwand und Übernahme deren Funktion durch die Apophysenwand führen zur echten Exospore. Einige morphologische Beobachtungen lassen vermuten, dass die Spore aktiv vom Sterigma springt und nicht passiv von der Basidie weggeschleudert wird.

In diesem Aufsatz soll versucht werden, die bisher bekannten Strukturen der Sporenwände der Agaricalen auf eine gemeinsame Basis zu stellen und Entwicklungstendenzen zu beschreiben. Insbesondere wird gezeigt, wie die Basidiosporen verschiedene Stufen auf dem Wege zur echten Exospore erreicht haben.

DIE ERSTE STUFE DER EXOGENISATION

Der Begriff der Exogenisation

Eine der mykologischen Grundideen ist die Exogenisation von Zellen, die räumlich verbreitet werden sollen, also der Konidien (im weitesten Sinne) und der Sporen. Klassisches Beispiel liefern die Zygomyceten mit dem Übergang von Sporangien mit vielen Endosporen (Typ *Mucor*) zu Sporangiolen mit wenigen (*Blakeslea*) oder nur einer einzigen Spore (*Cunninghamella*). Endstufe dieser Ent-

wicklung sind die von echten Konidien kaum unterscheidbaren Sporen von *Mycotypha*. Nur ihre doppelte Wand verrät die Sporangiolen-Natur.

Die Exogenisation, der ‚Drang nach aussen', liegt auch der Basidiospore zugrunde. Sie kann jedoch weitergehen, indem die eigentliche Sporenwand reduziert wird und im Extremfalle verschwindet. Damit ist die Stufe der echten Exospore erreicht. Ich behaupte nicht, dass die ursprüngliche Sporocyte ein Ascus war.

Erstes Produkt der Exogenisation, das Resultat der ersten Stufe, ist eine exponierte (exogenisierte) Endospore (Abb. 1). Diese besitzt eine eigene Sporenwand und ist von einer blasigen Ausstülpung der Sporocyte, der Apophyse, umschlossen. Morphologisch sind solche Sporen durchaus noch Endosporen, funktionell hingegen Exosporen, da sich die Apophysenwand wie eine Schicht der Sporenwand benimmt und zusammen mit der Spore die Sporocyte (Basidie) verläßt. Man könnte eine funktionelle, jedoch nicht morphologische Exospore dieser Art eine unechte Exospore nennen.

Unechte Exosporen dieser Stufe bilden innerhalb der Apophyse eine vollständige Sporenwand aus. Zur Zeit der Ablösung vom Sterigma ist die Apophysenwand weitgehend verschleimt.

Schöne Beispiele unechter Exosporen sind die Sporen von *Cortinarius* und der Russulaceen.

Die Wand des Sterigmas und der Apophyse und deren Differenzierungen auf der ersten Stufe der Exogenisation

Die Basidienwand ist mehr oder weniger deutlich aus zwei Schichten aufgebaut. Eine innere, festere, im Elektronenmikroskop graue und kaum strukturierte Schicht ist von einer aufgelockerten, dunkleren und schleimigen Schicht bedeckt.

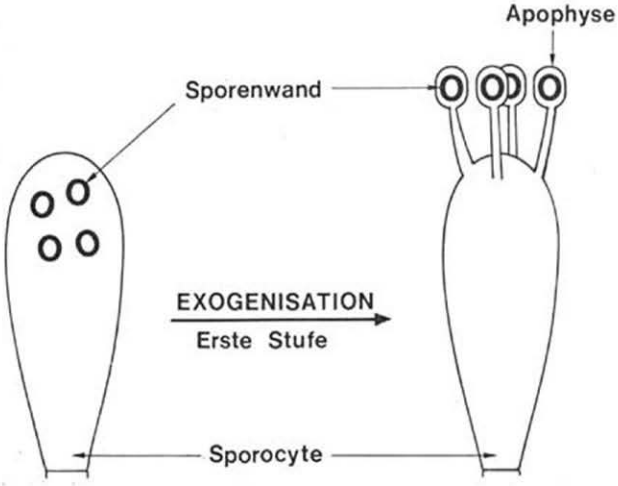

Abb. 1. Schema der Exogenisation, erste Stufe.

Die Sterigmenwand erscheint im Elektronenmikroskop homogen einschichtig und gegen außen scharf begrenzt. Die flockig-schleimige Außenschicht der Basidienwand verdünnt sich am Fusse des Sterigmas und wird unsichtbar (Taf. 38). Es kann nicht entschieden werden, ob sie auf dem Sterigma fehlt, oder ob sie so stark kondensiert ist, daß sie von der Innenschicht nicht mehr unterschieden werden kann.

Die Apophysenwand ist zunächst einschichtig, homogen und nach außen scharf begrenzt und entspricht genau der Sterigmenwand. Sehr bald aber können Veränderungen festgestellt werden. Zunächst tritt eine flockigschleimige Außenschicht auf. Es ist jedoch völlig unklar, ob es sich um eine Neubildung (Verschleimung) aus der nackten, homogenen Apophysenwand handelt, oder ob die äußere Schicht der Basidienwand hier wiederum sichtbar wird. Im ersten Fall sind die ganze Apophysenwand und ihre Differenzierungen nur der Innenschicht der Basidienwand homolog; im zweiten Fall ist die Apophysenwand der ganzen Basidienwand homolog.

Wie dem auch sei, die Apophysenwand ist frühzeitig in eine äußere und eine innere Schicht gegliedert, die sich während der Sporenreifung verschieden verhalten.

In den Schnitten durch Sterigma, Apikulus und Spore scheint die Sterigmenwand in die Sporenwand kontinuierlich überzugehen (Taf. 41A). Über der Sporenwand und von dieser getrennt durch das dünne, transparente Endosporothecium, liegt eine feine, heterogene, opake Schleimschicht, das Ektosporothecium. Beide zusammen bilden des Sporothecium, welches aus der äußeren Schicht der Apophysenwand hervorgegangen ist (Taf. 39A).

Die innere Schicht der Apophysenwand wird im Laufe der Sporenreifung stärker opak und verschleimt langsam, während die eigentliche Sporenwand daran angelagert wird (Taf. 39B). Die Anlagerung von Wandmaterial an die innere Schicht der Apophysenwand drückt sich in deren Verdickung aus, so dass die eigentliche Sporenwand und die innere Apophysenwand zu einer kontinuierlich aussehenden Einheit verschmelzen. Dies ist möglich, da die ersten Ablagerungen der Sporenwand ebenfalls schleimig oder gallertig sind. Die junge Apophyse ist in diesem Stadium im Lichtmikroskop stark cyanophil, was erfahrungsgemäß schleimigen oder gallertigen, elektronenopaken Schichten im Elektronenmikroskop entspricht.

Es sei gleich vorweggenommen, daß in der Endphase der zweiten Stufe der Exogenisation die innere Schicht der Apophysenwand nicht verschleimt und daß die ersten Ablagerungen der Sporenwand nicht oder kaum schleimig sind. Solche Apophysen sind acyanophil.

Die Differenzierungen der inneren Schicht der Apophysenwand sind also nicht überall die gleichen, sondern sind eng mit dem jeweiligen Stand der Exogenisation verbunden.

Allgemeine Struktur der Sporenwand und die Differenzierungen ihrer Tegumente auf der ersten Stufe der Exogenisation

Die Permanganat-Fixierung (Clémençon, *1973*) differenziert in der reifen Sporenwand zwei Arten von Substanzen, elektronenopake und elektronentransparente. Es ist unbekannt, ob es sich um je eine oder mehrere Substanzen handelt, doch ist

letzteres wahrscheinlicher. In Anlehnung an meine bisherigen Arbeiten (vor allem Clémençon, *1970*) werden die dunklen, opaken Substanzen Tunica-Material, die hellen, transparenten Corium-Material genannt.

Gleichzeitige Ablagerung von Coriummaterial und von Tunicamaterial (oder andere Vermengungs-Mechanismen), sowie mengenmäßige Unterschiede zwischen den beiden Materialien führen zu verschiedenartigen Mischungen. Sowohl die Proportionen, als auch die Art der Verteilung sind charakteristisch für die Vermengungen. Diese sind heterogen, und das dunkle Tunicamaterial befindet sich in gleichmäßiger oder ungleichmäßiger, grober bis feiner Suspension im hellen Coriummaterial verteilt.

Tritt das Coriummaterial in reiner Form auf, also ohne Beimischung dunklen Materials, so bildet es ein transparentes, homogenes Tegument, das Corium. In der Regel ist es eine innere Schicht, oft gegen das Cytoplasma grenzend und entspricht dann meist dem Endosporium der älteren Terminologie.

Wenn das Corium von dunklem Tunicamaterial durchsetzt ist, so sprechen wir von einem tunikisierten Tegument, welches Coriotunica genannt wird. Diese kann mehr oder weniger stark tunikisiert sein, so daß Zonierungen innerhalb der Coriotunica entstehen. Diese Zonen haben nicht den Wert von Tegumenten, denn sie gehören alle einem einzigen Tegument an. Solche Zonen brauchen weder vollständig, noch überall gleich dick zu sein, und sie können auf bestimmte Regionen beschränkt bleiben, oder unregelmäßig auftreten, oder auf kleine Flocken beschränkt bleiben. Als Beispiele seien *Pholiota* und *Kuehneromyces* genannt (Clémençon, *1974*; Taf. 39C).

Die Coriotunica ist weit verbreitet, und wegen ihrer relativ hohen mechanischen und chemischen Resistenz wird sie auch Sclerosporium genannt (Besson, *1970*; Besson & Kühner *1972*).

Corium und Coriotunica bilden die interne, feste und resistente Klasse der Tegumente, das Eusporium (Besson, *1972*).

Das Eusporium ist in vielen Fällen von einem weniger resistenten, meist gallertigen oder gar schleimigen Myxosporium bedeckt (Besson, *1972*). Bei manchen Sporen gelingt es, das Eusporium vom Myxosporium mechanisch zu trennen, indem die Sporen zwischen Deckglas und Objektträger gequetscht und gerieben werden (Taf. 39D, E).

Das Myxosporium entsteht aus der verschleimenden Innenschicht der Apophysenwand und daran zusätzlich angelagerten Mucosubstanzen. Die gesamte Schleimschicht, das primäre Mucostratum, wird vor der Synthese des Coriummateriales angelegt. In den meisten Fällen geht die Produkten von Mucosubstanzen auch nach dem Beginn der Coriummaterial-Synthese weiter. Auf diese Weise wird das transparente Coriummaterial von opakem Material durchsetzt. In der reifen Sporenwand kondensieren die Mucostratum-Partikel zum dispergierten Tunicamaterial der Coriotunica. Falls die Synthese des Coriummateriales nach Einstellung der Produktion der Mucosubstanzen weitergeht, entsteht als innerste Schicht des Eusporiums das Corium. Es ist wichtig zu verstehen, daß das Eusporium meist von myxosporialen Substanzen durchsetzt ist.

Das über dem Eusporium gelegene primäre Mucostratum wird während der Sporenreifung zum Myxosporium. Dieses kann in einer von vieren verschiedenen Formen auftreten, welche als verschiedene Tegumente gewertet werden.

(a) Die homogene, elektronenopake und verhältnismäßig feste Form des Myxosporiums ist die Tunica, wie sie bei *Rhodophyllus* auftritt (Taf. 40A). Sie ist eher selten und stellt eine Kondensation des primären Mucostratums dar. Ihr chemisches Verhalten, besonders die Löslichkeit in Kalilauge, charakterisieren dieses Tegument im Lichtmikroskop.

Die Tunica ist eine reine Form der Tunicasubstanz, wie sie auch in der Coriotunica vorkommt. In meiner ersten Arbeit über die Architektur der Sporenwände (Clémençon, *1970*), wird sie als eine von drei Grundtegumenten gewertet, und in meiner Zusammenstellung von 1973 (erschienen in Singer, *1975*) wird sie zum Eusporium gezählt. Dies ist ein Irrtum, bedingt durch die Verbindung Corium – Coriotunica – Tunica, wie sie in der reifen Spore zutage tritt. Die Ontogenie der Sporenwand lehrt uns nun, daß die opaken Substanzen zum Myxosporium gehören, und dass die Coriotunica, wie schon erwähnt, myxosporiale Elemente enthält. Das Grundschema der Sporenwand wird viel einfacher und verständlicher, wenn die Tunica zum Myxosporium gestellt wird.

Die Einstufung der Tunica als Myxosporium wird durch die Löslichkeit in Kalilauge bestätigt. Es ist auch diese Löslichkeit, welche Besson & Kühner überzeugte, daß die Außenschicht der *Rhodophyllus*-Sporen dem Myxosporium angehört (Besson, *1972*). Da ich damals die Tunica als zum Eusporium gehörend betrachtete, wurde die Bezeichnung Pseudotunica provisorisch vorgeschlagen (siehe Clémençon, *1974*). Diese fällt nun natürlich dahin.

(b) Weit häufiger ist die Epitunica, welche bei *Cortinarius* in Einzelheiten bekannt geworden ist (Clémençon, *1973*). Bei der Bildung einer vollständigen Epitunica spielen sich folgende Differenzierungen ab. Innerhalb der Apophyse wird zuerst das dunkle, primäre Mucostratum abgelagert. Nachdem eine bestimmte Dicke erreicht wurde, beginnt sich das Mucostratum an verschiedenen Stellen zu verfestigen und wird dabei zunehmend elektronentransparent. Auf der Oberfläche der Coriotunica bildet sich so eine dünne, helle und recht feste Schicht, das Podostratum, welches in Schnitten durch die Wand als feine, helle Linie die Coriotunica von der Epitunica trennt. Deshalb wurde das Podostratum auch als selbständiges Tegument aufgefaßt und Mediostratum genannt. Die viel voluminöseren, weniger transparenten und auch weniger harten Kondensationen in der Epitunica gehören dem Cerostratum an, so genannt wegen dessen wachsartiggallertigen Konsistenz. Diese Inseln reichen vom Podostratum bis oft zur Apophysenwand, können aber schmal und isoliert bleiben. Oder sie können größer werden, teilweise oder ausgedehnt anastomosieren oder zusammenfließen und nur isolierte Löcher frei lassen. Der Raum zwischen den Inseln oder Adern und die Löcher des Cerostratums sind einige Zeit mit dem Schleim des primären Mucostratums ausgefüllt. Mit zunehmender Reifung der Sporen vermindert sich dieser Schleim, und so werden die Warzen, Kreten oder

Löcher der Epitunica geformt. Ein weiterer Fall ist die Bildung von Höhlen, wie sie bei *Cortinarius*, besonders in der Untergattung *Phlegmacium*, häufig sind, oder wie sie sehr schön bei *Fayodia bisphaerigera* auftreten. Hier hat sich entlang der Apophysenwand eine dünne Schicht des primären Mucostratums verfestigt, so daß beim Schwund des Restschleimes eine Höhle auftritt, die von einer dünnen Decke des Cerostratums überdacht ist. Alle Oberflächen der Höhlen, Löcher und Warzen sind dauernd von einem dünnen Mucostratum bedeckt.

Neben diesen Formen der Epitunica, welche Ornamentationen bilden, kommt auch eine homogene Epitunica vor, die bei einigen glatten Sporen, z. B. bei *Galerina medullosa*, zu finden ist. Bei dieser Art ist das Cerostratum eine durchgehende, dicke, in das Mucostratum eingebettete Schicht mit nur wenigen, kleinen, helleren Kondensationen (Taf. 40B). Die solchermassen gleichmäßige Epitunica kann leicht mit einer Coriotunica verwechselt werden, aber die Auflösung in KOH oder in Chromtrioxid zeigt die Homologie mit der Epitunica der Cortinarien an.

(c) Eine weitere Differenzierung des primären Mucostratums ist das Holotectum, bestehend aus Tectum und Interstratum (Clémençon, *1970*). Das Tectum ist eine feste, elektronentransparente Schicht mit scholligem Aufbau. Die Schollen fügen sich in der Regel eng aneinander und können zum Teil zusammenfließen. Das restliche Mucostratum befindet sich zwischen dem Tectum und der zum Sporotheciun gewordenen äußeren Apophysenwand und heißt deshalb Interstratum. Von diesem dringen feine Adern zwischen die Schollen des Tectums, so daß dieses gegen die Oberfläche zu auf charakteristische Weise aufgelockert und geädert wird.

Es ist heute klar geworden, daß das Interstratum zum Tectum das gleiche Verhältnis hat, wie das Mucostratum zum Rest der Epitunica. Die Logik verlangt, daß das Interstratum mit der hellen Schicht zu einem einzigen Tegument vereinigt wird. Der Stabilität der Terminologie Willen soll die helle Schicht weiterhin Tectum genannt werden. So muß denn für das Tegument, 'Tectum+Interstratum' ein neuer Name gefunden werden. Es wird hier H o l o t e c t u m vorgeschlagen.

Das Tectum kann glatt sein ('Leiotectum'), oder es kann ausgeprägte Warzen und Kreten tragen, wie bei den Russulaceen.

(d) Die Leptotunica wurde von Capellano & Kühner (*1975*) eingeführt um eine opake, homogene, dünne, der Coriotunica direkt aufliegende Schicht der Sporen von *Pluteus* und *Volvariella* zu bezeichnen. Sie gleicht der Tunica im Aussehen, welche aber dicker und auf die Rhodophyllaceen beschränkt ist, und einen komplexeren Ursprung hat.

Die Leptotunica ist die opak und wahrscheinlich schleimig gewordene Innenschicht der Apophysenwand, die nicht durch sekundäre Schleimanlagerungen verdickt wurde.

Wir haben hier bereits einen Fall beginnender Reduktion der eigentlichen Sporenwand. Die Ablagerung von reinen Mucosubstanzen ist stark oder ganz reduziert, so daß das primäre Mucostratum dünn bleibt (dies ist bei der Tunica nicht der Fall). Die sekundären Mucosubstanzen werden gleich in die Coriotunica eingebaut.

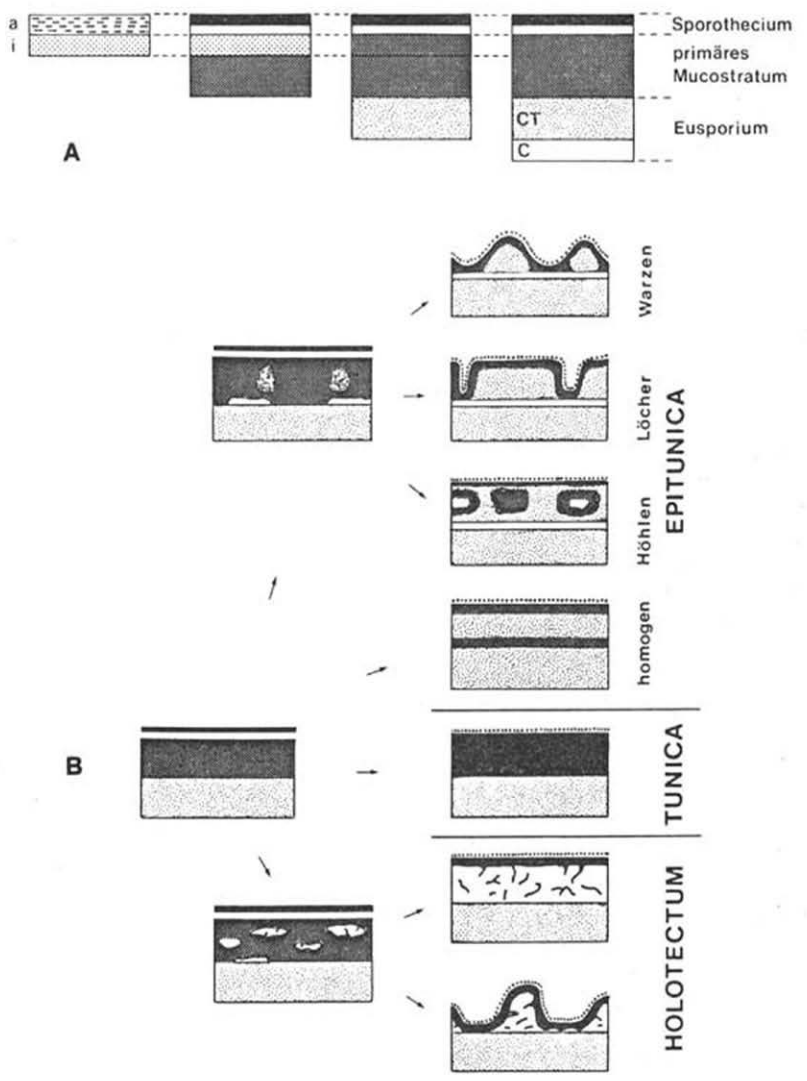

Abb. 2. Schema der Differenzierungen des primären Mucostratums. — A. Entstehung des primären Mucostratums aus der inneren Schicht (i) der Apophysenwand und der daran angelagerten Mucosubstanzen. Die äußere Schicht (a) der Apophysenwand wird zum Sporothecium. — B. Umwandlung des primären Mucostratums in das Myxosporium, das die Formen der Epitunica, der Tunica oder des Holotectums annehmen kann.

Das Ausbleiben eines verdickten primären Mucostratums führt zu Sporen mit reduziertem Myxosporium. Dies ist der erste Schritt zu einer weiterführenden Exogenisation.

Die Differenzierungen des primären Mucostratums und die sich daraus ergebenden Tegumente sind schematisch in der Abbildung 2 zusammengefaßt.

DIE ZWEITE STUFE DER EXOGENISATION. — REDUKTION DER SPORENWAND

Die zweite Stufe der Exogenisation führt von der unechten Exospore zur echten Exospore; die morphologische Endospore wird zur morphologischen Exospore. Die eigentliche Sporenwand wird reduziert und verschwindet im Extremfalle, und die Apophysenwand übernimmt die Funktionen der Sporenwand.

Die Reduktion der Sporenwand geht parallel mit einer entsprechenden Reduktion des Apikulus. Innerhalb der Agaricalen wurden verschiedene Grade der Reduktion erreicht, und es werden oft einzelne Tegumente stärker betroffen, als andere.

Auf der zweiten Stufe der Exogenisation werden drei Faktoren, nämlich die opaken Substanzen, die transparenten Substanzen und die Pigmente, unabhängig voneinander mehr oder weniger stark reduziert. Im folgenden werden einige Beispiele angeführt, die verschiedene Grade der zweiten Stufe der Exogenisation darstellen.

(a) In einem ersten Reduktionsschritt werden die Ablagerungen der opaken Substanzen an die Apophysenwand verringert oder unterdrückt. Das Myxosporium besteht dann aus einer dünnen, manchmal unregelmäßigen Schleimschicht oder aus einer Leptotunica.

Dieser Grad der Reduktion des Myxosporiums wird von einigen miteinander nicht enger verwandten Agaricalen erreicht, deren Eusporium verschiedene Strukturen zeigt. Bei vielen Coprinaceae bedeckt eine Leptotunica das gut ausgebildete und stark pigmentierte Eusporium (Taf. 41A), bei *Tubaria dispersa* und *Lyophyllum fumatofoetens* finden wir ein unregelmäßiges Mucostratum, das die schleimigen bis gallertigen Ornamentationen der Sporenwand bildet (Taf. 41B, 42, 43).

Es ist schwierig, oft sogar unmöglich, in den Schnittbildern reifer Sporen eine Leptotunica von einer äußeren, stark mit opaken Substanzen durchsetzten Zone der Coriotunica zu unterscheiden. In solchen Fällen können die Homologien mit den Schichten der Apophysenwand durch Untersuchung junger Sporen und deren Sterigmen erkannt werden. Es sollte auch möglich sein, durch differenzierende Ätzung das Myxosporium selektiv wegzulösen und solche Sporen mit intakten zu vergleichen.

(b) In einem weiteren Reduktionsschritt verschwindet das Myxosporium, nicht aber das Sporothecium. Die Innenschicht der Apophysenwand wird Bestandteil des Eusporiums. Bei *Inocybe*-Arten wird eine normale und heterogen strukturierte

Coriotunica direkt an die nicht verschleimende Apophysenwand angelagert. Die Apophysenwand wird zur Coriotunica verdickt, und in den Schnitten erscheint eine Kontinuität der Sterigmenwand mit dem Eusporium. Bei den Inocyben ist die Pigmentation reduziert, und das Sporothecium liegt direkt dem Eusporium auf (Taf. 44A).

(c) Eine weitere Reduktion der Pigmente führt zu farblosen Sporen. Bei *Lepiota*-Arten z. B. besteht die Sporenwand aus einer dicklichen bis dicken, schwach tunikisierten und pigmentlosen Coriotunica (Taf. 44B). Hier ist also die Synthese der opaken Substanzen und der Pigmente, nicht aber (oder nur wenig) die der transparenten Substanzen reduziert.

(d) Bei *Tubaria furfuracea* hat das Gegenteil stattgefunden. Das Eusporium ist durch die Vorherrschaft der opaken Substanzen gekennzeichnet. Die innere Apophysenwand wird opak und wahrscheinlich gallertig-schleimig. An diese Schicht wird nun das Eusporium angelagert, das aber reich an opaken, arm an transparenten Substanzen ist. Apophysenwand und Eusporium verschmelzen zu einer Einheit. Das so entstandene Eusporium ist eine sehr stark von opaken Substanzen durchsetzte, dünne Coriotunica in welcher ebenfalls die Pigmente reduziert sind (Taf. 44C). Wände solcher Bauart sind zart und mechanisch leicht verformbar, und auch chemisch nicht sehr widerstandsfähig.

(e) Eine dünne, pigmentlose, schwach tunikisierte Coriotunica ohne Myxosporium kommt bei einigen Pilzen mit farblosen, dünnwandigen Sporen vor, so bei *Leucocortinarius bulbiger* und bei *Amanita fulva* (Taf. 44D, E).

(f) Bei anderen dünnwandigen und farblosen Sporen ist sowohl das Myxosporium, als auch das Eusporium verschwunden. Die persistente Apophysenwand ersetzt die Sporenwand. Solche Sporen finden wir z. B. bei *Hydropus subalpinus*, *Mycena galopus*, *Oudemansiella* (?) *platyphylla* und vielen weiteren Tricholomataceen (Taf. 44F, G).

Die Phasen der zweiten Stufe der Exogenisation sind in der Abbildung 3 schematisch zusammengefaßt.

APIKULUS, PUNCTUM LACRYMANS UND SPORENABSPRUNG

Es besteht immer noch eine milde Kontroverse um die korrekte Bezeichnung des Stielchens, mit welchem die Spore dem Sterigma aufsitzt, obschon sie bereits von Josserand (*1952*) gut diskutiert wurde. Er entschied korrekt für ‚Apikulus', und ihm folgten Kühner & Romagnesi (*1953*), Horak (*1968*) und Clémençon (*1973*), während Pegler & Young (*1971*) ‚Hilarappendix' vorziehen. Falsch ist es, Hilum zu sagen, denn so wird die Ablösungsstelle des Apikulus (Narbe oder Loch) genannt. Das hohe Auflösungsvermögen des Elektronenmikroskopes verlangt diese Unterscheidung.

MORPHOLOGIE DES APIKULUS AUF DER ERSTEN STUFE DER EXOGENISATION

Der Apikulus dickwandiger Sporen (unechter Exosporen) ist anders gebaut, als der dünnwandiger, echter Exosporen. Dies hängt mit der besprochenen Reduktion der Tegumente in der zweiten Stufe der Exogenisation zusammen. Zuerst wird der Apikulus der dickwandigen Sporen besprochen, der noch nicht durch Reduktionen markiert ist.

Der vollständige Apikulus setzt sich aus Apikularwand, Apikulardeckel und Apikularmark zusammen (Clémençon, *1973*). Die Wand ist vom Myxosporium und Sporothecium bedeckt und besteht aus den äußeren Teilen, der Deckel aus den inneren Teilen der Coriotunica. Wand und Deckel bilden zusammen einen meist konischen Hohlraum, in welchem sich das schleimige bis gallertige Mark befindet. Einem Sporenpulver entnommene Sporen haben den Apikularraum nur teilweise mit Mark gefüllt, wobei dieses gegen den Deckel hin zu finden ist, beim Hilum hingegen fehlt. Deshalb stehen die verdünnten Apikularwände über, und es wird ein Loch sichtbar. Es hängt von der Höhe der frei überstehenden Wand und deren Festigkeit oder Schlaffheit ab, ob die Wände aufstehen oder zusammenfallen.

PUCTUM LACRYMANS UND SPORENABSPRUNG

Allgemein wird angenommen, die Spore werde bei ihrer Reife passiv abgeschleudert. Man spricht von Sporenabwurf oder Projektion der Sporen. Die wichtigsten dabei beobachteten Ereignisse sind die Ausscheidung eines Tropfens (Fayod, *1889*: 272; Buller, *1922*) oder einer Gasblase (Olive, *1964*), und darauf wurde versucht, eine Theorie der Sporenprojektion zu konstruieren (Salive, *1965*). Neuerdings wurden auch die seit Buller (*1909*) bekannten elektrostatischen Ladungen der Sporen zur Erklärung herbeigezogen (Leach, *1976*).

In einer interessanten Arbeit von van Niel *& al.* (*1972*) wurde vorgeschlagen, daß die Spore aktiv vom Sterigma springt. Die dabei auftretende Blase am Apikulus wird als Gasblase, nicht als flüssiger Tropfen angenommen.

Der Tropfen aber ist nicht eine Täuschung, wie Olive (*1964*) und van Niel *& al.* (*1972*) annehmen, sondern er existiert tatsächlich. Er ist aber nicht mit dem Sporenabsprung verknüpft, sondern wurde von Hugueney (Dissertation, 1978) bei *Coprinus* schon in frühen Phasen der Sporenreifung bei noch farblosen oder schwach gefärbten Sporen beobachtet. Nach seinen Untersuchungen dient eine besondere, stark differenzierte Stelle der dorsalen Seite des Apikulus der Ausscheidung des Tropfens. Diese Stelle ist das Punctum lacrymans (Hugueney, *1972*).

Das Punctum lacrymans kann mehrere Tropfen nacheinander ausscheiden. Seine Funktion liegt (nach Hugueney) in der Entwässerung des Cytoplasmas der reifenden Spore. Dies ist in guter Übereinstimmung mit den interferenzoptischen Messungen von Knecht (*1975*) an den Sporen von *Tricholomopsis rutilans*, die einen Wassergehalt von nur 23,8 $\pm$ 0,1 % aufweisen (berechnet nach den Angaben in Knechts Tabelle).

Das Punctum lacrymans von *Psathyrella subatrata* ist eine Differenzierung der

Leptotunica (Taf. 45A). Über das Punctum lacrymans der Pilze aus anderen Familien weiss man noch nichts oder nur sehr wenig.

Gestützt auf die beschriebenen Beobachtungen und Interpretationen gebe ich folgende, zum Teil hypothetische Beschreibung des Sporenabsprunges. Die Apophyse besitzt zuerst einer zwar dünne, doch feste Wand innerhalb derselben die Sporenwand aufgebaut wird, oder die zur Sporenwand wird (je nach der Stufe der Exogenisation). Mit zunehmender Reifung bildet sich der Apikulus aus, der oben vom Apikulardeckel verschlossen, gegen das Sterigma jedoch offen ist. Das Sterigma wird seinerseits gegen den Apikulus durch einen Pfropfen verschlossen. Die Spore wird, auf der ersten Stufe der Exogenisation, nur durch die modifizierten Schichten der Apophysenwand, also durch das Sporothecium und das Myxosporium, an das Sterigma gebunden. Während der Reifung wird durch das Punctum lacrymans Wasser ausgeschieden und das Cytoplasma der Spore kondensiert. Im Apikulus, zwischen Apikulardeckel und Sterigmapfropfen, entsteht im Mark ein gasgeladener Schleim unter relativ hohem Gasdruck (nach van Niel *& al.*, *1972*, um die 5 atm.). Es kommt nun der Augenblick, wo die Festigkeit der zunehmend verschleimenden Apo-physenwand, auch in der zweiten Stufe der Exogenisation, dem steigenden

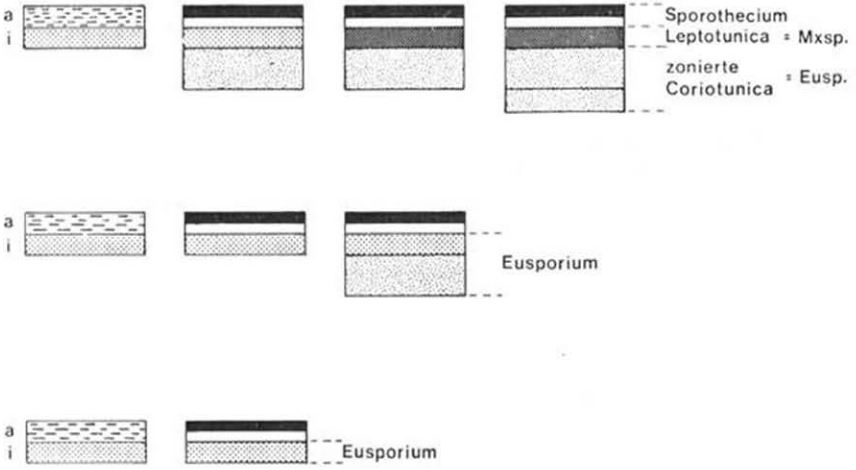

Abb. 3. Schema der zweiten Stufe der Exogenisation. Oben: die innere Schicht (i) der Apophysenwand wird zur Leptotunica, eine gut ausgebildete Coriotunica wird daran angelagert. Diese Stufe kann auch als letzte Phase der ersten Stufe der Exogenisation gewertet werden, wie das im Text geschah. Mitte: Die innere Schicht der Apophysenwand bleibt fest, das Eusporium wird daran angelagert, (i) wird Teil des Eusporiums. Unten: Die Anlagerung von Eusporium-Material unterbleibt, die Apophysenwand übernimmt die Funktionen der Sporenwand.

Druck nicht mehr gewachsen ist. Es bildet sich so die Gasblase und gleich darauf zerreißt die Apikularwand an ihrer dünnsten Stelle, d. h. über dem Sterigmapfropfen. Es ist durchaus möglich, daß das Punctum lacrymans die Riß-Stelle vormarkiert. Der unter Druck stehende Inhalt des Apikulus tritt rasch aber unvollständig aus, und durch einen Raketen-Effekt springt die Spore ab. Der Apikularinhalt ist aber nicht trockenes Gas, sondern besteht aus einer schleimigen Gaslösung, vielleicht einem Schaum. So kommt es, daß die abspringende Spore durch den Ablösemechanismus benetzt wird. Der Schub ist anfänglich recht groß, die Spore beschleunigt rasch, aber infolge des sehr beschränkten Volumens des Apikularmarkes dauert der Schub nur sehr kurze Zeit.

Diese Absprung-Hypothese wird durch die Morphologie des Apikulus, das Auftreten des Tropfens und der Gasblase und der Tatsache unterstützt, dass bei hohem Druck keine Sporen von den Sterigmen springen (Ingold & Dann, *1968*).

Es wird meist angenommen, daß Sporen aus einem Sporenpulver, also abgesprungene Sporen, reif sind. Dies wird wohl vielfach der Fall sein, doch sind die Entwicklung des Ablösemechanismus und die Wandsynthese nicht immer korreliert. Vielleicht sind auch andere Reifungsprozesse zur Zeit des Sporenabsprunges nicht vollständig durchgeführt. Ein schönes Beispiel für eine nach dem Absprung weitergehende Wandsynthese und Differenzierung finden wir bei *Hebeloma sinapizans*. Im Sporenpulver einer Kollektion dieser Art wurden von glatten bis stark ornamentierten Sporenwänden zahlreiche Übergänge gefunden (Taf. 45B, C).

Im Jahre 1969 haben Pegler & Young aufgrund Rasterelektronenoptischer Untersuchungen zwei Hilum-Typen unterschieden: den ‚nodulose type' und den ‚open pore type'. Letzterer ist mit großer Wahrscheinlichkeit aus Hilum und Punctum lacrymans zusammengesetzt (Hugueney, *1975*).

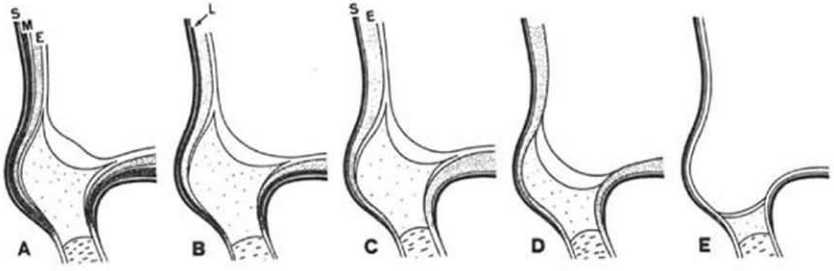

Abb. 4. Schema der Phasen der zweiten Stufe der Exogenisation. — A. Voll ausgebildetes Myxosporium (M) und Endosporium (E). Differenzierungen des Myxosporiums nicht berücktichtigt. S = Sporothecium. — B. Myxosporium reduziert auf eine Leptotunica (L). — C, D. Ohne Myxosporium. — C. Voll ausgebildetes Eusporium. — D. Reduziertes Eusporium, das 'Endosporium' ist auf den Apikulardeckel beschränkt. — E. Eusporium nur noch als Apikulardeckel rudimentär vorhanden. Die Apophysenwand hat die Funktionen der Sporenwand übernommen.

MORPHOLOGIE DES APIKULUS WÄHREND DER ZWEITEN STUFE DER EXOGENISATION

Die Reduktion des Eusporiums auf der zweiten Stufe der Exogenisation, wie sie im diesbezüglichen Abschnitt beschrieben wurde, hat auch eine Modifikation der Apikularstruktur zur Folge (Abb. 4).

Der Apikulardeckel und die Apikularwand werden vom Corium oder der innersten Zone der Coriotunica gebildet. Mit der Reduktion des Eusporiums werden diese Zonen ebenfalls zurückgebildet, bis davon nur noch ein dünner Apikulardeckel vorliegt, der wie in die Sporenwand eingehängt erscheint. Zugleich verschiebt er sich sterigmawärts, und der Apikulus wird zum Teil mit Cytoplasma der Spore gefüllt. Einige Beispiele mögen dies erläutern.

Bei *Pholiota caespitosa* (Taf. 46A) wird der linsenförmige Apikulardeckel von der inneren, durchgehenden Zone der Coriotunica gebildet. Die Apikularwand ist im oberen Teil von der Coriotunica bedeckt. Entspricht der Zeichnung C der Abbildung 4.

Bei *Agaricus abruptibulbus* (Taf. 46B) ist die innerste Zone der Coriotunica nicht durchgehend, sondern auf den Apikulardeckel beschränkt. Die Coriotunica bedeckt die Apikularwand.

Bei *Tubaria furfuracea* (Taf. 46C) beschränkt sich die innere, helle Schicht der Coriotunica auf den Apikulardeckel. Weder die Sporenwand, noch die Apikularwand sind von einer homologen Schicht bedeckt. Entspricht der Zeichnung D der Abbildung 4.

Bei *Hygrophorus melizeus* (Taf. 46D) ist der Apikulus vom Cytoplasma der Spore erfüllt. Der Apikulardeckel beschränkt sich auf einen dünnen, eingehängten Schild. Entspricht der Zeichnung E der Abbildung 4.

DIFFERENZIERUNGEN DES SPORENSCHEITELS

Viele Sporen, vor allem die dünnwandigen, weisen keine Scheitel-Differenzierung auf. Bei anderen Basidiosporen, besonders vielen dickwandigen, werden lichtoptisch seit 1866 der Keimporus (de Bary, *1866*: 127) und seit 1931 der Kallus (Heim, *1933*: 55) unterschieden. (Tulasne, *1853*, hat ‚pore germinatif' für Rostsporen gebraucht).

Die Scheitel-Differenzierungen vieler Sporen wurden von Meléndez-Howell (*1962*) elektronenoptisch untersucht. Die Autorin unterscheidet 6 verschiedene Strukturen, die im Text allgemein als ‚différenciations', seltener als ‚pore germinatif' beschrieben werden, und nur am Schluß wird des Kallus erwähnt (l. c.: 591): „Le terme de cal répondrait bien à certains pores de nos types δ et ω, ..."

KEIMPOREN

Die porusförmige Scheiteldifferenzierung kann sehr eng bis sehr breit, gerundet oder gestutzt sein und kann sich sogar im vorgezogenen Scheitel befinden. Charakteristisch ist, daß die Tegumente in dieser Scheitelzone (oft verhältnismäßig brüske)

Veränderungen ihrer gegenseitigen Proportionen aufweisen, aber in ihrer Feinstruktur nicht verändert sind (Beispiel Taf. 47B; vgl. Clémençon, *1974*).

Papillen

In der Arbeit von Meléndez-Howell (*1962*) werden keine Cortinarien untersucht. Die papillenförmige Scheiteldifferenzierung vieler Cortinariensporen weist eine besondere Struktur auf, die vielleicht teilweise der Struktur ω von Meléndez-Howell entspricht.

Das Besondere an der Papille besteht darin, daß eine Veränderung der Feinstruktur der Tegumente auftritt. Diese sind schwammig-schaumig bis löcherig aufgedunsen (Taf. 47A). Es ist aber zu bemerken, daß diese Veränderungen auch an flachen Scheiteln auftreten können, wo sie lichtoptisch kaum oder nur als im Brechungsindex veränderte Stelle gesehen werden können (Clémençon, *1973*).

Kallus

Es besteht eine gewisse Unsicherheit darüber, was der Heim'sche Kallus eigentlich ist, und in der auf lichtoptischen Beobachtungen beruhenden Literatur können drei einander oft widersprechende Auffassungen gefunden werden.

(a) De Kallus wird als dünne Stelle verstanden. Singer (*1975*): „a thinner-walled apical region that is more or less convex or even callously protracted rather than truncate." Smith & Singer (*1964*: 6): „... the existence of a callus (thin spot) ...", Moser (*1967*): „dünnwandige, konvexe (nicht abgestutzte) Stelle der Sporenwand am apikalen Ende."

(b) Der Kallus wird auch der apikalen Papille vieler Cortinariaceen gleichgestellt. Singer (*1975*) schreibt für *Hebeloma*: „with a callus at the apex", für *Rozites* „without germ pore but more or less mucronate with a callus", für *Cortinarius* „without a germ pore but often with a distinct callus." In diesem Sinne wurde die Scheitelpapille von *Cortinarius* auch von Clémençon (*1973*) als Kallus bezeichnet, was von Kühner (mündlich) beanstandet wurde.

Es sei bemerkt, daß viele *Hebeloma*-Arten eine Papille, andere aber einen Kallus aufweisen, aber man ist geneigt, die Papille als Kallus zu bezeichnen, da *Hebeloma* eine Cortinariacee ist und die einzige europäische Art von *Rozites* eine deutliche Papille hat.

(c) Die Abgrenzung des Heim'schen Kallus gegenüber dem Keimporus wird als schwierig und unsicher empfunden. Singer (*1975*) schreibt: „Undoubtedly, the transition from a callus to a pore is not quite a sharp one." Kühner & Romagnesi (*1953*): „différenciation ... qui peut être comparée au pore germinatif, mais qui est sensiblement moins large et plus difficilement visible...." Josserand (*1952*): „ce terme ... désigne une sorte de pore étroit et surtout mal individualisé".

In der Erstbeschreibung („Definition") des Kallus braucht Heim (*1931*: 55) Bezeichnungen wie „discontinuité", „réfringence différente" und „disposition caractéristique", die nichts über die Struktur des Kallus aussagen. Als Beispiele werden *Pholiota carbonaria* und *Hebeloma radicosum* genannt.

Das Elektronenmikroskop zeigt, daß die Sporenscheitel von *Pholiota carbonaria* (Taf. 48A) und von *Hebeloma radicosum* (Taf. 48B) von innen her verdünnt sind. Das Cytoplasma ist papillenförmig in eine entsprechende Vertiefung der Sporenwand vorgezogen.

Diese Struktur hat eine gewissen Ähnlichkeit mit der porusförmigen Scheiteldifferenzierung, so dass kaum ein fundamentaler Unterschied zwischen Kallus und Porus besteht, es sei denn, die vom Cytoplasma ausgefüllte Verdünnung der Sporenwand werde als fundamental betrachtet.

Von allen bereits zitierten lichtoptischen Beschreibungen treffen nur diejenigen zu, die eine dünne Stelle für wesentlich halten. Die Papillen der Cortinariaceen sind keine Kallen.

Die Scheiteldifferenzierungen können zusammenfassend in zwei Klassen und drei Gruppen gegliedert werden.—

(1) Differenzierungen ohne wesentliche Veränderung der Feinstruktur:
  (1a) Porus, ohne merkliche Verdünnung von innen her.
  (1b) Kallus, mit einer merklichen Verdünnung der Wand von innen her.
(2) Differenzierungen mit wesentlicher Veränderung der Feinstruktur,
  (2a) Papillen, mit schaumig bis löcheriger Veränderung der Tegumente.

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Summary

In an attempt to find the basic architecture underlying the known structures of the basidiospore walls some developmental patterns of the formation and reduction of the wall teguments are described.

Spore walls are built from two classes of substances differing in their aspect in the electron microscope: an electron dense material and an electron transparent material. These two classes, by mixing and separation, form two classes of teguments, the eusporium and the myxosporium. The teguments are modified by differentiation and reduction processes.

A processus called exogenisation leads from an endospore to a false exospore and

eventually to a true exospore. A false exospore is morphologically an endospore but functionally an exospore. The wall of the apophyse contributes to the formation of the spore wall. The external layer becomes the sporothecium, the internal layer contributes to the myxosporium if it gelatinizes or to the eusporium if it does not gelatinize. Total reduction of the true spore wall leads to a replacement of the spore wall by the apophyse wall and thus to a true exospore.

Some morphologic observations suggest that the basidiospore is not projected by the basidium, but that it actively jumps off the sterigma.

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ERLÄUTERUNGEN DER TAFELN 38–48

TAFEL 38

Übergang der Basidienwand in die Sterigmenwand: Verschwinden der äußeren, schleimigen Schicht. *Psathyrella subastrata*, × 33.000.

TAFEL 39

Fig. A. Sporothecium mit Endo- und Ektosporothecium (oberer und unterer Pfeil). *Agrocybe splendida*, × 100.000.

Fig. B. Anlagerung der eigentlichen Sporenwand (Pfeil) and die Apophysenwand. *Lepista sordida*, × 50.000.

Fig. C. Unregelmäßig gezonte Coriotunica, *Pholiota* (*Kuehneromyces*) *caespitosa*, × 25.000.

Fig. D, E. Mechanisch getrennte Eusporien und Myxosporien. *Hebeloma mesophaeum*, × 1600. — Fig. D. Phasenkontrast. — Fig. E. Hellfeld, Toluidinblau, Endosporium gefärbt und am unteren Ende aufgesprungen. C = Cytoplasma, E = Endosporium, M = Myxosporium.

TAFEL 40

Fig. A. Tunica, *Rhodophyllus incanus*, × 50.000.

Fig. B. Homogene Epitunica von *Galerina medullosa*, eine glattsporige Art, × 50.000.

TAFEL 41

Fig. A. Sterigma und basaler Teil der noch unreifen Spore von *Psathyrella subatrata*, × 50.000 Die äußere Schleimschicht tritt wieder auf, und die Sterigmenwand ist in die dunkle Leptotunica fortgesetzt. Die Coriotunica wird gegen innen vom Plasmalemma begrenzt.

Fig. B. Unregelmäßiges Mucostratum, *Tubaria dispersa*, × 30.000.

TAFEL 42

Unregelmäßiges Mucostratum, *Tubaria dispersa*, × 10.000.

TAFEL 43

Unregelmäßiges Mucostratum, *Lyophyllum fumatofoetens*, × 10.000.

TAFEL 44

Fig. A. Lockeres, flockiges Sporothecium, direkt auf der Curiotunica aufliegend. *Inocybe geophylla*, × 50.000.

Fig. B. Lockeres Sporothecium, direkt auf der Coriotunica aufliegend. Die äußerste Zone der Coriotunica ist stärker tunikisiert und erscheint deshalb dunkler. *Lepiota cristata*, × 50.000.

Fig. C. Stark tunikisierte, fast gallertige Coriotunica von *Tubaria furfuracea*, × 50.000.

Fig. D. Nackte, schwach tunikisierte Coriotunica von *Leucocortinarius bulbiger*, × 50.000.

Fig. E. Zwei sich berührende Sporen von *Amanita fulva*, × 50.000. Coriotunica schwach tunikisiert und pigmentlos. Die dünnen Sporothecien verschmelzen beim Kontakt.

Fig. F. Reife Spore von *Hydropus subalpinus*, × 50.000. Die eigentlichte Sporenwand ist durch die persistente Apophysenwand ersetzt worden.

Fig. G. Reife Spore von *Oudemansiella* (*Tricholomopsis?*) *platyphylla*, × 50.000. Die eigentliche Sporenwand ist durch die persistente Apophysenwand ersetzt worden.

TAFEL 45

Fig. A. Punctum lacrymans, eine Differenzierung der Leptotunica bei *Psathyrella subatrata*. P. L. = Punctum lacrimans, ST = Sterigma, SP = Spore. Vgl. Tafel 41A, die eine andere Schnittebene darstellt und das Punctum lacrimans auf der rechten Seite tangiert.

Figs. B, C. Verschiedene Ausbildungs-Stadien der Epitunica bei Sporen aus frisch abgefallenem Sporenpulver von *Hebeloma sinapizans*, × 50.000.

TAFEL 46

Figs. A–D. Apikularstrukturen verschiedener Stufen der Exogenisation, × 50.000.— Fig. A. Voll ausgebildete Struktur mit Myxosporium und Endosporium. Der Apikulardeckel setzt sich allseitig in ein ‚Endosporium' fort. *Pholiota* (*Kuehneromyces*) *caespitosa*. — Fig. B. Eusporium reduziert. Apikulardeckel setzt sich nicht seitlicht fort, und wirkt wie eingehängt. *Agaricus abruptibulbus*. — Fig. C. Die Synthese der elektronentransparenten Substanz ist stark reduziert, die Coriotunica wird dadurch weich und dunkel. Nur der Apikulardeckel ist schwächer tunikisiert und ist auf den Apikulus beschränkt. *Tubaria furfuracea*. — Fig. D. Letzte Stufe der Exogenisation. Das Eusporium ist nur noch als schlecht individualisierbarer Apikulardeckel zu finden (Pfeil). Die Sporenwand wurde durch die persistente Apophysenwand ersetzt. *Hygrophorus melizeus*. Vgl. Tafel 44G.

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Fig. A. Beispiel einer Papille. *Cortinarius orechalcius*, × 50.000.

Fig. B. Beispiel eines Porus. *Pholiota* (*Kuehneromyces*) *bridgei*, × 50.000.

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Fig. A. Kallus von *Pholiota carbonaria*, × 50.000.

Fig. B. Kallus von *Hebeloma radicosum*, × 50.000.

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A KEY TO THE SPECIES OF MORTIERELLA

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A key is provided covering only those species of *Mortierella* of which living cultures are available and which are recognized as specifically distinct. Two subgenera, *Micromucor* subgen. nov. and *Mortierella*, and nine sections in the latter are distinguished. The recognized species are listed with some new synonymies and bibliographic documentation. Three species which were invalidly published by Linnemann in 1936 are validated.

After Linnemann's (*in* Zycha & Siepmann, *1970*) and Mil'ko's (*1974*) fairly complete compilations of the species so far described in *Mortierella*, it now seems inappropriate and premature to provide another revision of the genus. This key is mainly written for practical purposes, arising from the need to provide a concise survey of the recognized species. It covers the species of which living cultures are available and which are considered sufficiently distinct to deserve a specific status. A considerable number of species has not been found again since their original description and their status is somewhat doubtful; others are considered to be synonyms of recognised species from their diagnosis and yet others have been synonymized on the basis of available type cultures and, further, some species are not recognized because they have not been validly published. All these taxa have been omitted from this key.

The species grouped around *Mortierella ramanniana* (Möller) Linnem. and *M. isabellina* Oudem. with velvety growth and mostly pigmented sporangia form a distinct group without affinity to other species of the genus. They deserve distinction at a higher than sectional rank but are retained in *Mortierella* for the time being as long as it cannot be decided objectively whether they belong to the Mortierellaceae A. Fischer or rather the Mucoraceae Dumort.

Mortierella subgen. **Micromucor** W. Gams, *subgen. nov.*

Mucor sect. *Ramannianus* Zycha *in* Krypt.-Fl. Brandenb. **6**a: 57. 1935 (nom. inval.; Intern. Code Bot. Nomencl., ed. 1972, Art. 36).

Mucor sect., *Micromucor* Naumov, Opredel. Mukorovykh (Mucorales) (Izd. 2): 27. 1935 (nom. inval., Art. 36).

Mortierella isabellina group Turner *in* Trans. Br. mycol. Soc. **46**: 262. 1963 — *Mortierella* sect. *Isabellina* Linnem. *in* Zycha & Siepm., Mucorales: 156. 1970 ('1969') (nom. inval., Art. 36).

MISAPPLIED: *Mortierella* sect. *Pusilla* Linnem., Mucorineen-Gatt. *Mortierella*: 16. 1941 (*M. pusilla* Oudem., a species of doubtful identity, obviously does not belong to this group).

Coloniae velutinae nec arachnoideae, non distincte olentes. Sporangiophora erecta, plus minusve ramosa; sporangia plerumque rubra vel ochracea, pluri- vel unispora, columella parva praesente vel absente. Species typica *Mortierella ramanniana* (Möller) Linnem.

Species of this subgenus show their characters most clearly on 2% malt extract agar. The monographic treatment of this group by Turner (*1963*) provides a sound base for species delimitation, and her arrangement is followed with some additions.

The other subgenus, *Mortierella*, is characterized by white, arachnoid colonies often with lobed or rosette patterns and mostly with a garlic-like odour. The morphological features of this group are described from cultures growing on soil extract agar or potato-carrot agar, as outlined by Gams (*1970*), and the arrangement in nine sections, proposed in that paper, has been retained.

While a considerable number of species remains doubtful and might eventually be elucidated when isolates become available which cannot be identified with this key, some old species have already been rediscovered recently and a number of new species has been added (Gams, *1976*). The locations of the diagnoses and the first discoveries of zygospores of the recognized species, as well as some synonymies, are given at the end of this study.

KEY TO THE SUBGENERA, SECTIONS AND SOME ISOLATED SPECIES

1a. Colonies velvety, not exceeding 3 mm in height; sporangia mostly ochraceous or vinaceous, often with a small columella; without distinctive odour . subgen. *Micromucor* (I)
b. Aerial mycelium consisting of longer, ascendent or prostrate hyphae, white, cottony or arachnoid; sporangia usually not pigmented, without or with a rudimentary columella; mostly with a garlic-like odour . . . . . subgen. *Mortierella* (II) 2
2a. Only chlamydospores present (recognizable as *Mortierella* by colony habit and odour) 3
b. Sporangiophores and sporangia (sporangioles) present 6
3a. Chlamydospores smooth-walled: no further species identification possible
b. Chlamydospores ornamented, not exceeding 30 µm diam. (if bigger, cf. *M. alliacea*) 4
4a. Chlamydospores covered with relatively few blunt spines up to 4 × 1 µm, terminal or intercalary, mostly 15–26 µm diam.; homothallic. . . . . *M. chlamydospora*
b. Chlamydospores more densely fimbriate 5
5a. Chlamydospores mostly terminal, sometimes intercalary, densely covered with straight 1–2 µm long spines, mostly 14–21 µm diam.; heterothallic . . . . . *M. indohii*
b. Chlamydospores mostly intercalary, sometimes terminal, with sometimes flexuous blunt spines up to 5 × 1 µm, mostly 17–28 µm diam.; zygospores unknown . . *M. echinosphaera*
6a. Sporangiophores always unbranched 7
b. Sporangiophores branched (at least sometimes) 9
7a. Sporangiophores usually exceeding 200 µm in length . . . . . Sect. *Simplex* (1)
b. Sporangiophores less than 150 µm in length 8
8a. Sporangia, at least partly, many-spored; sporangiophores with distinctly widening base (cf. also *M. horticola* in sect. *Stylospora*) . . . . . Sect. *Alpina* (2)
b. Sporangia one-spored; very slender sporangiophores arising in dense rows from the aerial hyphae . . . . . Sect. *Schmuckeri* (3)
9a. Sporangiophores racemosely branched with a thick main stem and thin, short branches 10
b. Branching in another way 11
10a. Branches arising above the middle of the sporangiophore . . . . Sect. *Mortierella* (4)
(if sporangiophores shorter than 100 µm with strongly swollen base,
cf. Sect. *Haplosporangium*)

10b. Branches arising from the uppermost part of the sporangiophore in clusters from an inflated region . . . . . Sect. *Actinomortierella* (5)
11a. Branches arising mainly from the lower part of the sporangiophore (basitonous) . 12
b. Branches arising from the middle or upper part of the sporangiophore (mesotonous or acrotonous) 13
12a. Sporangia containing many, or at least several, smooth or ornamented spores Sect. *Hygrophila* (6)
b. Sporangia one-spored, often ornamented . . . . . Sect. *Stylospora* (7)
13a. Sporangia many-spored; sporangiophores often bent upwards above an ascendent basal part and with a minute columella . . . . . Sect. *Spinosa* (8)
b. Sporangia one- or two-spored; sporangiophores short, with broad base, strongly tapered in the middle part and arising in dense rows from the aerial hyphae Sect. *Haplosporangium* (9)

I. Subgenus MICROMUCOR

1a. Sporangia one-spored 2
b. Sporangia many-spored 3
2a. Sporangia hyaline; colonies white . . . . . *M. nana*
b. Sporangia reddish . . . . . *M. roseo-nana*
3a. Colonies shades of ochraceous-grey; spores slightly angular, 2–3 µm diam.; small chlamydospores scarcely produced . . . . . *M. isabellina*
b. Colonies pink, russet or lilac 4
4a. Chlamydospores filled with lipid droplets, abundantly produced; sporangiophores always with a small distinct columella 6
b. Chlamydospores small and scarce or absent 5
5a. Sporangiophores slightly widened below the sporangium, sporangial wall mostly remaining as a large collarette; small columella often present; spores angular, 2–3 µm diam. . . . . *M. longicollis*
b. Sporangiophores not widened below the sporangium, without a collarette; columella hardly developed; spores angular, 3–4 µm diam. . . . . *M. vinacea*
6a. Spores angular; colonies somewhat brownish red . . . . *M. ramanniana* var. *angulispora*
b. Spores rounded; colonies in other red to vinaceous shades 7
7a. Spores ellipsoidal; fungus requiring thiamin . . . . . *M. ramanniana* var. *ramanniana*
b. Spores globose; fungus not requiring thiamin . . . . . *M. ramanniana* var. *autotrophica*

II. Subgenus MORTIERELLA

1. Section SIMPLEX W. Gams

in Nova Hedwigia **18**: 37. 1970 ('1969')

1a. Sporangia equal; all many-spored 2
b. Sporangia unequal; partly many-spored, partly few- or one-spored 9
2a. Clusters of vesicles present near the base of the sporangiophores 3
b. Clusters of vesicles absent 5
3a. Spores globose, finely warted, 5–7 µm diam. . . . . *M. globulifera*
b. Spores ellipsoidal to cylindrical, smooth-walled 4
4a. Spores 11–16 × 6–8 µm . . . . . *M. tuberosa*
b. Spores 7–9 × 4–5 µm . . . . . *M. pilulifera*
5a. Amoeba-like chlamydospores with irregular appendages present . . . *M. amoeboidea*
b. Amoeba-like chlamydospores absent 6

6a. Sporangiophores markedly constricted below the sporangium; spores 9–11 × 6–7 µm *M. strangulata*
b. Sporangiophores hardly constricted below the sporangium 7
7a. Columella conspicuous; spores globose, 2–3 µm diam.. cf. *M. turficola* (Sect. *Hygrophila*)
b. Columella absent; spores much larger 8
8a. Spores 5–6.5 × 3.5–4 µm, smooth-walled . . . . . *M. rostafinskii*
b. Spores 10–20 µm diam., with strongly undulate outer membrane and angular outline *M. ornata*
9a. Sporangiophores to 1000 µm long and 70 µm wide; spores subglobose, almost smooth-walled, about 10 µm diam., formed in many-spored sporangia; in addition verrucose spores, 12–25 µm diam., are formed in few-spored sporangia; chlamydospores absent *M. simplex*
b. Sporangiophores to 600 µm long and 30 µm wide; spores subglobose, either 8–11 µm diam., almost smooth-walled and formed in many-spored sporangia, or 12–24 µm and coarsely verrucose and formed in one- or few-spored sporangia; chlamydospore-like hyphal swellings present . . . . . *M. angusta*

2. Section ALPINA Linnem.

Mucorineen-Gatt. *Mortierella*: 35. 1941

1a. Sporangia always one-spored, globose, finely echinulate cf. *M. horticola* (sect. *Stylospora*)
b. Sporangia, at least partly, many-spored 2
2a. Spores of many-spored sporangia elongate 3
b. Spores of many-spored sporangia of other shapes 4
3a. Fimbriate chlamydospores, 20–60(–120) µm diam., present . . . . . *M. alliacea*
b. Only small, indistinct, smooth-walled chlamydospores occasionally present . *M. alpina*
4a. Spores irregularly lobulate . . . . . *M. polygonia*
b. Spores more or less globose 5
5a. Spores 3–10 µm diam; globose chlamydospores, 6–15 µm diam., fairly numerous *M. antarctica*
b. Spores 3–5 µm diam.; chlamydospores absent or scanty and little differentiated, elongate *M. globalpina*

3. Section SCHMUCKERI W. Gams

in Nova Hedwigia **18**: 38. 1970 ('1969')

1a. Sporangia globose 2
b. Sporangia flattened, 10–15 µm diam.; sporangiophores mostly 20–50 µm long *M. schmuckeri*
2a. Sporangiophores 7–17 µm long; spores 5–6 µm diam. . . . . *M. claussenii*
b. Sporangiophores 25–45 µm long; spores 7–12 µm diam. . . . . *M. camargensis*

4. Section MORTIERELLA

Syn.: Section *Polycephala* Linnem., Mucorineen-Gatt. *Mortierella*: 24. 1941
emend. W. Gams *in* Nova Hedwigia **18**: 38. 1970 ('1969')

1a. Spores with reticulate walls . . . . . *M. reticulata*
b. Spores with smooth or granulate walls 2
2a. Sporangia up to 5-spored; spores finely warty, 11–16 µm diam.; irregularly lobate chlamydospores present in the agar . . . . . *M. oligospora*

2b. Sporangia many-spored; aerial chlamydospores regularly spinulose 3
3a. Spores smooth-walled, 10–12 μm diam. . . . . *M. polycephala*
b. Spores finely echinulate, 12–15 μm diam. . . . . *M. echinulata*

5. Section ACTINOMORTIERELLA (Chalabuda) W. Gams

in Nova Hedwigia **18**: 38. 1970 ('1969')

Actinomortierella Chalabuda *in* Nov. Sist. niz. Rast. 1968: 129

1a. Sporangiophores with an apical inflation from which short branches arise; chlamydospores absent 2
b. Sporangiophores without an apical inflation but with numerous short branches arising close together in the uppermost part of the sporangiophore; chlamydospores present, covered with irregular appendages . . . . . cf. *M. wolfii* (sect. *Spinosa*)
2a. Apical inflation forming an apophysis bearing a terminal large sporangium and giving rise to several narrow branches with smaller sporangia; spores ellipsoidal, 4–9 × 3–6 μm *M. ambigua*
b. Inflation some distance below the terminal sporangium giving rise to numerous narrow branches; spores globose, 8.5–10 μm diam. . . . . *M. capitata*

6. Section HYGROPHILA Linnem.

Mucorineen-Gatt. *Mortierella*: 45. 1941

emend. W. Gams *in* Nova Hedwigia **18**: 39. 1970 ('1969')

1a. Sporangiophores not exceeding 120 μm in length; spores more or less globose . . . 2
b. Sporangiophores longer or spores ellipsoidal-cylindrical 5
2a. Sporangiophores with branches arising almost from the same point very close to the base; sporangia few-spored; spores 4.5–12 μm diam., finely verrucose cf. *M. verticillata* (sect. *Stylospora*)
(If spores larger than 12 μm diam., cf. *M. hyalina*)
b. Sporangiophores with branches arising at different levels; sporangia many-spored. . 3
3a. Spores 4–7(–10) μm diam.; chlamydospores absent . . . . . *M. minutissima*
b. Spores not exceeding 4 μm diam.; chlamydospores present. 4
4a. Chlamydospores globose, 20–100(–300) μm diam.; spores 2–3 μm diam. *M. macrocystis*
b. Chlamydospores consisting of widened hyphal branches of irregular shape; spores 2.5–4.0 μm diam. . . . . *M. clonocystis*
5a. Chlamydospores aggregated in rows or clusters. 6
b. Chlamydospores, if present, not aggregated 8
6a. Sporangiophores with an inflation below the sporangium; spores more or less globose, 8–12 μm diam. . . . . *M. beljakovae*
b. Sporangiophores not inflated apically; spores ellipsoidal to cylindrical 7
7a. Spores with a single membrane, 8–11 × 4–6 μm . . . . . *M. zychae*
b. Spores with a double membrane, 3.5–8 × 2.0–3.3 μm . . . . . *M. parazychae*
8a. Chlamydospores usually exceeding 20 μm diam. 9
b. Chlamydospores smaller or absent 12
9a. Spores globose, 6–10 μm diam., minutely striate; chlamydospores 50–100 μm diam., covered with short fimbriate hyphae . . . . . *M. sclerotiella*
b. Spores ellipsoidal or reniform, smooth-walled 10
10a. Spores irregularly reniform, 18–26 × 8–12 μm; chlamydospores 40–60 μm diam. *M. armillariicola*
b. Spores ellipsoidal, smaller. 11

11a. Spores short-ellipsoidal, 14–16 × 9–11 µm; chlamydospores 35–50 µm diam., thick- and smooth-walled . . . . . *M. gemmifera*
b. Spores ellipsoidal-fusiform, 5.5–8.5 × 2.0–3.0 µm; chlamydospores to 40 µm diam., thin-walled, sometimes with papillate appendages . . . . . *M. elongatula*
12a. Spores globose to subglobose 13
b. Spores distinctly elongate 17
13a. Spores completely or almost smooth-walled 14
b. Spores with distinctly ornamented wall 16
14a. Spores 3–5 µm diam. . . . . *M. basiparvispora*
b. Spores much larger 15
15a. Sporangiophores with apophysis-like inflation; spores smooth-walled, 8–12 µm diam.; chlamydospores often in groups . . . . . *M. beljakovae*
b. Sporangiophores without any inflation; spores minutely roughened, 8–25 µm diam.; chlamydospores formed solitarily . . . . . *M. hyalina*
16a. Sporangiophores 320– over 500 µm long; spores 8–10(–14) µm diam., echinulate *M. echinula*
b. Sporangiophores 60–160(–260) µm long; spores 6–12(–16) µm diam., verrucose *M. verrucosa*
17a. Spores crescent-shaped, 15–20 × 5–9 µm. . . . . *M. selenospora*
b. Spores cylindrical or ellipsoidal 18
18a. Sporangiophores 2–3 mm long, 18–20 µm wide at the base; spores 5–10 × 3–5 µm; chlamydospores absent . . . . . *M. bainieri*
b. Sporangiophores shorter and/or more slender and/or spores smaller 19
19a. Sporangiophores with 8–14 µm wide apophysis-like inflation; spores 8–12(–17) × 4–5 (–7) µm . . . . . *M. kuhlmanii*
b. Sporangiophores without any inflation 20
20a. Homothallic species with numerous naked zygospores produced on malt extract agar; spores fusiform with rounded ends, 9–14 × 3–6 µm; chlamydospores absent *M. epigama*
b. Heterothallic species or zygospores unknown; spores ellipsoidal to cylindrical. . . 21
21a. Sporangiophores usually with a rather long (to 600 µm) and mostly 10–12 µm wide, unbranched basal portion; spores 3.5–4 × 2.0–2.5 µm . . . cf. *M. jenkinii* (sect. *Spinosa*)
b. Sporangiophores branched near the base and/or spores larger and/or more slender 22
22a. Sporangiophores 100–200(–400) µm long; spores 6–9 × 3.0–4.5 µm; chlamydospores absent . . . . . *M. sarnyensis*
b. Sporangiophores longer. 23
23a. Sporangiophores up to 1 mm and longer, at the base usually not exceeding 6 µm diam., branching in the middle; spores 4.5–8 × 3–5 µm . . . . . *M. dichotoma*
b. Sporangiophores mostly not exceeding 400 µm, 5–15 µm wide at the base and 1.5–3.5 µm at the tip, with typically basitonous ramification; spores 7–13(–16) × 3.5–7 µm *M. elongata*

7. Section STYLOSPORA Linnem.

Mucorineen-Gatt. *Mortierella*: 20. 1941

1a. Sporangiophores always unbranched; sporangia 7–12 µm diam., minutely spinulose *M. horticola*
b. Sporangiophores basitonously branched. 2
2a. Sporangia with reticulate walls . . . . . *M. stylospora*
b. Sporangia with spinulose or smooth walls 3
3a. Sporangiophores 5–7 µm wide at the base, strongly tapering in the middle part to 1.0–1.8 µm at the tip; sporangia echinulate, 8–18 µm diam. . . . . *M. lignicola*
b. Sporangiophores tapering gradually to 1.5–3.0 µm at the tip 4

4a. Sporangia smooth-walled, 10–25 μm diam. . . . . *M. zonata*
b. Sporangia finely ornamented, smaller. 5
5a. Sporangia finely spinulose, always one-spored, with the outermost layer firmly attached to the spore. . . . . *M. humilis*
b. Sporangia often few-spored; spores irregularly warty, with a loose outer layer *M. verticillata*

8. Section SPINOSA Linnem.

Mucorineen-Gatt. *Mortierella*: 52. 1941
emend. W. Gams *in* Nova Hedwigia **18**: 39. 1970 ('1969').

1a. Sporangiophores generally not exceeding 200 μm in length. 2
b. Sporangiophores typically much longer 4
2a. Spores globose, 18–25 μm diam., with a double membrane . . . . . *M. acrotona*
b. Spores much smaller, with a single membrane 3
3a. Chlamydospores constantly absent; spores 3–4 μm diam. . . . . *M. pulchella*
b. Chlamydospores scarcely produced, lemon-shaped, about 6 μm diam.; spores 4–7(–10) μm diam. . . . . *M. epicladia*
4a. Sporangiophores with umbellate branches arising from the same level; spores plano-convex, 12–14 × 5–7 μm . . . . . *M. umbellata*
b. Sporangiophores with branches inserted at different levels; spores of other shapes 5
5a. Spores globose to subglobose 6
b. Spores ellipsoidal to cylindrical 8
6a. Spores not exceeding 4 μm diam. . . . . *M. parvispora*
b. Spores larger 7
7a. Sporangiophores often exceeding 1 cm in length; spores more than 10 μm diam. *M. nantahalensis*
b. Sporangiophores 200–800 μm long; spores less than 10 μm diam. . . . . *M. gamsii*
8a. Chlamydospores densely covered with blunt spines; spores 4.0–5.5 × 2.0–3.0 μm *M. fimbricystis*
b. Chlamydospores if present, smooth-walled or irregularly lobate. 9
9a. Spores not exceeding 5.5 μm in length; chlamydospores regularly globose, lemon-shaped, or absent 10
b. Spores larger; chlamydospores bearing irregularly lobate appendages 11
10a. Chlamydospores absent or tardily produced and lemon-shaped; sporangiophores 400 to more than 1500 μm tall; spores 3.5–4.0(–5.0) × 2.0–2.5 μm . . . . . *M. jenkinii*
b. Chlamydospores abundantly produced, globose, 20–60 μm diam., thick-walled; sporangiophores usually not exceeding 300 μm; spores 3–4 × 1.2–2.0 μm *M. cystojenkinii*
11a. Sporangia leaving a pronounced collarette; spores with a double membrane *M. wolfii*
b. Sporangia not leaving a collarette but with a trace of a columella; spores with a single membrane . . . . . *M. exigua*

9. Section HAPLOSPORANGIUM (Thaxt.) W. Gams

in Nova Hedwigia **18**: 40. 1970 ('1969')
Haplosporangium Thaxt. *in* Bot. Gazette **58**: 362. 1914.

Sporangia one- or two-spored . . . . . *M. bisporalis*

THE RECOGNIZED SPECIES OF MORTIERELLA

Epithets in alphabetical order with references to the first descriptions, some important redescriptions and first descriptions of zygospores (Z.), followed by facultative synonyms (S.). Other information is to be found in Zycha & Siepmann (*1970*), Mil'ko (*1974*) and Linnemann (*1941*).

acrotona W. Gams *in* Persoonia **9**: 133. 1976.
alliacea Linnem., *in* Zentbl. Bakt. ParasitKde (II. Abt.) **107**: 225. 1953.
alpina Peyron., Germi atmosferici, Diss. Padova: 17. 1913. Z.: Kuhlman *in* Mycologia **67**: 674. 1975.
S.: *M. renispora* Dixon-Stewart *in* Trans. Br. mycol. Soc. **17**: 214. 1932. Z.: ibid.
M. thaxteri Björling *in* Bot. Notiser 1936: 116.
M. monospora Linnem. *in* Flora **130**: 210. 1936 (nom. inval., Art. 36).
M. acuminata Linnem., Mucorineen-Gatt. *Mortierella*: 21. 1941.
ambigua B. S. Mehrotra *in* Mycologia **55**: 291. 1963.
amoeboidea W. Gams *in* Persoonia **9**: 116. 1976.
angusta (Linnem.) W. Gams *in* Ber. naturw.-med. Ver. Innsbruck **53**: 73. 1963. — *M. polycephala* var. *angusta* Linnem., Mucorineen-Gatt. *Mortierella*: 29. 1941.
antarctica Linnem. apud Zycha & Siepmann, Mucorales: 198. 1970 ('1969') ex Linnem. *in* Nova Hedwigia **19**: 565. 1971 ('1970').
armillariicola W. Gams *in* Persoonia **9**: 128. 1976.
bainieri Cost. *in* Bull. Soc. mycol. Fr. **4**: 150. 1889; Z.: Kuhlman *in* Mycologia **64**: 325. 1972.
basiparvispora W. Gams & Grinbergs *in* Persoonia **9**: 130. 1976.
beljakovae Milko *in* Nov. Sist. niz. Rast. 1973: 83; Gams *in* Persoonia **9**: 124. 1976. Z.: Kuhlman *in* Mycologia **64**: 325. 1972 (as *M.* '*candelabrum*').
bisporalis (Thaxt.) Björling *in* Bot. Notiser 1936: 126. — *Haplosporangium bisporale* Thaxt. *in* Bot. Gaz. **58**: 363. 1914.
S.: *M. decipiens* (Thaxt.) Björling *in* Bot. Notiser 1936: 126. — *Haplosporangium decipiens* Thaxt. *in* Bot. Gaz. **58**: 364. 1914.
camargensis W. Gams & R. Moreau *in* Annls Univ. Besançon (Sér. 2) **3**: 103. 1960. — *Haplosporangium gracile* Nicot *in* Bull. trimest. Soc. mycol. Fr. **73**: 87. 1957.
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M. dichotoma Linnem. ex W. Gams, *spec. nov.* Mortierellae elongatae Linnem. similis, sed sporangiophoris angustioribus, cito procumbentibus, 200 — amplius 750 µm longis, c 5–6 (–10) µm sursum ad 2–4 µm angustatis, irregulariter quasi dichotomice ramosis differt. Sporangia 20–40 µm diam., dilapsa collare minimum relinquunt. Sporangiosporae ellipsoideae vel breviter cylindricae, plerumque 4–7 × 2.5–4 µm. Chlamydosporae elongatae vel irregulares, 5–10 µm diam. Typus: CBS 221.35, isolatus ex excrementis murinis prope Marburgum in Germania a *G. Linnemann*. Nov. 1933.
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M. humilis Linnem. ex W. Gams, *spec. nov.* Coloniae rapide crescunt et fortiter olent. Sporangiophora basitone ± ramosa, 50–200 µm longa, e 2–4 sursum ad circa 1 µm angustata. Sporangia constanter monospora, 6–15 µm diam., pariete externo verruculoso firme adhaerente, dilapsa nonnumquam collare minutum relinquunt. Species heterothallica; zygosporae inter hyphas compatibiles appropinquantes formantur, hyalinae, leves nec involutae; pariete 2–6 µm crasso circumdatae, (34–)46(–62) µm diam.; alteri suspensores ad diametrum zygosporae similem inflati. Chlamydosporae absunt. Typus: CBS 222.35, isolatus e terra prope Marburgum in Germania, a *G. Linnemann*, 1934.

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NOTES ON GYMNOASCACEAE

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Based on type studies, the following genera are reclassified: *Petalosporus*, *Disarticulatus*, and *Plunkettomyces* as synonyms of *Arachniotus*; *Gymnascella*, *Gymnoascoides*, *Macronodus*, *Tripedotrichum*, and *Uncinocarpus* as synonyms of *Gymnoascus*, and *Kuehniella* as a synonym of *Arachnotheca*. The question of the type species of *Arachniotus* is discussed. *Rollandina* is considered to be a nomen confusum; sensu Apinis (*1970*) it belongs to *Nannizzia*. The accepted genera of the Gymnoascaceae are briefly reviewed.

Recent research on Gymnoascaceae has been based on pure cultures. The older genera described in the 19th century, however, were based on material collected on plant debris, dung, spoiled food and similar substrates. In general no type-material was preserved and the taxa have to be judged from descriptions which are usually short and insufficient for recognition of the fungus. In some cases type specimens are available, but these have mostly proved to be too poor for reidentification. Some older taxa have been provided with 'neotypes' which are usually living (and dried) cultures.

The results of a comparative study of some type specimens, some neotype cultures and type cultures will be discussed under the following.

1. ARACHNIOTUS Schroeter (*1893*)

Schroeter (*1893*) erected the genus for 3 species earlier described as *Gymnoascus*, viz. *G. candidus* Eidam (*1886*), *G. aureus* Eidam (*1886*), and *G. ruber* van Tieghem (*1887*). No generic type was indicated and no type specimens of the three species have been maintained. In general the first mentioned species was regarded as type, its description, however, is insufficient to recognize the fungus; a *Talaromyces* or *Neosartorya* species was probably meant. *Arachniotus aureus* (Eidam) Schroeter belongs to *Amauroascus* as *A. aureus* (Eidam) v. Arx; it has been redescribed by Kuehn *& al.* (*1964*) based on a neotype culture (CBS 593.71) isolated in Japan by K. Tubaki.

The description of *Arachniotus ruber* (v. Tiegh.) Schroet. allowed recognition of the fungus. The recent isolate IMI 92796 (=CBS 194.64) has been designated as neotype by Kuehn & Orr (*1964*). Several additional strains have become available (Apinis, *1964*). This species has been designated as lectotype of the genus by von Arx (*1970*, *1971*) among others. Without mentioning this decision, Orr *& al.* (*1977*) again regard *Arachniotus candidus* (Eidam) Schroet. as type. They do not, however,

give an adequate description of the species and no type specimen is designated. The remaining species of *Arachniotus* they partly classify in *Pseudoarachniotus*, partly in *Gymnascella*, but no characters are given for the separation of the two genera. In fact all species are congeneric and should preferably be retained in *Arachniotus*, with *A. ruber* as type of the genus.

2. GYMNASCELLA Peck (*1885*)

The genus was described for the single species, *Gymnascella aurantiaca* Peck. The diagnosis is very short and inadequate for recognition of the fungus. The specimen, maintained in the New York State Museum, Albany (NYS), was studied some years ago. It contained two small pieces of plant stem, on which only traces of fungi, mainly belonging to *Cladosporium*, *Chrysosporium*, and *Rhodotorula*, could be found. In one small patch, clusters of roughened, yellow hyphae and roundish or oblate, thin-walled, yellow spores, 3–4.5 × 2–3 µm in size, were observed. These hyphae and spores agree in size and shape with the peridial hyphae and ascospores of *Gymnoascus reessii* Baranetzky, the type species of the genus *Gymnoascus*. The classification of *Gymnascella aurantiaca* Peck in *Gymnoascus* by Saccardo (*1889*) could therefore be confirmed.

Recently, Orr & *al.* (*1977*) reintroduced the genus *Gymnascella* and identified its type species with a fungus described by Orr & Kuehn (*1971*) as *Arachniotus verruculosus*. A study of specimens received from G. F. Orr (CBS 636.72, 637.72) showed, however, that this fungus can be easily distinguished from *Gymnascella aurantiaca* (=*Gymnoascus reessii*) by its larger, rather thick-walled, pigmented, 4.5–6.2 × 3.5–4 µm ascospores. Compare in this respect Figs. 3, 4 with Fig. 6 in Orr & *al.* (*1977*). *Arachniotus verruculosus* proved to represent a species very close to or identical with *Arachniotus aurantiacus* (Kamyschko) v. Arx. The latter species in turn is very close to *Arachniotus dankaliensis* (Cast.) van Beyma=*Pseudoarachniotus roseus* Kuehn=*Arachniotus flavoluteus* Kuehn & Orr.

3. ROLLANDINA Patouillard (*1905*)

The genus was described with a single species, *R. capitata*, which is thus the type. The type specimen is maintained in the Farlow Herbarium, Cambridge (FH) and has been re-examined by Benjamin (*1956*) and Apinis (*1968*, *1970*). The material (in formalin) is now very poor, but the slides prepared by R. K. Benjamin and A. E. Apinis (also maintained in FH) proved to be useful. The fungus is described as having stalked ascomata, but these stalks belonged to another organism, as pointed out by Apinis (1970). The fungus forms densely and minutely asperulate peridial hyphae, oblate ascospores with an equatorial band, 3.5–4.5 × 2.5 µm in size, and large, fusiform, verrucose, 5-septate, 40–60 × 9–13 µm aleurioconidia. This fungus is without doubt a *Nannizzia* species, probably *N. fulva* Stockdale, and its *Microsporum-conidial* state is similar to *M. fulvum* Uriburu.

The genus *Rollandina* can be considered to be a nomen confusum as it was based on two different organisms. *Rollandina* sensu Apinis (*1970*), however, is a synonym of *Nannizzia* Stockdale (*1961*).

Roy, Orr, and Ghosh in Orr & *al.* (*1977*), identified *Pseudoarachniotus hyalinosporus* Kuehn & *al.* as *Rollandina capitata*. The former species has no conidial state and has a different ascigerous state with no peridial hyphae and hyaline, lenticular ascospores with an equatorial frill. It is similar to the type species of the genus *Narasimhella* (von Arx, *1972*).

Rollandina vriesii Apinis (*1970*) has spherical, pitted ascospores and *Chrysosporium*-like conidia. It may belong to *Apinisia*, but its type culture (CBS 407.72) is at present only conidial.

4. PETALOSPORUS Ghosh & *al.* (*1963*)

The examination of the type culture (CBS 577.63) of the type species *Petalosporus nodulosus* Ghosh & *al.* showed its resemblance to a fungus, usually treated as *Arachniotus citrinus* Mass. & Salm. (Apinis, *1964*; van Arx, *1971*). The type cultures of the later described species, *Petalosporus anodosus* Kuehn & *al.* (CBS 518.68) and *P. afilamentosus* Orr & Kuehn (CBS 658.71), also proved to represent forms of *Arachniotus citrinus*. This species is close to *A. dankaliensis* and intermediates exist. Both species do not usually include a conidial state. In some sulphur-yellow strains in the CBS-collection, swollen, rather large arthro- or aleurioconidia (*Chrysosporium*-like) were observed and these strains may represent undescribed taxa.

The genus *Petalosporus* has been considered to be a synonym of *Arachniotus* by von Arx (*1974*).

5. KUEHNIELLA Orr (*1976*)

The genus was based on *Myxotrichum racovitzae* Lagarde (*1913*), but no type specimen of this species has been maintained. Orr (*1976*) based the description on the culture ATCC 28557 (=NRRL 6154=CBS 156.77) which has been designated as neotype. This culture completely agrees with the type strain of *Arachniotus albicans* Apinis (IMI 100875=CBS 151.65). The fungus has been provided with an adequate diagnosis by Apinis (*1964*); that given by Orr (1976) is incomplete and misleading as the typical initials and asci and the sheath of the ascospores are not mentioned.

Arachniotus albicans is close to *Arachnotheca glomerata* (Müller & Pacha-Aue) v. Arx and has been classified as *Arachnotheca albicans* (Apinis) v. Arx (*1974*). Typical of both species are the white (or yellow) colonies and ascomata, the clavate ascogonia surrounded by an antheridial coil, the clavate asci borne from croziers and the spherical, hyaline ascospores which are surrounded by a persistent, ornamented sheath and are bluish or violet en masse.

The genus *Kuehniella* has to be considered to be a synonym of *Arachnotheca*.

6. UNCINOCARPUS Sigler & Orr (*1976*)

This genus has been described in a paper by Sigler & Carmichael (*1976*). Its type species, *Uncinocarpus reesii* Sigler & Orr, is very close to *Gymnoascus uncinatus* Eidam, as described by Orr & *al.* (*1936*) or Samson (*1972*). The neotype culture RSA 56 (=NRRL 3610 = CBS 408.72) of *Gymnoascus uncinatus* has been illustrated by Benjamin (*1956*) under the name *Myxotrichum uncinatum* (Eidam) Schroet.

Gymnoascus uncinatus is rather peculiar within the genus *Gymnoascus* by its uncinate appendages and the apically swollen initials. *Uncinocarpus reesii* is heterothallic and has 'bulbous' initials and similar uncinate appendages. Sigler & Orr in Sigler & Carmichael (*1976*) did not compare it with *G. uncinatus*.

Consequently the genus *Uncinocarpus* should be considered to be a synonym of *Gymnoascus*.

7. TRIPEDOTRICHUM Orr & KUEHN (*1964*)

The only species *Tripedotrichum herbariensis* Orr & Kuehn was based on some fructifications found on a herbarium specimen of *Myxotrichum chartarum* (Nees) Kunze, distributed on Rabenhorst's Fungi Europaei No. 179 (NY). No cultures of the fungus are known and the description is incomplete. The uncinate, dark, 80–260 µm long and 4–7 µm broad appendages and the pigmented, oblate, 3.5–5.5 ×2.2–3.5 µm ascospores indicate that the fungus is identical to *Gymnoascus uncinatus* Eidam or *Uncinocarpus reesii* Sigler & Orr.

The genus *Tripedotrichum* should therefore also be considered a synonym of *Gymnoascus*.

8. MACRONODUS Orr (*1977a*)

The genus *Macronodus* with *Macronodus bifurcatus* Orr as type is characterized by discrete ascomata surrounded by a peridium with uncinate or bifurcate appendages and by oblate, yellow-brown ascospores; the initials are not described. The genus is mainly compared with *Auxarthron*; an unrelated genus with a dark peridium and with spherical, ornamented ascospores. *Macronodus bifurcatus*, however, is again very close or identical to *Gymnoascus uncinatus*. A decision concerning the identity can only be taken after comparison of a larger number of strains. The genus *Macronodus* has to be considered a synonym of *Gymnoascus*.

9. GYMNOASCOIDES Orr, Roy & Ghosh (*1977*)

Several strains of *Gymnoascoides petalosporus* Orr & *al.*, the type species of the genus, were studied (a.o. CBS 630.72=O–2067 and CBS 629.72=O–2060). The fungus is rather variable in its cultural characters, in the formation of peridial hyphae (which may be absent) and in the size of the ascospores. The latter are oblate, yellowish or

brownish and 3–4.5 × 2–3 µm. The peridial hyphae are branched at right angles, brownish, thick-walled, 2–3 µm broad and terminate in lighter, appendage-like, blunt cells.

The species is intermediate between *Arachniotus* and *Gymnoascus*, is close to *Gymnoascus reessii* and has to be classified as **Gymnoascus petalosporus** (Orr & al.) v. Arx, *comb. nov.* (basionym: *Gymnoascoides petalosporus* Orr *& al. in* Mycotaxon **5**: 460. 1977).

10. PLUNKETTOMYCES Orr (*1977b*)

The type and some more strains of *Plunkettomyces littoralis* Orr, the type species of the genus, were maintained in the CBS collection as *Arachniotus* spec. (CBS 454.73, 455.73) and have been studied.

The slow growing colonies are rather flat and sulphur-yellow. The ascogonial initials are small, form irregular coils and are composed of hyaline, 2.5–3.5 µm broad hyphae. The clusters of asci have a diameter of 30–60 µm, but are often aggregated in masses, up to 200 µm. Characteristic peridial hyphae are absent, but some yellow, often verruculose, hyphae may develop around the ascal clusters and in the mycelial mat. The asci are spherical, botryose or in short chains, deliquescent, 9–11 µm in diameter and contain 8 oblate-lenticular, golden yellow, 4.5–6 × 3–4 µm ascospores which show a band-like equatorial thickening of the wall. The catenate conidia, separated from one another by empty parts of the conidiogenous hyphae, are slightly swollen, smooth, 1-celled, hyaline and 5–13 × 3.5–6.5 µm.

The genus *Plunkettomyces* has to be considered a synonym of *Arachniotus*. Its type species has to be renamed **Arachniotus littoralis** (Orr) v. Arx, *comb. nov.* (basionym: *Plunkettomyces littoralis* Orr *in* Mycotaxon **6**: 33. 1977). The fungus is close to *Arachniotus dankaliensis* and *Arachniotus citrinus*. It can be distinguished from the former by its sulphur-yellow colonies, from the latter by its equatorially thickened ascospore walls and from both by its *Chrysosporium*-like conidial state and by the adaption to marine environments.

11. DISARTICULATUS Orr (*1977b*)

A strain maintained in the CBS collection as *Arachniotus* spec. (CBS 546.72), isolated by C. Devroey from Somalian soil, has been studied. It is, without doubt, identical to the fungus described as *Disarticulatus devroeyi* Orr.

The description given by Orr (*1977b*) is incomplete. The colonies are initially whitish-yellow, but soon become cinnamon. The initials are composed of elongated, dense coils of hyaline gametangial hyphae. The clusters of asci are small, dispersed or aggregated and are not surrounded by a peridium. The asci are spherical, thin-walled, 12–17 µm; the ascospores are oblate, rather thick-walled, smooth, golden yellow, 5.5–6.5 × 4–5 µm, without an equatorial rim or thickening. Thick-walled, hyaline or brownish, swollen, 17–26 × 8–12 µm cells especially develop from swollen

parts of racquet-hyphae and may disarticulate with age. A *Malbranchea*-like conidial state was also observed: the conidia are cylindrical, not swollen, 1-celled, hyaline, 10–15 × 3–5 µm and separated from one another by empty cavities of the conidiogenous hyphae.

The genus *Disarticulatus* cannot be separated from *Arachniotus*. Its type species has to be classified as **Arachniotus devroeyi** (Orr) v. Arx, *comb. nov.* (basionym: *Disarticulatus devroeyi* Orr *in* Mycotaxon **6**: 35, 1977).

Discussion of the Gymnoascaceae

The Gymnoascaceae represent a small group of often keratinophilic Ascomycetes with or without arthric or aleuric conidial states (phialo- or blastoconidia absent). Von Arx (1974) keyed out 18 genera with about 60 species, but delimitation is partly based on conidial states. Formerly the genera were delimited mainly by the presence or absence and form of the peridial hyphae and their appendages. These characters, however, are often variable and only of limited taxonomic value. In one and the same strain of *Gymnoascus reessii* peridial hyphae and appendages may be absent or present, depending on medium, humidity, light, and age.

Von Arx (*1971*, *1974*) introduced the size and the shape of the ascospores and the type of the initials as useful characters for the delimitation of genera. Genera with ellipsoidal-fusiform, genera with oblate and genera with spherical ascospores are distinguished.

In the group with oblate ascospores, two genera can be distinguished without or with reduced peridial hyphae, viz. *Arachniotus* and *Narasimhella*. The latter genus is characterized by ring-like initials surrounding a central cell, clavate asci borne from croziers and inequally lenticular, hyaline or greenish ascospores with a small, equatorial frill. In *Arachniotus* the initials consists of two coiling gametingial hyphae, the asci are spherical and develop directly on the ascogenous hyphae. The oblate ascospores are pigmented and often have equatorial rims or thickenings. Both genera have no conidial states or form arthroconidia (*Malbranchea*- or *Chrysosporium*-like).

Arachniotus is close to *Gymnoascus* and intermediates exist, but in the latter genus smooth or verruculose peridial hyphae with long or short, blunt or uncinate appendages are usually present. The ascospores are generally smaller (3–4.5 µm in diameter) than those of *Arachniotus* (5–7 µm in diameter).

Most of the other genera with oblate ascospores have light ascomata with coiled appendages but have been mainly based on their conidial state. The genera *Arthroderma* and *Shanorella* comprise keratinophilic species with *Chrysosporium* or *Trichophyton* conidial states. *Nannizzia* is erected for the ascigerous states of *Microsporon*. In *Ctenomyces* the ascomata have a rather compact, dark wall and it is further characterized by dark, comb-like (ctenoid) hyphal structures (Eidam, *1883*).

The genera *Ajellomyces*, *Emmonsiella*, *Apinisia*, *Auxarthron*, *Amauroascus*, and *Arachnotheca* are characterized by spherical ascospores. *Ajellomyces* and *Emmonsiella* are

monotypic and heterothallic; *Ajellomyces dermatitidis* McDonough & Lewis being the ascigerous state of *Blastomyces dermatitidis* and *Emmonsiella capsulata* Kwon-Chung that of *Histoplasma capsulatum*. Both have small, smooth, hyaline ascospores and densely spirally coiled peridial appendages. In *Apinisia* the ascospores are pitted and the conidial state is *Chrysosporium*-like. In *Amauroascus* and *Auxarthron* the spherical ascospores are usually pigmented, thick-walled and ornamented, often spiny. Both genera are close, but in *Auxarthron* the ascomata have peridial hyphae with long, uncinate or branched appendages which are absent in *Amauroascus*.

In *Arachnotheca* the initials are composed of a clavate cell surrounded by a hyphal coil, the ascomata have a rather thick colourless peridium composed of hyphae, the asci develop from croziers and the ascopores are hyaline (bluish or violet en masse) and sheathed.

The genera *Myxotrichum*, *Pseudogymnoascus*, and *Byssoascus* have ellipsoidal fusiform ascopores. *Byssoascus* has no peridial hyphae and the ascopores are striated by flutes; *Pseudogymnoascus* has brownish peridial hyphae without spines and smooth (or indistinctly striate) ascopores; *Myxotrichum* has dark peridial hyphae with spines or long appendages and smooth or striate ascopores. The three genera are close to each other. Most of the species include *Oidiodendron*, *Malbranchea*, or *Chrysosporium* conidial states (Sigler & Carmichael, *1976*).

The Gymnoascaceae are close to the Onygenaceae (Malloch & Cain, *1971*). The genera *Xynophila* Malloch & Cain and *Neoxenophila* Apinis & Clark with a reduced ascocarp wall, oblate ascopores and arthroconidia may be intermediate.

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THE GENUS MYCELIOPHTHORA

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(With four Text-figures and Plate 49)

The hyphomycetous genus *Myceliophthora* Cost. is reintroduced with its type species, *M. lutea* Cost., and two new combinations are proposed: *Myceliophthora thermophila* and *M. fergusii*. The genus is characterised by blastoconidia with narrow basal attachments (sometimes borne on ampulliform swellings) and by lacking arthroconidia. All three species are more or less thermophilic, with temperature optima between 30 and 45 °C.

In 1894 Costantin & Matruchot described the 'vert de gris' mat disease or cultivated mushrooms and named the pathogen *Myceliophthora lutea* Cost. Carmichael (*1962*) included Costantin's species in *Chrysosporium* Corda as *Chrysosporium luteum* (Cost.) Carmichael. Von Arx (*1973*) suggested that *C. luteum* should be removed from this genus and returned to *Myceliophthora* Cost. *Myceliophthora lutea* produces blastoconidia with narrow basal attachments, borne directly on hyphae or pedicels or ampulliform swellings, and has no arthroconidia. *Chrysosporium* Corda becomes a more homogeneous group, with perfect states only in the Gymnoascaceae, when it is defined as having arthroconidia and aleurioconidia which are terminal, intercalary or lateral, occasionally formed in chains and have broad basal attachments (see Fig. 1).

MYCELIOPHTHORA Cost.

Myceliophthora Cost. *In* C.r. hebd. Séanc. Acad. Sci., Paris: **2**. 1892.
Type species: *M. lutea* Cost.

Colonies on 2% malt agar initially white, later pale yellow, pale brown, cream or even occasionally dark green; reverse pale yellow, bright yellow, honey brown, brown, cream or occasionally green. Colonies powdery and felty with a defined margin, or cottony and floccose without a defined margin; growing rapidly, reaching 30–80 mm diam. in 7 days at 30 °C. More or less thermophilic, with optima between 36 and 45 °C. Some species are cellulolytic, some keratinolytic. Hyphae septate, hyaline, branched, the submerged occasionally broader than the aerial hyphae, thin-walled (rarely bearing blastoconidia). Aerial hyphae arising individually from submerged hyphae, erect, 1–2 mm high, sterile at the base, profusely branched and usually fertile at the apex. Blastoconidia borne directly on the sides of the hyphae, on long or short pedicels or in groups of 1–4 on ampulliform swellings; globose, pyriform, clavate or obovoid with narrow basal attachments, smooth- or rough-walled at maturity.

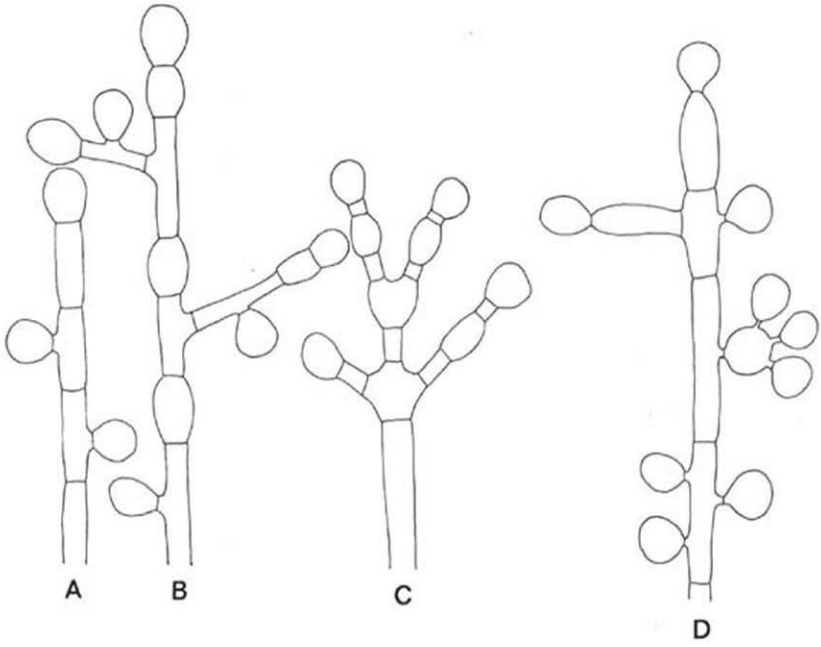

Fig. 1. Schematic diagram to illustrate varying conidiogenesis. — A–C. *Chrysosporium*-type with arthrospores and 'aleuriospores'. — D. *Myceliophthora*-type with blastoconidia.

Myceliophthora Cost. may be distinguished from the blastoconidial genera, *Emmonsia* Cif. & Montemartini (*1958*) and *Beniowskia* (*1900*) by the smaller (up to 10 µm diam.), almost globose conidia of the former, and the larger (up to 10 µm diam.), globose conidia (borne on denticles all over the hyphal surface) of the latter. In addition *Emmonsia* produces white, felty colonies. The genus *Trichosporiella* Kamyschko ex Gams & Domsch (*1969*) also has blastoconidia but differs by having moist colonies which usually lack an aerial mycelium.

The cellulolytic and keratinolytic properties of the species were tested by inoculation onto suitable media at optimal temperatures; a strip of cellophane or a number of human hairs being placed on the agar 2–3 cm from the point of inoculation.

KEY TO THE SPECIES

1a. Hyphal width not exceeding 3.0 µm; cultures felty, woolly, not floccose 2
b. Hyphal width 3.2–5.2 µm; cultures pinkish-cream, floccose; cellulolytic and keratinolytic; blastoconidia 4.8–12.0 × 2.8–5.2 µm . . . . . *M. fergusii* (3)

2a. Cultures yellow, felty; cellulolytic; blastoconidia 3.8–9.0 × 3.0–6.0 µm . . . *M. lutea* (1)
b. Cultures brown, occasionally green, woolly; keratinolytic but not cellulolytic; blastoconidia smooth or rough, 4.5–11.0 × 3.0–4.5 µm . . . . . *M. thermophila* (2)

(1) MYCELIOPHTHORA LUTEA Cost.—Fig. 2

Myceliophthora lutea Cost. *in* C.r. hebd. Séanc. Acad. Sci., Paris: 2. 1892. — *Chrysosporium luteum* (Cost.) Carmichael *in* Can. J. Bot. 40: 1158. 1962.
Sporotrichum carthusio-viride Rai & Mukerji *in* Mycopath. Mycol. appl. **18**: 122. 1962.

Colonies on 2% malt agar initially white, later pale yellow, felty, with a defined, dented margin, reaching 23–31 mm diam. in 7 days on 2% malt agar at 30 °C; reverse pale or bright yellow. Thermotolerant with optimal growth at 33 °C, temperature minimum 20 °C, maximum 40 °C. Cellulolytic, not keratinolytic. Submerged hyphae occasionally wider than aerial hyphae (up to 6.0 µm diam.), thin-walled; aerial hyphae 0.75–3.0 µm wide. Blastoconidia borne terminally or laterally on aerial hyphae, sometimes with short or long pedicels and occasionally a secondary blastoconidium being produced from the distal end of the first; 1–4 blastoconidia may be borne on one hyphal cell or on an ampulliform swelling; conidia pyriform to globose, smooth and fairly thick-walled, hyaline, 3.8–9.0 × 3.0–6.0 µm.

MATERIAL EXAMINED.—CBS 146.50, isolated from mushroom beds, Delaware, U.S.A., *E. T. Reese*, 1940; CBS 147.50, isolated from mushroom beds, Pennsylvania, U.S.A., *J. W. Sinden*, 1942; CBS 157.51, *P. J. Bels*, 1951; CBS 157.59, isolated from air in pig sty, Baarn, Netherlands, *G. A. de Vries*, 1959; CBS 227.67, isolated from soil, India, *J. P. Tewari* (type of *Sporotrichum carthusio-viride* Rai & Mukerji); CBS 145.77, (neotype) isolated from hay, Newmarket, U. K., *M. Archer*, 1974; CBS 146.77, isolated from *Hordeum vulgare*, Carlow, Ireland, *B. Dunne*, 1970; CBS 147.77, isolated from dust in stable, Newmarket, U. K., *M. Archer*, 1973.

No living or herbarium material is known of the original isolates of *M. lutea* described by Costantin & Matruchot in 1894 (Hawksworth, *1974*) but the origin from yellow patches in mushroom compost and the careful description leaves no doubt about the identity of this species. There is one discrepancy, however, in that the conidia described in 1894 were 3–4 × 2 µm, while the strains listed above have larger conidia (3.8–9.0 × 3.0–6.0 µm). The richly sporulating strain CBS 145.77 (IMI 182034) is here designated as neotype.

(2) **Myceliophthora thermophila** (Apinis) Oorschot, *comb. nov.*— Fig. 3, Plate 1A, B

Sporotrichum thermophilum Apinis *in* Nova Hedwegia **5**: 74. 1963 (basionym). — *Chrysosporium thermophilum* (Apinis) Klopotek *in* Arch. Microbiol. **98**: 366. 1974.
Ascerigerous state: *Thielavia heterothallica* Klopotek *in* Arch. Microbiol. **107**: 223–224. 1976.

Colonies on 2% malt agar initially white, cottony, later pale brown, occasionally greenish, woolly, without a well-defined margin; reaching 60–70 µm diam., in 7 days at 30 °C. Moderately thermotolerant, with optimal growth at 30–36 °C, minimum 24 °C, maximum 54 °C (von Klopotek, *1974*). Keratinolytic but not markedly

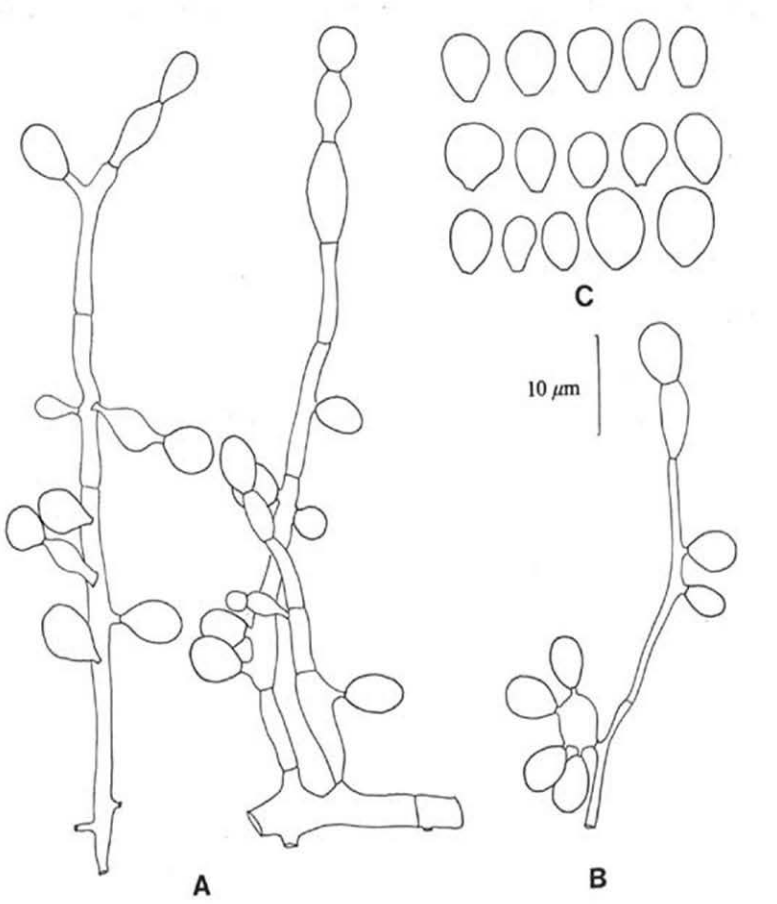

Fig. 2. *Myceliophthora lutea*. — A. Strain CBS 379.76. Aerial hypha bearing conidia. — B, C. Strain CBS 157.51. — B. Part of aerial hypha bearing an ampulliform swelling with 4 conidia. — C. Conidia.

cellulolytic. Submerged hyphae occasionally wider than aerial hyphae (up to 6.0 µm diam.); aerial hyphae 0.8–3.0 µm in diam. Blastoconidia borne terminally or laterally on hyphae, sometimes with short or long pedicels and occasionally a secondary blastoconidium being produced from the distal end of the first; 1–4 blastoconidia may be borne on one hyphal cell or on an ampulliform swelling; conidia obovoid to pyriform, 4.5–11.0 × 3.0–4.5 µm, hyaline, smooth- and thick-walled.

MATERIAL EXAMINED.—CBS 117.65 (type strain) isolated from dry pasture soil, Attenborough, England, *A. E. Apinis*, 1951; CBS 131.65 isolated from birch chips, Stockholm, Sweden, *T. Nilsson*, 1965; CBS 375.69 isolated from woodpulp, New Brunswick, Canada, *J. W. Carmichael*, 1969; CBS 173.70 isolated from wheat straw compost, Cambridge, England, *H. J. Hudson*, 1970; CBS 663.74 isolated from soil beneath *Adansonia* sp., Senegal, *H. Lindner*, 1974; CBS 202.75 isolated from garden soil, Giessen, Germany, *A. van Klopotek*, 1974; CBS 203.75 isolated from soil, Indiana, U. S. A., *M. R. Tansey*, 1974.

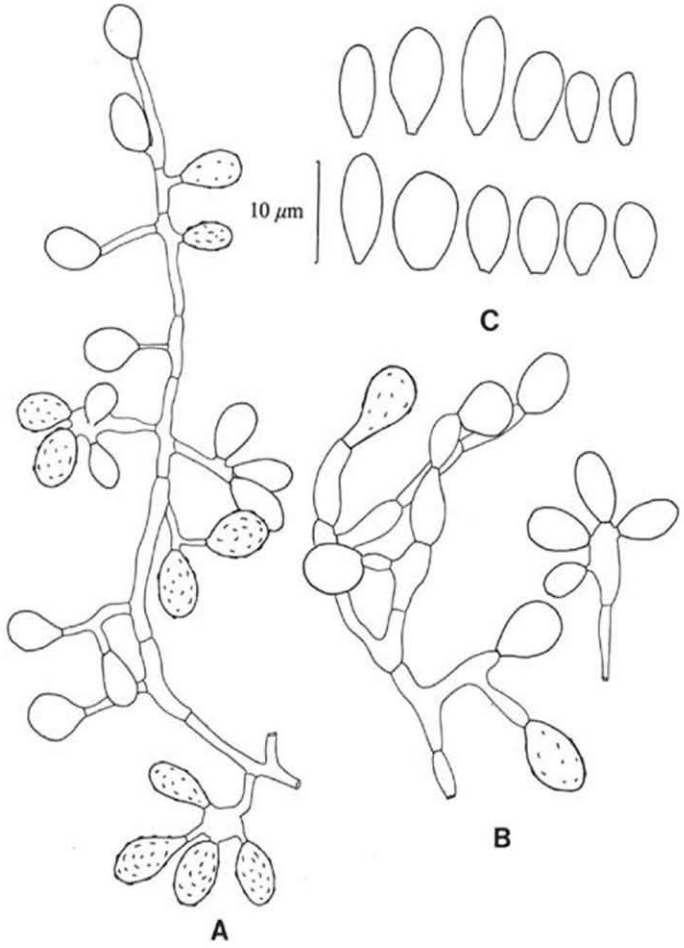

Fig. 3. *Myceliophthora thermophila*. — A. Strain CBS 202.75. Aerial hypha bearing conidia. — B, C. Strain CBS 131.65. — B. Parts of aerial hypha showing branching and ampulliform swelling with conidia. — C. Conidia.

Sporotrichum thermophilum was originally isolated amongst other thermophilic fungi from soild and plant debris in swamps in Britain (Apinis, *1963*). Von Klopotek (*1974*) transferred it to *Chrysosporium* because the hyphae lacked basidiomycete-type clamp connections which are present in *Sporotrichum aereum* Link ex Fr., the lectotype species of the genus. Moreover, *Sporotrichum thermophilum* has an ascomycetous perfect state. As the hyphae bear blastoconidia with narrow basal attachments, hyphal cells which may each produce up to 4 blastoconidia and ampulliform swellings, *M. thermophilum* is very close to *M. lutea*. Fresh isolates of *M. thermophila* always have rough conidia but older cultures tend to produce smooth conidia. Even an old isolate of the type strain CBS 117.65 (maintained since 1951) which was originally described as having smooth conidia (Apinis, *1963*) produced some rough conidia after 30 days on YpSs agar at 30 °C.

MATING EXPERIMENTS.—Von Klopotek (*1976*) obtained a perfect state which she called *Thielavia heterothallica*. The isolates which she used, CBS 202.75 and CBS 203.75, plus another strain, CBS 663.74, were mated. Single conidial isolates of CBS 203.75 with either CBS 202.75 or CBS 663.74, mated and produced mature ascomata of *T. heterothallica* Klopotek on 2% malt agar at 30 °C. In both cases the asci formed on the CBS 203.75 side of the dividing line between the two colonies. This would seem to indicate that either CBS 203.75 is homothallic and is induced by the other strains to produce ascomata, or that CBS 203.75 is heterothallic and acts as the 'female' partner.

(3) **Myceliophthora fergusii** (Klopotek) Oorschot, *comb. nov.*—Fig. 3

Chrysosporium fergusii Klopotek *in* Arch. Mikrobiol. **98**: 366. 1974 (basionym).
Ascigerous state: *Thielavia thermophila* Fergus & Sinden *in* Can. J. Bot. **47**: 1635. 1969. — *Corynascus thermophilus* (Fergus & Sinden) Klopotek *in* Arch. Mikrobiol. **98**: 366. 1974.

Colonies on cornmeal agar initially white, cottony, later pinkish-cream, floccose, covering an 8.5 cm petri dish within 72 h at 40 °C; reverse cream. Thermophilic with optimum growth at 45 °C, minimum 20 °C, maximum 56 °C. Cellulolytic and keratinolytic. Submerged hyphae of the same width as aerial hyphae (3.2–5.2 µm); aerial hyphae fertile at the apex or sterile, up to 5 mm high. Blastoconidia borne laterally or terminally on aerial hyphae, sometimes with short pedicels; up to 5 conidia being borne per hyphal cell. A secondary blastoconidium may be produced from the distal end of the first and ampulliform swellings are globose or slightly obovoid with one (occasionally two) blastoconidia per swelling. Conidia 4.8–12.0 × 2.8–5.2 µm, pyriform to clavate, occasionally somewhat globose, smooth- and thick-walled, hyaline, with narrow basal attachments.

MATERIAL EXAMINED —CBS 405.69 (type-strain) (+), isolated from mushroom compost, U. S. A., *C. L. Fergus*, 1969; CBS 406.69 (—) isolated from mushroom compost, U. S. A., *C. L. Fergus*, 1969; CBS 174.70 isolated from wheat straw compost, Cambridge, England, *H. J. Hudson*, 1969.

In 1969 Fergus & Sinden described the imperfect state of *Thielavia thermophila* Fergus & Sinden as resembling *Sporotrichum thermophilum* (i.e. *M. thermophila*) except in

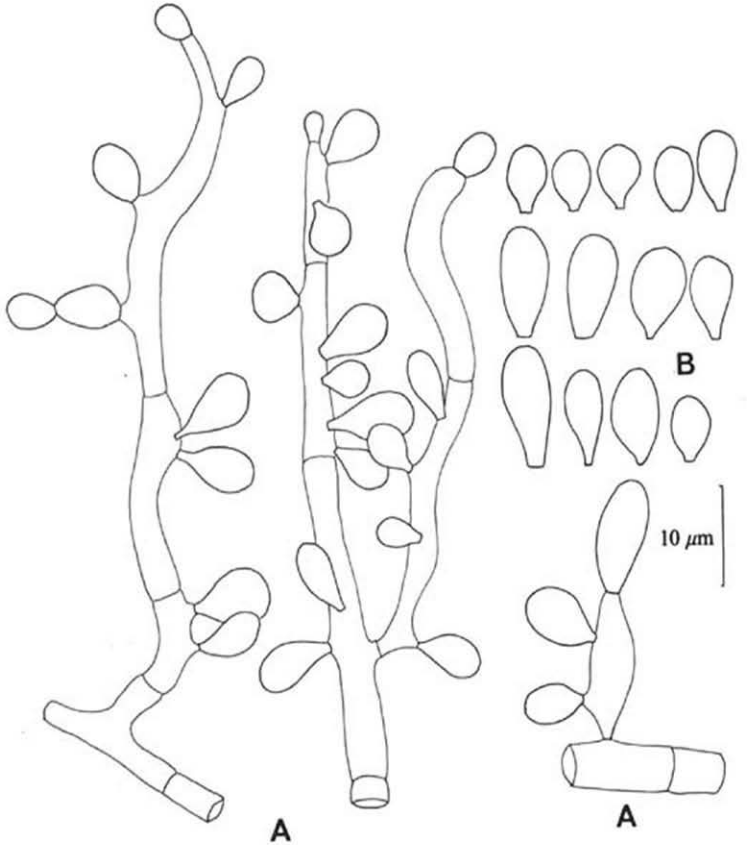

Fig. 4. *Myceliophthora fergusii*. — A, B. Strain CBS 406.69. — A. Parts of aerial hyphae bearing conida. — B. Conida.

cultural characteristics and temperature range. Hedger & Hudson (*1970*) pointed out most of the differences between *M. thermophila* and the conidial state of *Thielavia thermophila*. In addition it should be noted that the latter species has wider hyphae (3.2–5.2 μm) than *M. thermophila* (0.75–3.0 μm) and fewer, usually more elongate ampulliform swellings with less conidia per swelling. This species is transferred to *Myceliophthora* for the same reasons as *Myceliophthora thermophila*.

Excluded species

MYCELIOPHTHORA SULPHUREA Goddard *in* Bot. Gaz. **56**: 263. 1963.

Type material of this species probably does not exist. The drawings and descriptions

of the colonies strongly suggest *Chrysosporium merdarium* (fide Carmichael, *1962*).

MYCELIOPHTHORA INFLATA Burnside *in* Pap. Mich. Acad. Sci. **8**: 82–84. 1928. — *Paecilomyces inflatus* (Burnside) Carmichael *in* Can. J. Bot. **40**: 1148. 1962 (syn. *Paecilomyces flavescens* Brown & Smith *in* Trans. Br. mycol. Soc. **40**: 56. 1957).

MYCELIOPHTHORA FUSCA Doyer *in* Meded. phytopath. Lab. Willie Commelin Scholten **10**: 32. 1927. — *Ptychogaster rubescens* Boud. (fide von Arx, *1973*).

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EXPLANATION OF PLATE 49

Scanning electron micrographs of *Myceliophthora thermophila* strain CBS 202.75. — A. Young aerial hypha showing development of blastoconida. — B. Aerial hypha bearing smooth and slightly rough blastoconida on pedicels and on an ampulliform swelling (top left).

The scale-markers represent 10 μm.

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CLAVARIA LUTEA VITT., EINE EIGENE ART

E. Schild

Brienz, Schweiz

(Mit zwei Abbildungen)

Clavaria lutea Vitt. wird als eine selbständige Art anerkannt, für welche die neue Kombination *Ramaria lutea* vorgeschlagen wird. Die vorliegende Arbeit enthält eine teilweise Wiederbeschreibung des Neotypus, welcher im ZT aufbewahrt ist. Ausserdem ist eine vollständige Beschreibung, basierend auf frischem Material hinzugefügt. Einige der verwirrenden Beschreibungen in der früheren Literatur werden diskutiert.

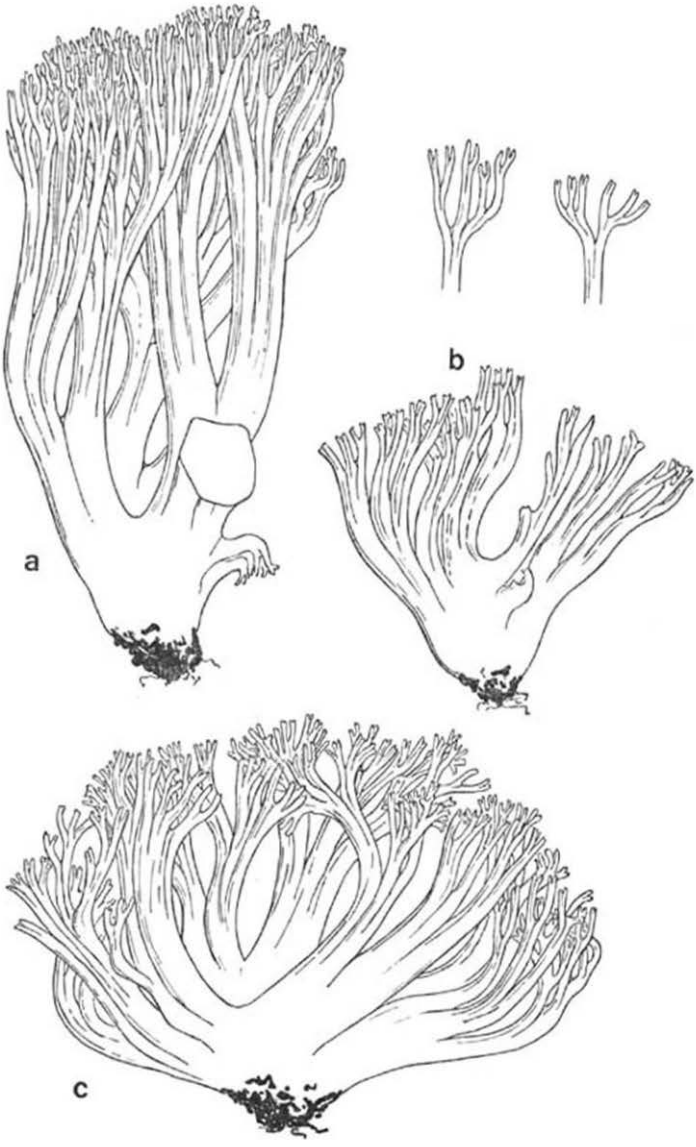
Nachdem Petersen im Jahr 1974 die Schaefferschen Korallenpilze *Clavaria aurea*, *C. flava* und *C. flavescens* endlich geklärt und von diesen Arten je einen Neotypus aus Bayern aufgestellt hatte, wurde im weiteren auch die rotfleckende *Clavaria sanguinea* Pers. geklärt, die in der Literatur oft verwechselt wird, oder unter verschiedenen nomenklatorisch falsch angewendeten Namen figuriert (siehe weiter unten).

Nun wurde dieser Kreis von orangefarbigen bis hell gelben Arten durch die neu aufgestellten europäischen Arten *Ramaria eosanguinea* Petersen und *R. neoformosa* Petersen noch erweitert (*1974*: 739 und *1976*: 309).

Indessen findet man in der Literatur noch den Namen *Clavaria lutea* Vitt., dem man aber — vor allem in der neueren Literatur — nur als Synonym unter *Clavaria*, oder *Ramaria flava* (Schaeff. per Fr.) Quél. begegnet. Die Tatsache, daß einige Mykologen für letztere Pilzart rote Flecken angeben, während andere diese wiederum nicht erwähnen, ließ in mir den Verdacht aufkommen, daß hier vielleicht mehrere Arten im Spiel sein könnten und Verwechslungen nicht ohne weiteres auszuschließen seien. In der Folge studierte ich Vittadinis Originaldiagnose von *C. lutea*, worin jedoch absolut nichts von einer roten Verfärbung dieser Pilzart zu erfahren ist, im Gegenteil, die Bezeichnung „sulphurei" und wiederum „di color giallo zolfino piu o meno risentito", scheint mir ein ziemlich klarer Begriff zu sein.

Im Gegensatz zur Diagnose von *C. lutea* schreibt Vittadini über die Farbe von *C. flava* Schaeff. folgendes: „rami flavi... ramuli sublutei". Diese Auffassung dürfte Vittadini im Sinne Schaeffers (lacte flavis) verstanden haben (dies gilt auch für die Beschreibung von *C. flava* bei Bourdot & Galzin), woraus ersichtlich ist, daß er *C. flava* und *C. lutea* für zwei verschiedene Arten hielt.

Während ich nun Vittadinis Farbtafel betrachtete, welche *C. lutea* als einen sehr hellen bleich gelben Korallenpilz ohne rote Flecken darstellt, erinnerte ich mich, vor einigen Jahren in Bologna (Italien) zwei schöne, blaß gelbe und auf Vittadinis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Farbbild gut passende Korallenpilze in die Hände bekommen zu haben, die ich noch im Frischzustand untersuchte, skizzierte und beschrieb. Infolge des Ausbleibens der von mir damals erwarteten roten Verfärbung, wie sie von *Ramaria flava* bekannt war, wollte mir die Bestimmung dieser zwei Funde nicht gelingen. Durch die Feststellung, dass diese Pilze keine Schnallen besitzen und ihre Sporen merklich kleiner sind als bei *R. sanguinea* und der Schnallen aufweisenden *R. flava* sensu Petersen, konnte ich letztere beide Arten mit Sicherheit ausschließen. Indessen bestätigte sich meine Vermutung, daß es sich bei den zwei Kollektionen aus Bologna um *C. lutea* handeln könnte. Aus Vittadinis Sammelgebiet der Lombardei, wenn möglich aus der Gegend um Milano noch Material zu beschaffen, war dann mein nächstes Ziel. Dank der freundlichen Mithilfe von Herrn Renato Tomasi aus Brescia, bekam ich im November 1976 ein Paket mit mehreren Exsikkaten verschiedener Ramarien, die er im Herbst des gleichen Jahres in der Gegend von Brescia — Milano, als „gelbe Clavarien" gesammelt hat.

Da nun vor allem Milano sich stark industrialisierend vergrößert hat und ein Suchen nach dem damaligen Standort von *C. lutea* heutzutage aussichtlos ist, muß man schon froh sein, daß in der weiteren Region um die genannte Stadt überhaupt noch Ramarien gefunden werden können.

Nach eingehender Untersuchung dieser Kollektionen (es waren etwa 10), konnte ich eine Probe aussondern, die in allen mikroskopischen und makroskopischen Merkmalen eindwandfrei mit den zwei Pilzfunden aus Bologna identich ist! Von dem Moment an gab es für mich keine Zweifel; ich habe mich denn auch entschieden, dieses eine Exsikkat das in der Gegend zwischen Brescia—Milano gefunden wurde, als den Neotypus von *Clavaria lutea* Vitt. aufzustellen.

Somit gebe ich eine hauptsächlich mikroskopische Beschreibung dieser Exsikkatprobe der nun wie folgt zu nennenden Pilzart.—

Ramaria lutea (Vitt.) Schild, *comb. nov.*

Clavaria lutea Vitt., Descr. fung. mang. Italia: 228, 1835 (Basionym).

Fruchtkörper 50 mm hoch, 35 mm breit; Strunk allein 35 mm hoch, 8 mm breit. Die Farbe der trockenen Äste ist créme-beige-oliv. Das vorhandene Exsikkat stellt jedoch nur einen Teil des gesamten Fruchtkörpers dar, da der Pilz zerschnitten wurde, wodurch leider auch die Stammbasis fehlt.

Sporen blaß graugrünlich-graulicholiv 6–9,6 × 3,7–5,4 µm, Wand um 0,2 µm dick, cyanophil, Apiculus 0,7–1,3 µm lang, Apiculuswand nicht oder nur schwach cyanophil, Warzen mittelgroß, sehr unregelmäßig angeordnet, bisweilen etwas reihig miteinander verbunden, ± stark cyanophil. Basidien blaß graugrünlich, glatt oder teilweise mit tropfig-körnigem Inhalt, keulig, 40–56 × 6,5–9,5 µm, an der Basis ohne Schnallen, mit 4 oder 3 (2) relativ kurzen Sterigmen, (2,4)–3,2–6,5 µm

Abb. 1. *Ramaria lutea*, Fruchtkörper in frischem Zustand, × 0,8 — a. Von Bologna (Herb. Schild 569). — b. Von Hofstetten, Brienz (Herb. Schild 1045). — c. Von Bologna (Herb. Schild 572).

lang. Basidiolen meist etwas kürzer, im Inhalt fast gleich wie die Basidien. Zystiden keine. Hymenium um 60–80 µm dick, olivgrün. Hyphen von einer Sorte, fast hyalin, im ganzen Fruchtkörper ohne Schnallen, im Subhymenium oder nahe dem Hymenium stark irregulär, meist 2–3,5 µm dick, Wände dünn, 0,2–0,4 µm und blaß olivlich; in der Trama der Äste im allgemeinen subregulär, ziemlich langzellig, 2–10,5 (13) µm dick, parallelwandig bis etwas langbauchig, oder nur gegen die Septen etwas verjüngt oder eingeschnürt, bisweilen sekundär septiert, Wände blaß graugrünlich-olivlich, glatt, dünn, zwischen 0,3–0,5 µm. Hier und da ampullenförmige Anschwellungen mit und ohne Fortführung der Hyphenzellen bis um 12 µm dick und mit ± ausgeprägt fein-tropfigkörnigem Inhalt und Wände hier etwas stärker, zwischen 0,7–1 µm (Abb. 2c). Hyphen im Strunk 2,5–10 µm dick, Wände ± dünn bis leicht verdickt, zwischen 0,3–0,5 (0,7) µm, einzelne Glieder ähnlich wie diejenigen in den Asthyphen, hier und da auch sekundär septiert. Ampullenförmige Anschwellungen hier etwas häufiger als in den Asthyphen, etwa 12–16 µm dick, mit gleichem Inhalt, Wände hier etwas stärker, zwischen 0,7–1,3 µm. Stellenweise viele einzeln herumliegende Kristallaggregate, in der Form sehr unterschiedlich (etwa rosetten-mosaikartig zusammengesetzt, oder unregelmäßig quadratförmig), meist zwischen 4–18 µm groß, bisweilen jedoch auch in zusammenhängenden Gruppen

Oleiferen im Strunk zerstreut, etwas spärlicher in den Ästen, parallelwandig bis unregelmäßig, 2,5–6,5 µm dick, an den angeschwollenen, seltener aber kopfigen Enden bis 16 µm.

UNTERSUCHTES MATERIAL.—ITALIEN, Gegend zwischen Brescia und Milano, bei Laubbäumen, Oktober 1976, *R. Tomasi*, (Neotypus, ZT).

Der Vollständigkeit halber folgt noch eine Beschreibung wie ich sie anhand von frischem Material angefertigt habe.—

Fruchtkörper 60–120 mm hoch, 70–110 mm breit (Abb. 1). Strunk abwärts ± konisch, an der Basis 10–15 mm dick, oben etwa 20–35 mm, glatt, seltener mit tiefer gelegenen Seitenästchen, unten weiß, aufwärts allmählich in weiß-gelblich, dann in die Farbe der Äste übergehend. Äste aufrecht bis stark verbogen, unten 4–15 mm dick, aufwärts bis zur nächsten Astteilung entweder gleichdick und nur kurz vor der Teilstelle dicker werdend, oder allmählich gegen die Teilung sich erweiternd und manchmal etwas flach gedrückt, im allgemeinen wenig rundlich, meist unregelmäßig kantig und ± stark längsgefurcht speziell unterhalb der fast überall spitzen Astwinkel (charakteristisch!), gegen oben mehrfach dichotom geteilt, dabei sich immer verfeinernd und Enden junger Fruchtkörper meist „zweizahnig", an älteren Pilzen mehr zangenartig verlängert, einzelne Spitzchen 3–5 (10) mm lang und stumpfspitzig. Farbe der Äste im allgemeinen wenig variabel, bei jüngeren, frischen Pilzen sehr hell schwefelgelb (am nächsten etwa Séguy 289/290/319) und Spitzen gleichfarbig oder etwas lebhafter gelb, eintrocknende Fruchtkörper eher noch bleicher (etwa Séguy 320), an Exsikkaten créme–beige–oliv, wie beim Neotypus. Auf Druck unveränderlich. (Einer der Pilze aus Bologna hatte auf dem Strunk und den unteren Hauptästen schmutzig grauviolettliche, zum Teil nur punktförmig kleine Flecken, was von einem Parasiten herrühren dürfte.) Hymenium die Äste bis zu den Spitzen bedeckend, matt. Fleisch bei feuchten Pilzen etwas wässerig weiß und schwach beige-graulich marmoriert, speziell im Strunk, bei eintrocknenden Pilzen eher milchweiß, weich, biegsam brüchig. Geruch etwas variabel und schwer definierbar; im allgemeinen ähnlich wie die meisten anderen gelben bis orange- oder rosa-gelben Arten, schwach oder

herber grasartig, bei einem Exemplar aus Bologna mit eigenenartigen, entfernt an *Tricholoma sulphureum* erinnernden Beikomponenten. Geschmack mild aber schwer definierbar.

Sporenpulver in Masse auf weißem Papier abgeworfen hell ocker, auf Glas abgeworfen sehr blaß ockergelb. Sporen (5,5–)6–10,5(–10,8) × 3,2–5,5 µm, manchmal mit einem oder zwei Tropfen (vermutlich wenn nicht ganz ausgereift), Apiculus zwischen 0,7–1,3 µm lang. Sporenform, Farbe, Wand und Warzen gleich wie beim Neotypus. Basidien (34–)40–56(–64) × (5,5–)6,5–9,5(–11) µm, mit 4 oder 3 (2) Sterigmen, (2,5–)3–7(–8,5) µm lang, sonst gleich wie beim Neotypus. Basidiolen 34–56 × 4,8–7,5 µm, im Inhalt fast gleich wie die Basidien. Keine Zystiden. Hymenium wie beim Neotypus. Subhymenium schmal, um 10–20 µm dick, jedoch gegen die Trama schlecht abgegrenzt, bestehend aus stark irregulär verlaufenden, dünnen und kürzerzelligen Hyphen.

Generative Hyphen, Oleiferen und Kristallaggregate im allgemeinen wie beim Neotypus.

UNTERSUCHTES MATERIAL — ITALIEN, Bologna, in Laubwald, Sept 1972, Finder unbekannt (Herb. Schild 569 und 572). SCHWEIZ, Hofstetten bei Brienz, in Laubwald, hauptsächlich *Fagus*, 1 Sept. 1976, *E. Schild* (Herb. Schild 1045); Tessin, bei *Fagus* und *Quercus*, 5. Okt. 1976, *G. Lucchini* (Herb. Schild 1073).

Größere Pilze von *Ramaria lutae* können sehr leicht mit zarteren Fruchtkörpern von *R. flava* verwechselt werden. Beide Arten röten nicht. Oberflächlich gesehen haben sie zwar fast die gleiche gelbe Farbe, bei genauer Betrachtung stellt man aber fest, daß *R. lutea* meist ein helleres bleiches Gelb aufweist. Ihre Sporen sind zudem viel kleiner und die Hyphen haben im Gegensatz zu *R. flava* keine Schnallen. Von *R. sanguinea* (Pers. per Secr.) Quél. unterscheidet sie sich ebenfalls durch eher noch bleicheres Gelb, völliges fehlen einer roten Verfärbung und kleinere Sporen. Schließlich möchte ich noch *R. eosanguinea* Petersen erwähnen, die sich durch schwaches Röten an Druckstellen, am Strunk oder im Fleisch, größere Sporen und Hyphen mit Schnallen von unserem Pilz unterscheidet.

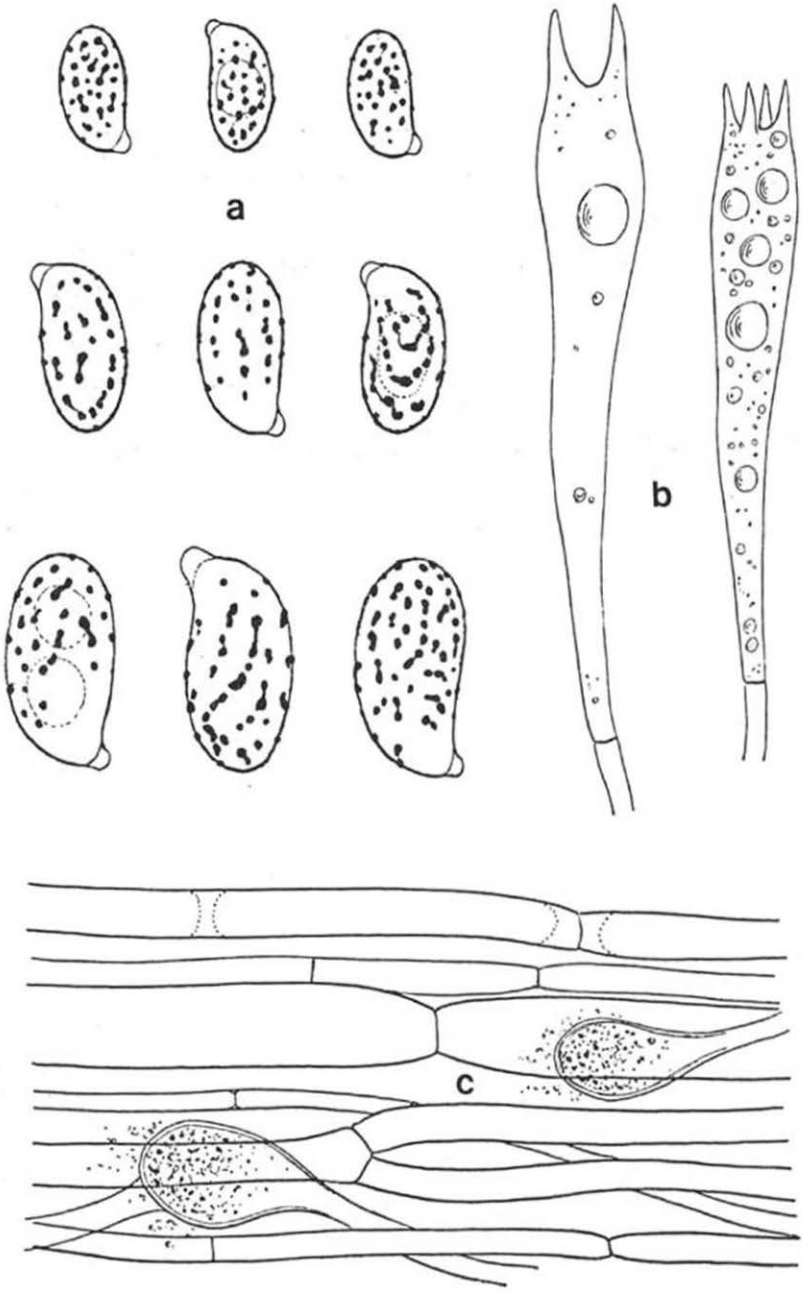
Anhand der bis jetzt nur wenigen sicheren Funde nehme ich an, daß *R. lutea* in der Schweiz eine seltenere Art ist und wärmere Regionen vorzieht. Wie weit diese Pilzart gegen Norden heraufsteigt sowie auch ihre allgemeine geographische Verbreitung, ist mir nicht bekannt.

Im Folgenden werden einige der vielen in der Literatur vorkommenden Vermischungen und Verwechslungen zwischen *Clavaria sanguinea*, *C. flava* und *C. lutea* näher beleuchtet.

Bresadola (*1932*: Taf. 1086) beschreibt die Farbe bei *C. flava* mit „flavo-sulphurini" und gibt kein Röten an, während er auf der Farbtafel einen rotfleckenden Strunk zeigt. Die Sporen werden mit 10–14 × 4–5 µm angegeben. Er muß somit *C. sanguinea* mit *C. flava* vermischt haben.

Saccardo (*1916*: 1227) beschreibt die Äste bei *C. flava* mit „flavis" und erwähnt nichts von Röten. Die Sporen gibt er mit 8–10 × 4–5 µm vel 10–13 × 4 µm an. Hier scheint eine Vermischung von *C. lutea* und *C. flava* vorzuliegen.

Cotton & Wakefield (*1918*: 169) geben die Farbe bei *C. flava* wie folgt an: „ochra-


a
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ceous ... reddish when bruised" und die Sporen werden mit 11–14 (15) × 4–5 µm angegeben. In diesem Fall stimmt die Farbe mit einer reifenden *C. sanguinea* überein, während die Sporen besser für *C. flava* zutreffen.

Corner (*1950*: 577) schreibt in seiner Monographie über die Farbe bei *R. flava* folgendes: „sulphur-yellow or lemon-yellow, ageing ochraceous: stem whitish at the base, often reddish or bloodred on bruising or with age". Die Sporen gibt er mit 11–18 × 4–6,5 µm an. Dies sind hohe Masse, deshalb müssen hier nebst *C. sanguinea* Pers., auch noch andere Arten im Spiel sein.

Donk (*1933*: 107) gibt die Farbe für *R. flava* folgendermassen an: „Strunk ... vielfach rot gefleckt. Äste ... leuchtend hell schwefel- bis zitronengelb". Die Sporenmasse übernimmt er von Konrad & Maublanc wie folgt 9–12 × 4–5 µm. Für den Standort schreibt er „In Laub- wie in Nadelwäldern". Hier dürfte *R. sanguinea* vorliegen, zugleich aber auch eine andere Art, da *R. sanguinea* meines Wissens nur im Laubwald vorkommt, ja vermutlich sogar eine Symbiose mit *Fagus* eingeht.

Hennig (*1958*: 237, Tafel 177) hat die Sache wohl nur von Donk abgeschrieben und schreibt: „*Ramaria flava* hat schwefelgelbe Äste und einen weissen Strunk der oft weinrote Flecken aufweist", Sporen 9–12 × 4–5 µm. Nach eigener Beobachtung schreibt er nur: „Bei Pilzen des Tieflandes sind rote Flecken meist nicht festzustellen". Auch dieser Äußerung ist zu entnehmen, daß neben *R. sanguinea* noch andere Arten darin verwickelt sein müssen, denn *R. sanguinea* weist früher oder später immer Rötungen auf, und beim „Übergehen" werden die Fruchtkörper oft fast gänzlich schmutzig weinrot-purpurbraun.

Coker (*1923*: 120, Taf. 39, Fig. 1) beschreibt *C. flava* als gelb ohne rote Verfärbung. Für die Sporen gibt er 7,4–10 × 3–4 µm an. Anhand dieser Sporenangabe hat der Pilz nichts mit der heutigen *R. flava* zu tun, könnte aber mit *R. lutea* identisch sein.

Schließlich möchte ich noch *Ramaria flaviceps* Corner, Thind & Anand (Thind, *1961*: 59) erwähnen, deren Existenz als selbständige Art ich jedoch bezweifle, da sich dieser Pilz gemäß den Literaturangaben weder makroskopisch noch mikroskopisch eindeutig von *R. lutea* unterscheiden läßt.

Wie aus diesen Beispielen ersichtlich ist, findet man *Ramaria sanguinea* in der Literatur fälschlicherweise meist unter dem Namen als *Clavaria flava* oder *Ramaria flava* und von Corner (*1970*: 262) wird der Pilz noch als *Ramaria flava* var. *sanguinea* aufgeführt.

Summary

Clavaria lutea Vitt. is recognized as a species in its own right, for which the new combination *Ramaria lutea* is proposed. A partial redescription is given of the neotype preserved at ZT, and a full description based on fresh material is added. Some of the confusing descriptions in earlier literature are discussed.

Abb. 2. *Ramaria lutea*. — a. Sporen, × 3000. — b. Basidien, × 2000. — c. Hyphen und Anschwellungen in der Trama der Äste, × 1000.

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ON TWO SPECIES OF THE GENUS TRECHISPORA (CORTICIACEAE)

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Two species formerly placed in *Trechispora* have been studied and are now transferred to two different genera. The following new combinations are proposed: *Ramaricium albo-ochraceum* (Bres.) Jülich and *Lindtneria leucobryophila* (P. Henn.) Jülich. The genus *Lindtneria* has been emended.

The genus *Trechispora* is characterized by its ampulliform hyphal swellings, relatively small basidia and small spores with smooth or ornamented surface. In his excellent revision of the genus, Liberta (*1973*) accepted two species which differ from all other members in having larger basidia and spores. On re-examining these species I realized that the relationships are to be sought with other genera.

The first species studied is *Corticium albo-ochraceum* Bres. The type material shows pale brownish and elongated spores with flat warts of irregular diameter, thus contrasting with the typical finger-like excrescences of most species of *Trechispora*. As a whole the strongly cyanophilous spores with its large apiculus remind one very much of the spores of a *Ramaria*. For specimens with corticioid basidiocarps J. Eriksson (*1954*) described the genus *Ramaricium* — now a member of the Gomphaceae — with *R. occultum* J. Erikss. as its only species. *Corticium albo-ochraceum* Bress. clearly belongs to *Ramaricium* and might even be an older name for *R. occultum*. —

Ramaricium albo-ochraceum (Bres.) Jülich, *comb. nov.* (basionym: *Corticium albo-ochraceum* Bres. *in* Annls mycol. **1**: 96. 1903).

The second species restudied is *Thelephora leucobryophila* P. Henn. The type material shows large basidia (up to 55 μm long) and large spores with an ornamentation of spines and some wing-like crests. These spores, too, exhibit a strongly cyanophilous reaction. Since the basidia in younger stages contain numerous cyanophilous globules which unite in mature basidia to form one to three large guttules, a possible relationship with the genera *Cristinia* (Corticiaceae) and *Lindtneria* (Polyporaceae) comes to mind. The genus *Christinia* deviates because of its smooth spores, but species of *Lindtneria* seem to be very similar both with regard to the soft-membranaceous basidiocarps as well as to the spiny, globose to broadly ellipsoid spores. The only difference seems to be the poroid hymenial surface. An examination of material of *Lindtneria trachyspora* (the generic type species) strongly suggests a relationship with the Corticiaceae. The soft basidiocarp, the monomitic hyphal system and the structure of the hymenium indicates that it belongs to this family (a view already expressed

by Parmasto (*1968*). Up to now three species of *Lindtneria* are known viz. *L. trachyspora* (Bourd. & Galz.) Pilát (widespread but rare in Europe), *L. flava* Parm. (described from Russia), and *L. pterospora* Reid (from West Africa). I do not think that the poroid basidiocarps of these three species is a highly advanced character which should separate them from species with a smooth hymenophore, and so I prefer to place the corticioid *Thelephora leucobryophila* together with the poroid species in an emended genus *Lindtneria*, characterized also by the cyanophilous globules in the basidia. The genus *Cristinia* shows different hyphal structures and smooth spores, and should remain a genus on its own.

LINDTNERIA Pilát (*1938*), emend. Jülich

Basidiocarp soft-membranaceous. Hymenial surface smooth, merulioid to poroid. Hyphal system monomitic. Hyphae hyaline, thin-walled, with or without clamps, often inflated where branching occurs. Basidia hyaline, clavate to suburniform, four-spored, with strongly cyanophilous globules or guttules in the cytoplasma. Spores hyaline to mostly pale brown, somewhat thick-walled, globose to broadly ellipsoid, with an ornamentation of spines or wing-like crests, the spore-wall as well as ornamentation strongly cyanophilous.

TYPE SPECIES.—*Lindtneria trachyspora* (Bourd. & Galz.) Pilát (*1938*).

EXAMPLES.—*Lindtneria flava* Parmasto (*1968*); *Lindtneria pterospora* Reid (*1976*); **Lindtneria leucobryophila** (P. Henn.) Jülich, *comb. nov.* (basionym: *Thelephora leucobryophila* P. Henn. *in* Verh. Bot. Ver. Prov. Brandenb. **39**: xcvi. 1898).

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PERSOONIA
Published by the Rijksherbarium, Leiden
Volume 9, Part 3, p. 419 (1977)

BOOKS RECEIVED BY THE RIJKSHERBARIUM LIBRARY

G. BECKER, *Les champignons.* (Gründ, Paris, 1977.) Pp. 96, 4 Text-figs., 109 colour-photographs.

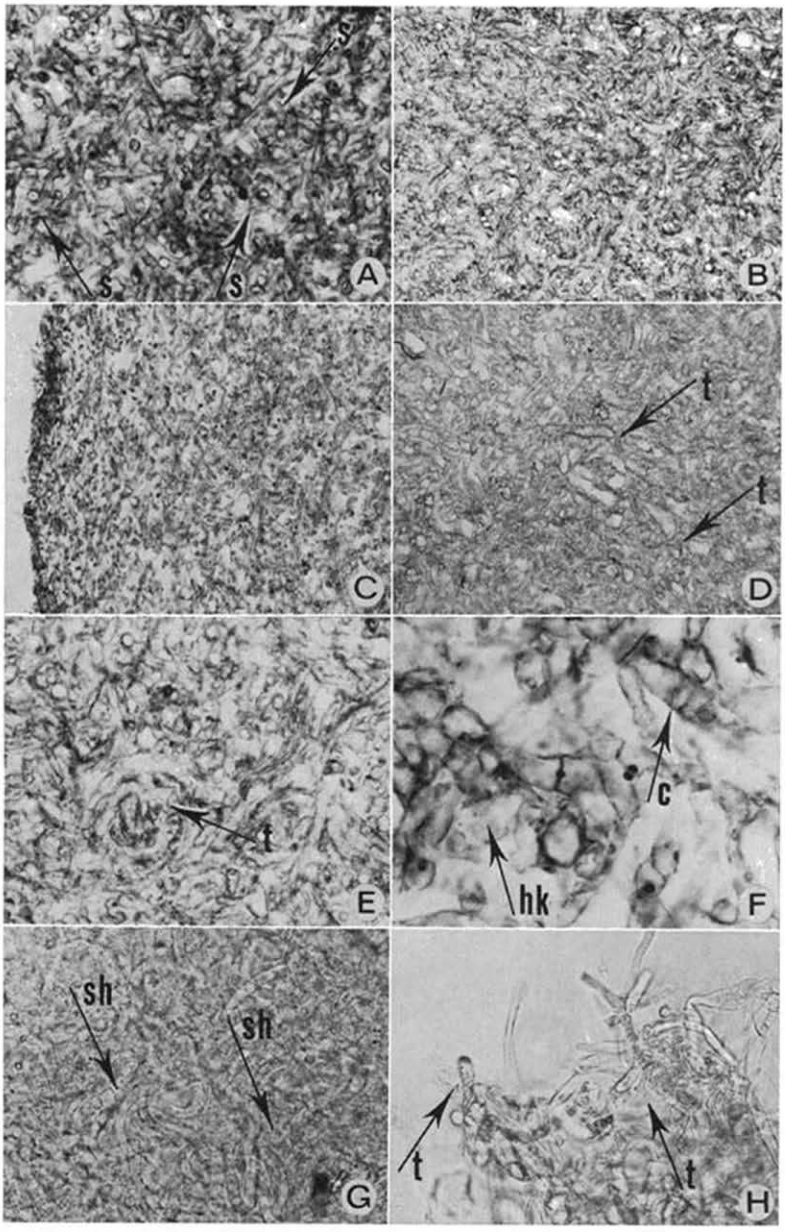
This richly illustrated book shows many of the most common and most spectacular species of fungi found in Western Europe. The text is very popular and touches such items as poisionousness, edibility, culinary instructions, prejudices, and folklore.

M. V. LOCQUIN, *Mycologie du goût.* (J.-F. Guyot, Paris, 1977.) Pp. 97. Price: 30 Frs.

In this book, after a comprehensive culinary introduction, 24 menus and 176 recipes with mushrooms are presented.

D. M. PEGLER, *A premilinary Agaric Flora of East Africa.* (*In* Kew Bull., Additional Series VI, 1977.) Pp. 615, 129 Text.-figs. Price: £ 45.

This agaric flora is mainly based on the author's collections and on material deposited in the Kew Herbarium from Kenya, Tanzania, and Uganda. The East African fungus flora is extremely rich. In this flora 17 families are considered containing 94 genera and 389 species. Each of the accepted genera and species are described in detail. Line-drawings are given of both the habitus and the microscopic characters for each species. Author citations, synonymy, and collecting data are quoted. Many new species (63) and new combinations (23) are proposed. Idented keys are provided for the determination of all taxa treated.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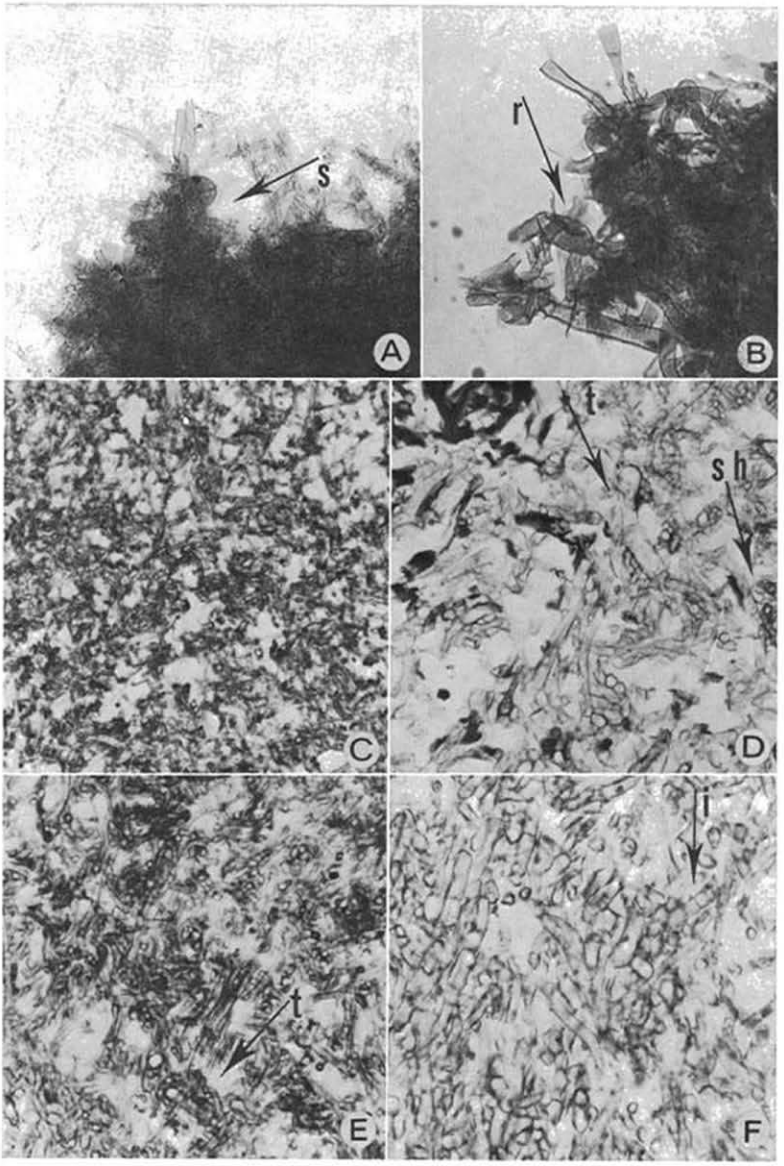
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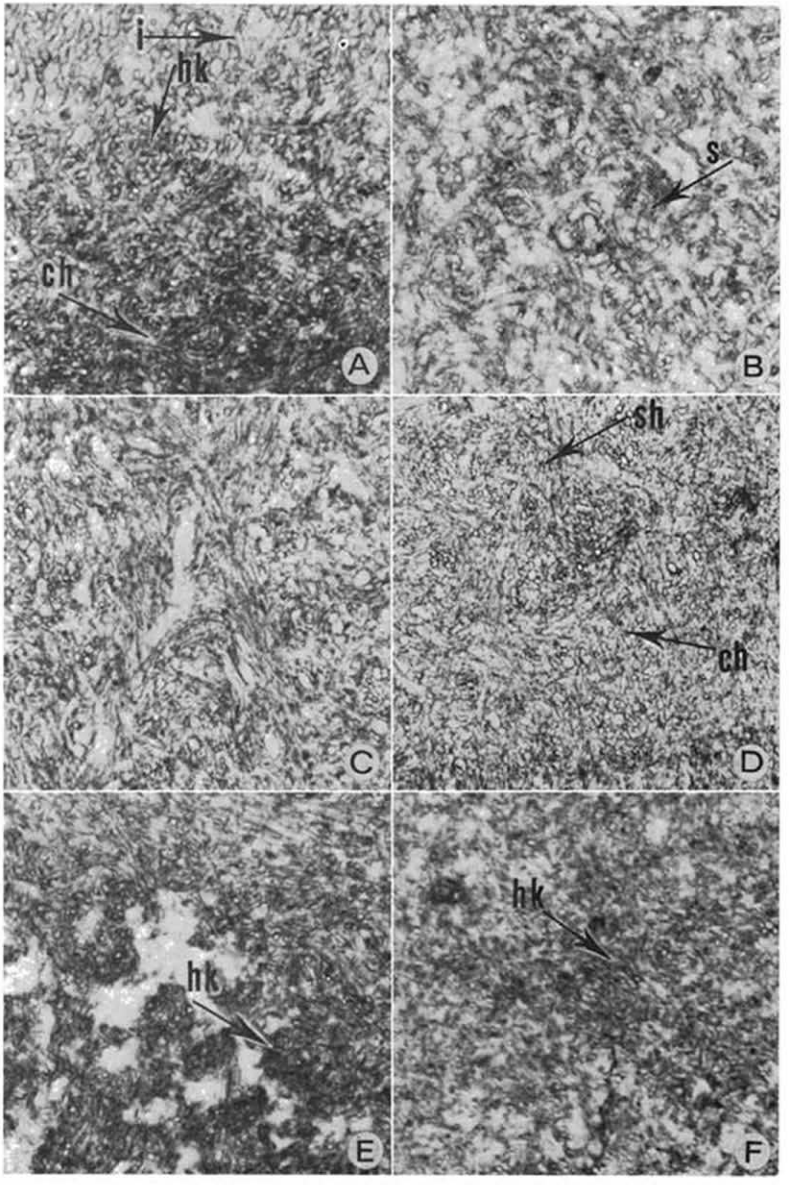
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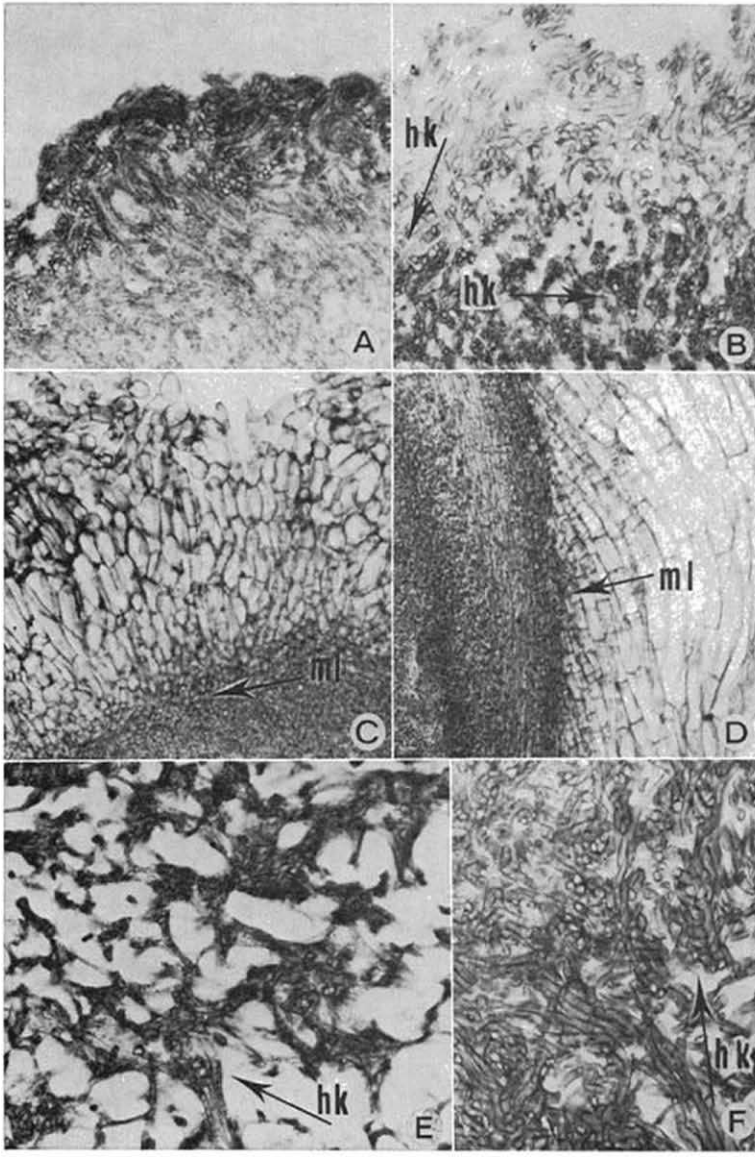
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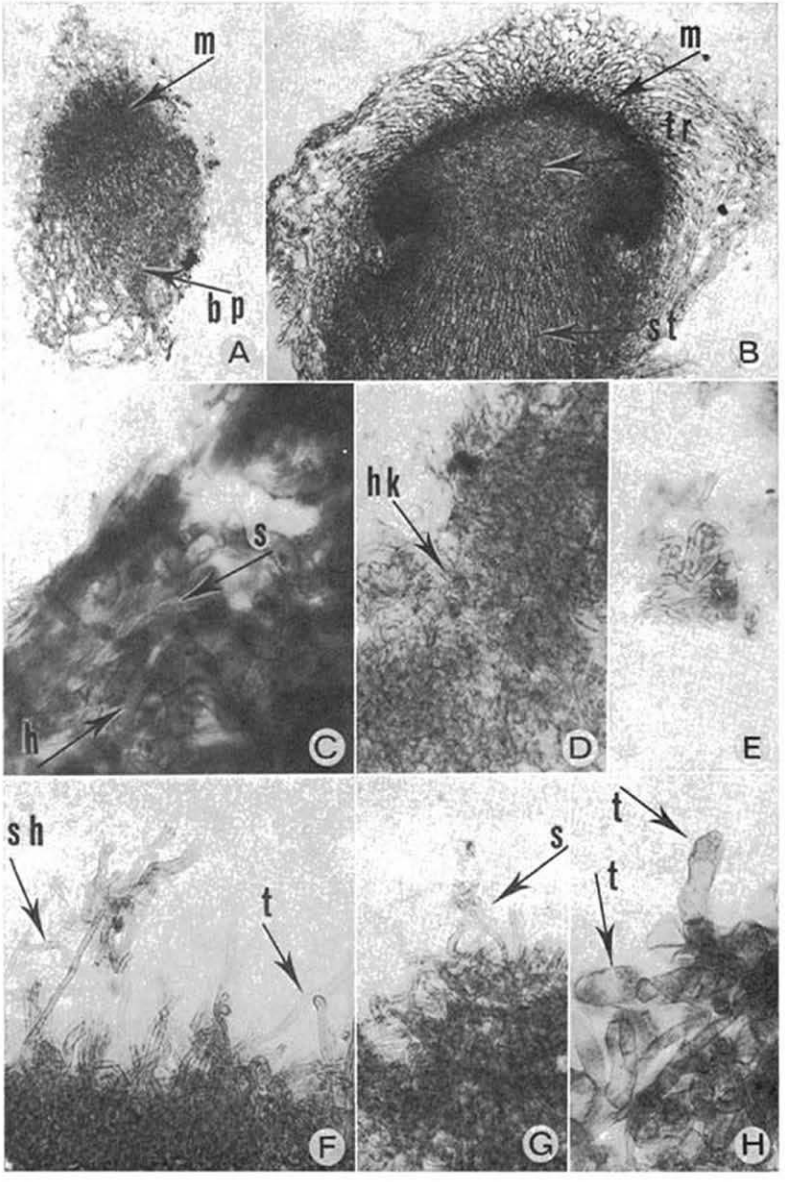
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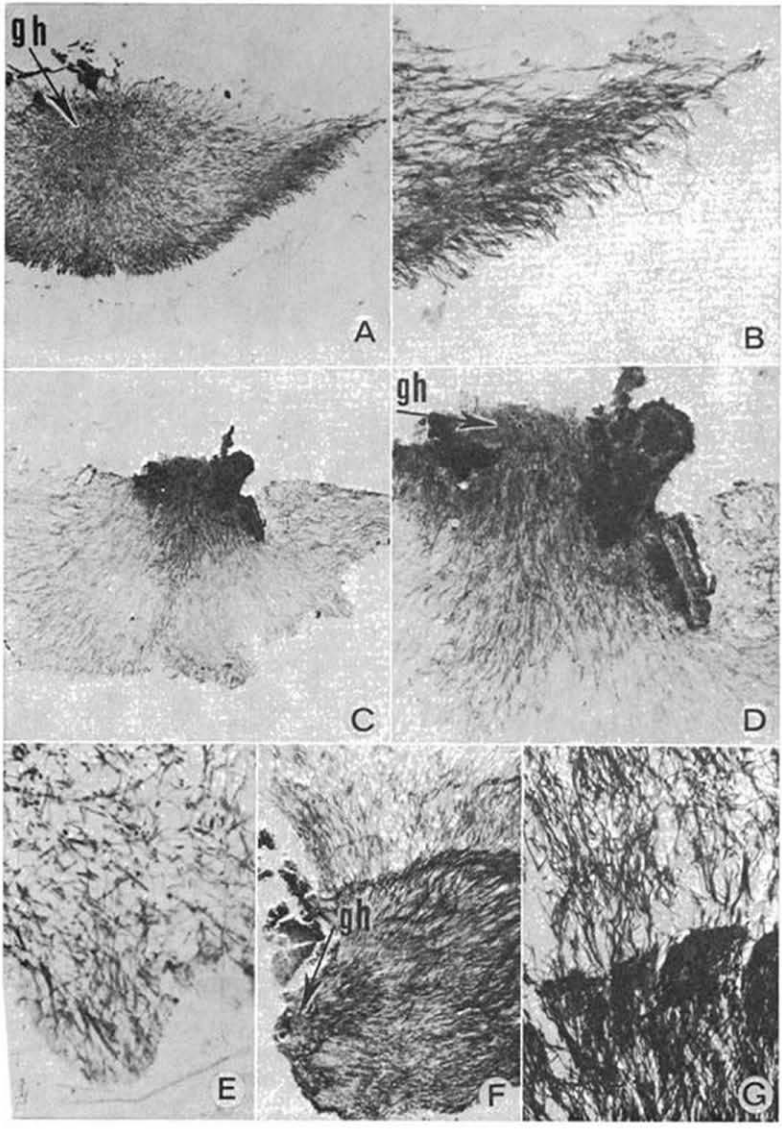
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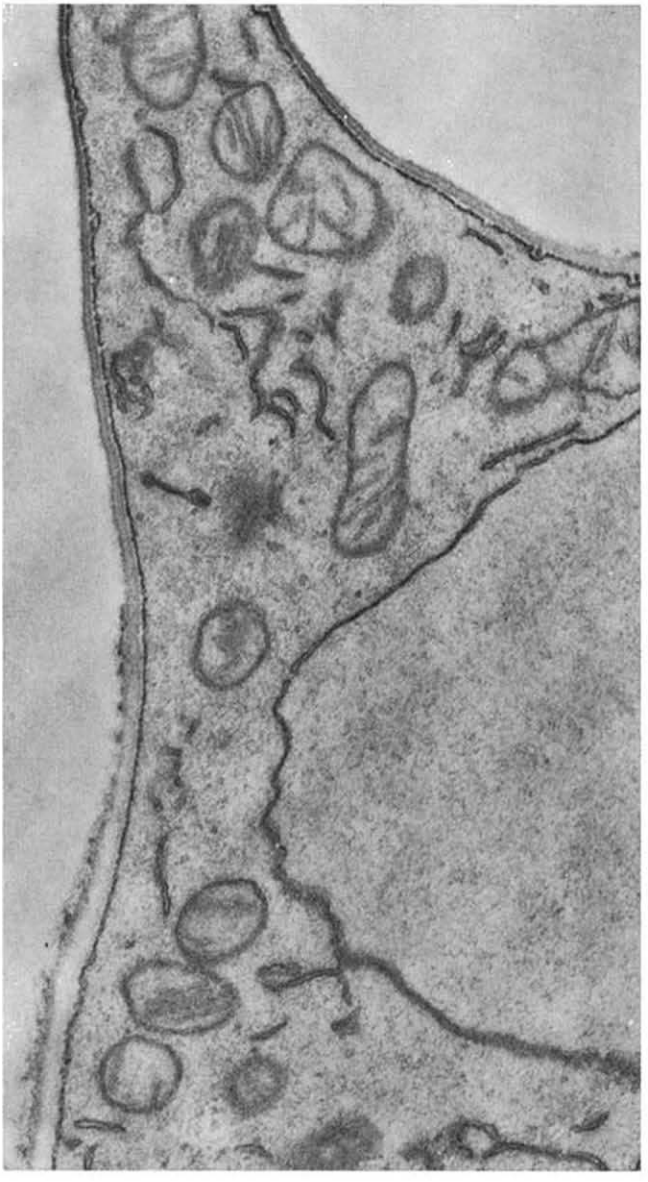

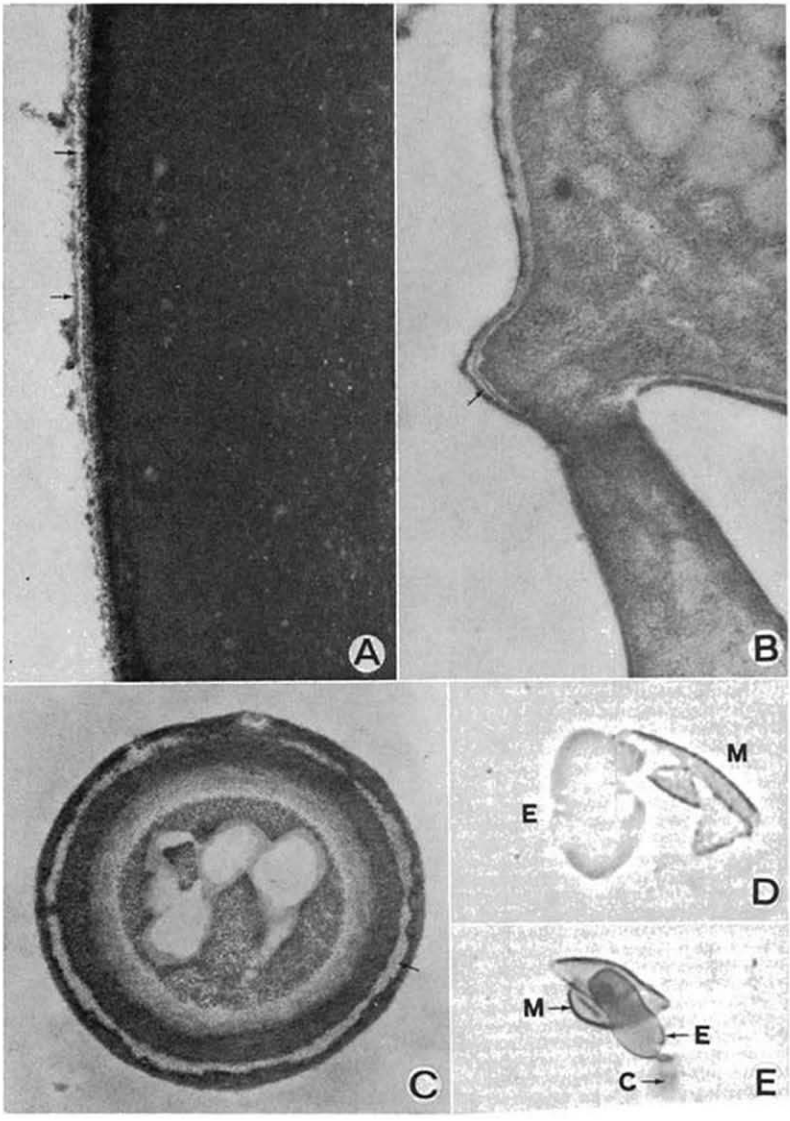
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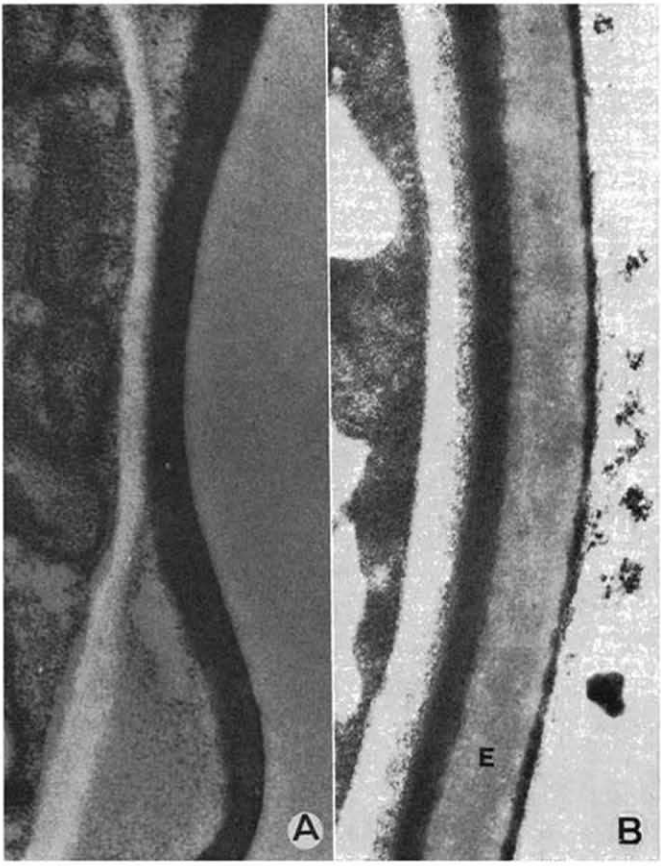
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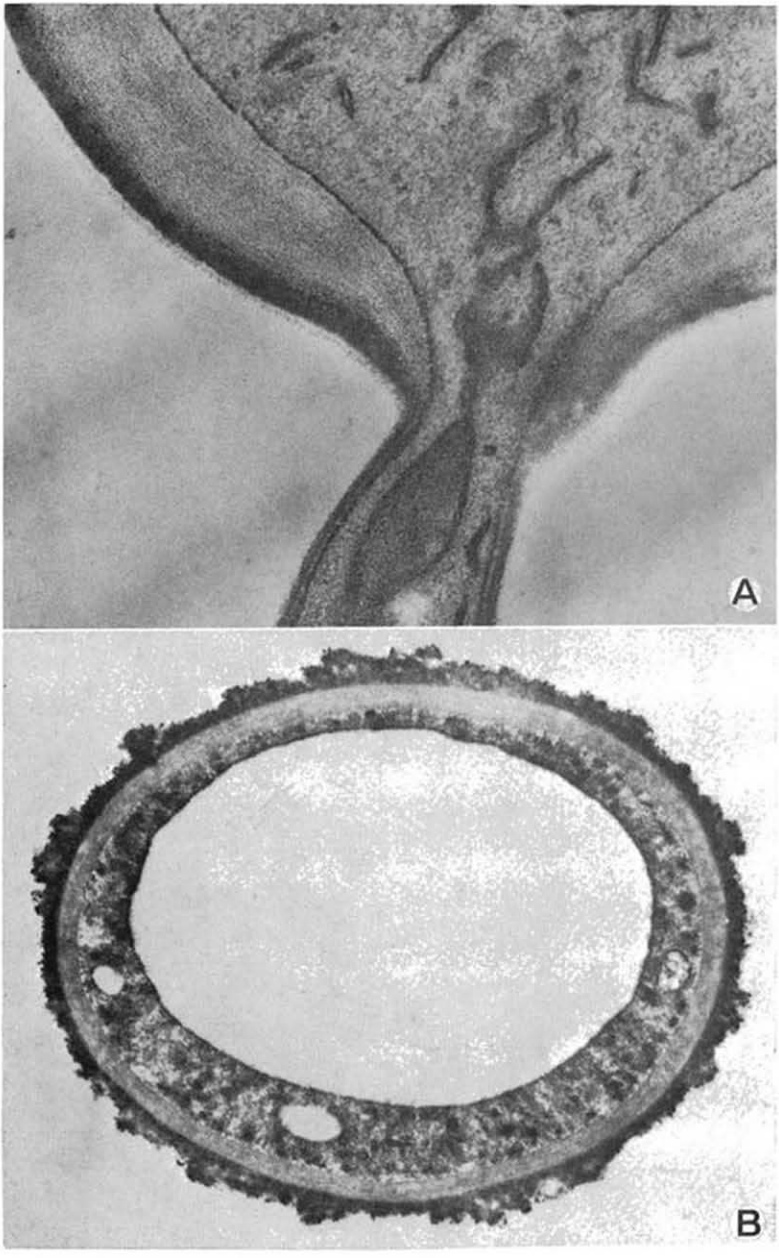
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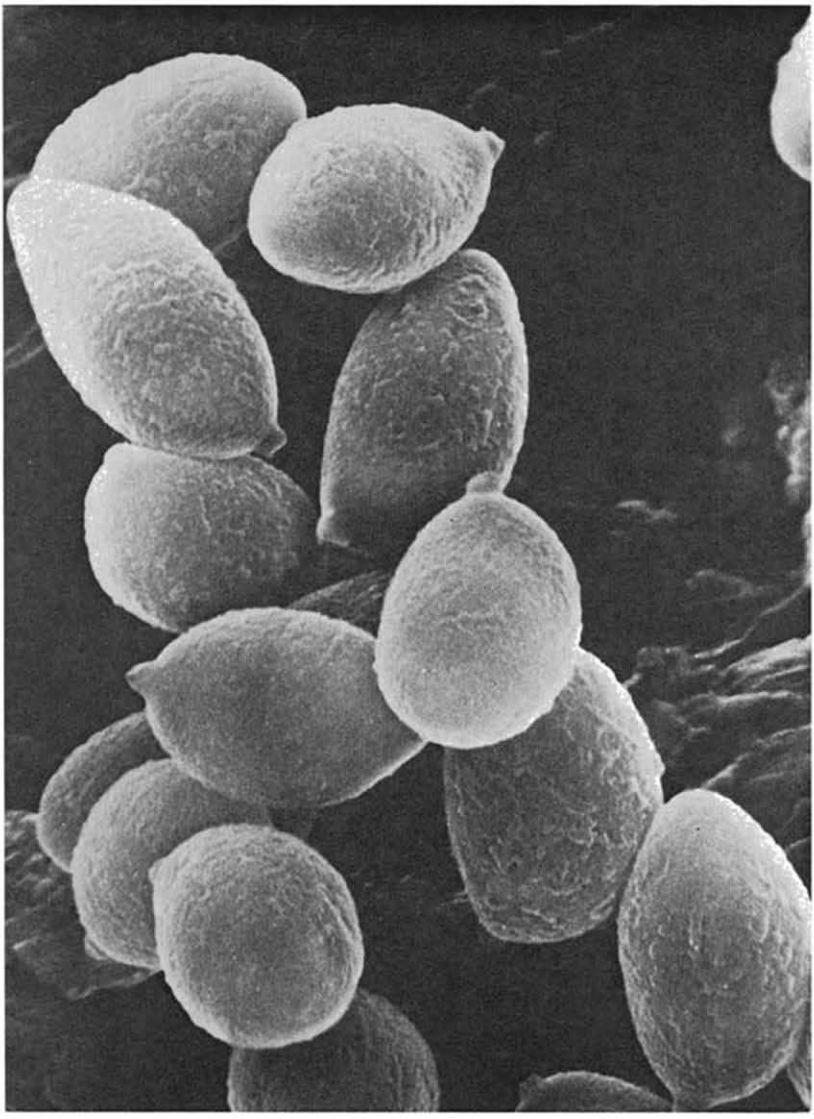

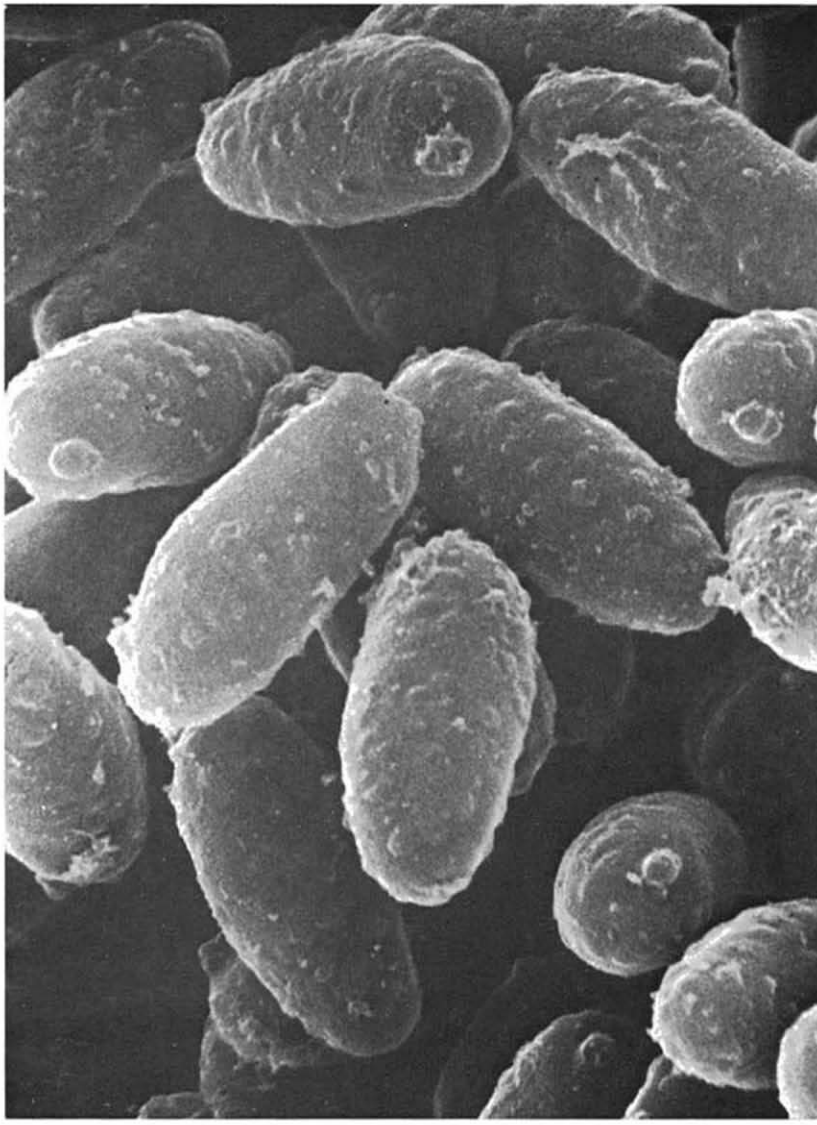

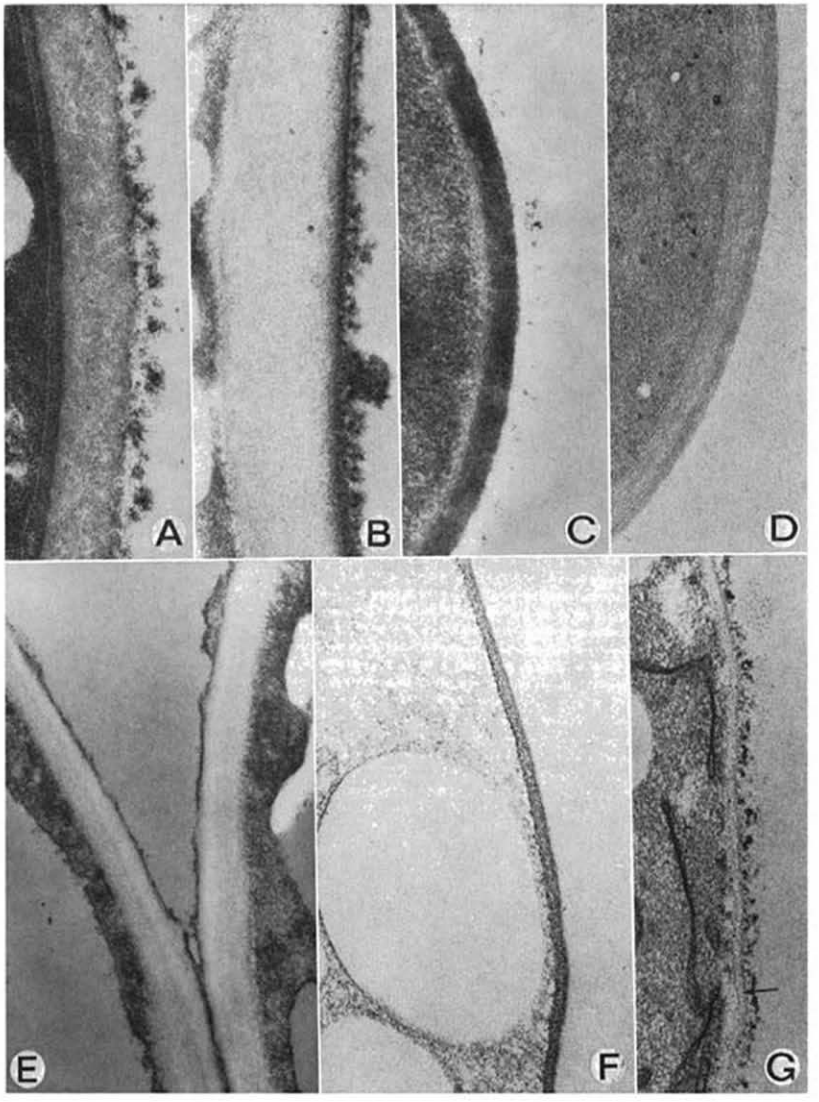
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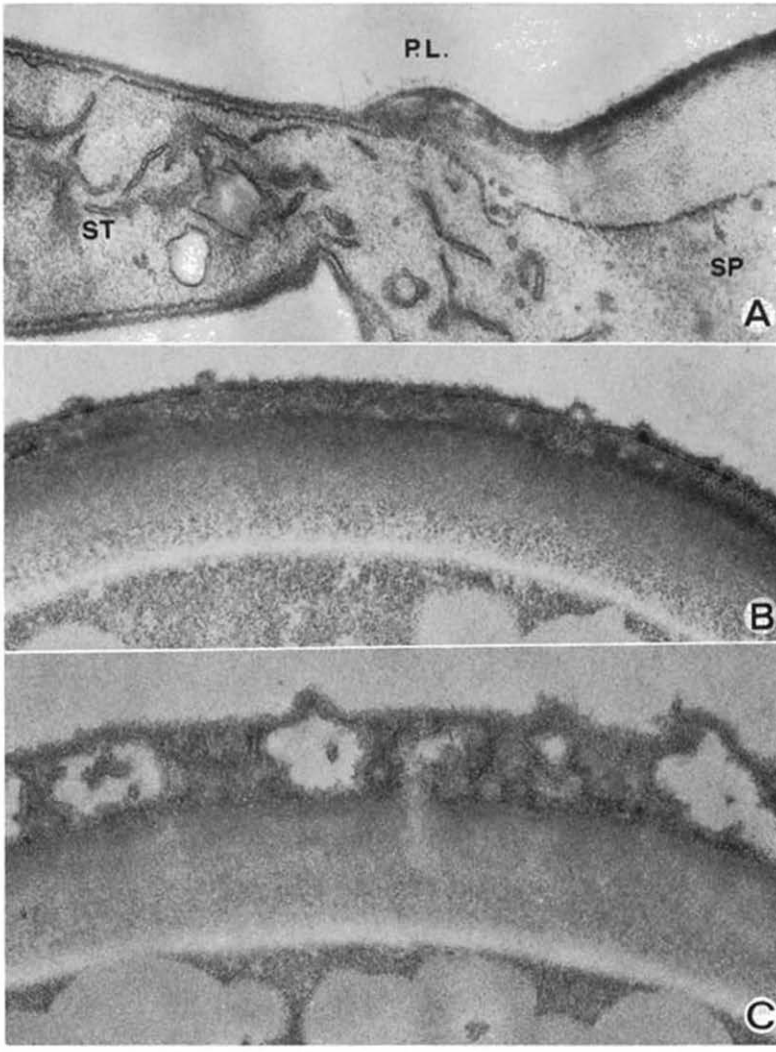
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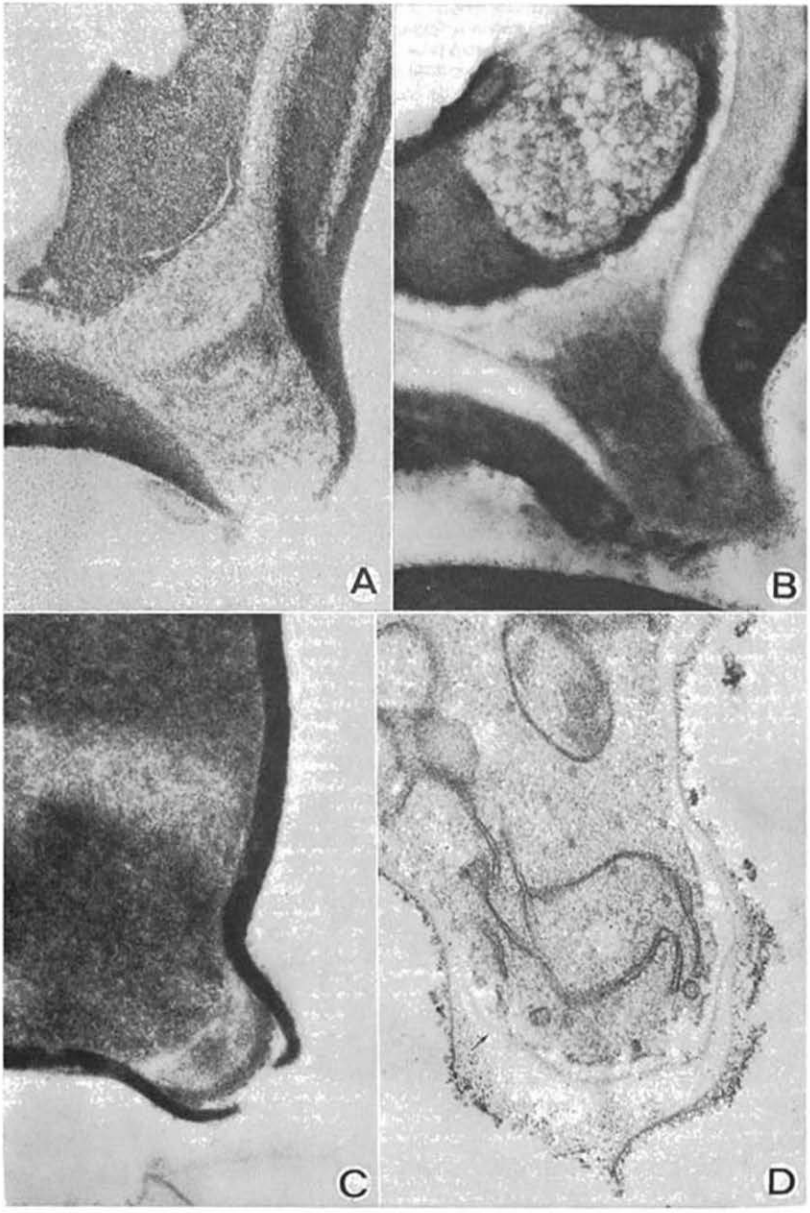
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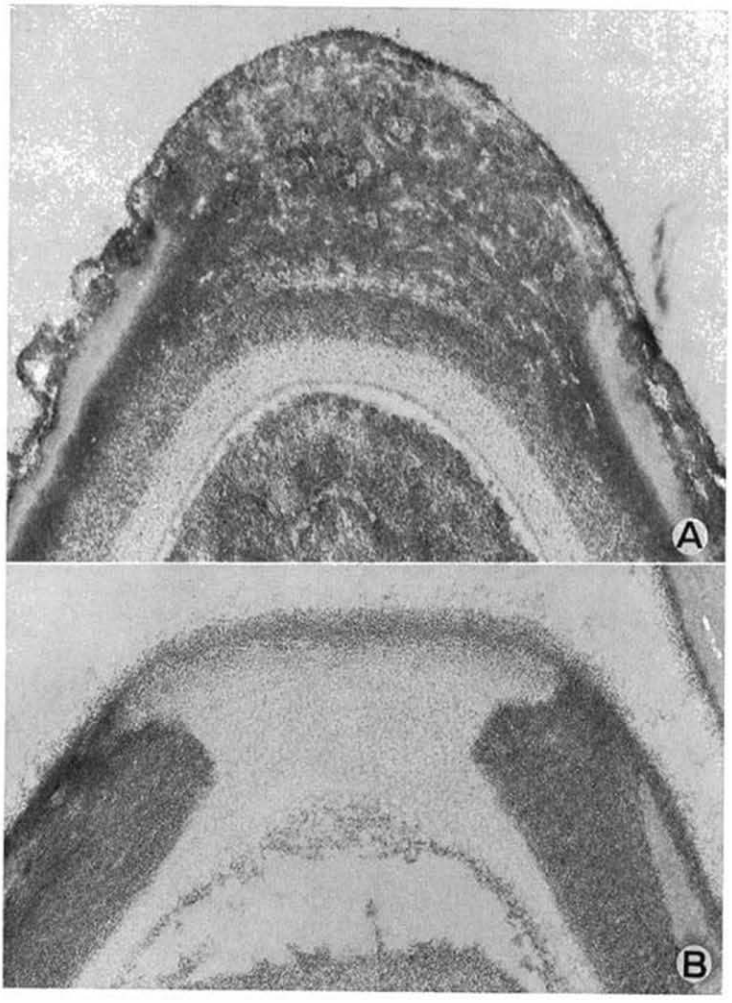
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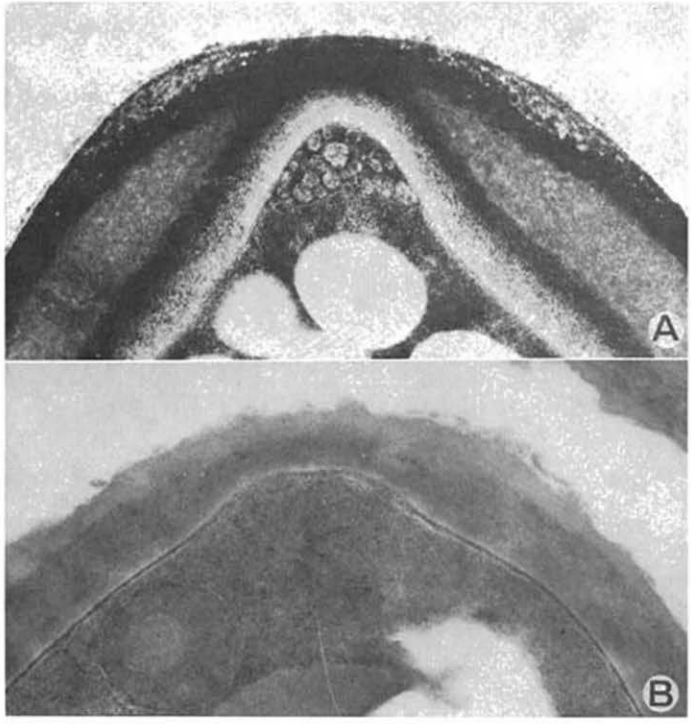
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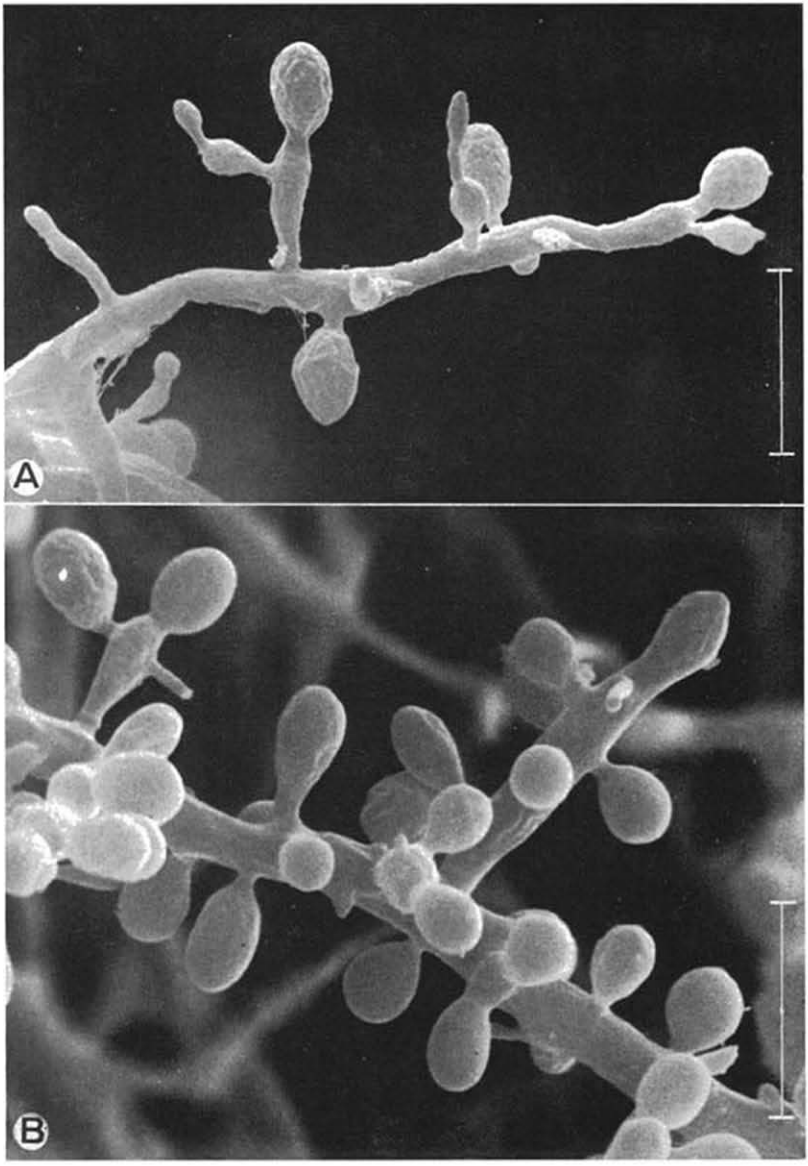
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