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STEREUMS WITH ACANTHOPHYSES, THEIR POSITION AND AFFINITIES

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Stereum peculiare spec. nov. and *S. reflexulum* Reid are described. Two new subgenera are distinguished in the genus *Stereum:* subg. *Aculeatostereum* and subg. *Acanthostereum*. The authors compare them with other genera having acanthophyses.

The genus *Stereum* S. F. Gray emend. Boid. 1958 is restricted to species having smooth, amyloid, and binucleate spores, dimitic basidiocarps without clamps and with pseudocystidia; it is also characterized by a holocenocytic nuclear behaviour with sparse, opposite or verticillate clamps on the bigger hyphae of mono- and polysporous cultures.

In this genus, Bourdot & Galzin (*1921*) distinguished two sections – section *Luteola* which contains the type species and section *Cruentata* for the species which redden upon injury. The distinction between the species is based on external appearance, while microscopic characteristics are rarely used because they display little variation.

As far back as 1960 Boidin (p. 67, note 6) proposed the term 'pseudoacanthophyses' for those sterile, aculeolate elements which replace the basidioles, have the same size but bear a few short outgrowths at their apex. True acanthophyses or acanthohyphidia, called 'bottle-brush paraphyses' by Burt (*1920*), are more differentiated, with many apparently massive, cylindrical, finger-like elements, covering the top and, more or less, the sides. These elements can be observed in many species of *Aleurodiscus* subg. *Aleurodiscus* and subg. *Acanthophysium* Pilát 1926 and with a more regular shape, in all members of *Aleurodiscus* subg. *Aleurobolus* Boid. *& al.* (*1968*), as well as in the genus *Xylobolus* and, as we will see, in various species of *Stereum* sensu stricto such as *Stereum peculiare*, and *S. reflexulum* Reid (*1969*) abundantly collected in the Mediterranean island of Port-Cros (France), both of which are described below.

Stereum peculiare Parmasto, Boidin & Dhingra, *spec. nov.* – Figs. 1, 2

Carposoma resupinatum vel resupinato-reflexum, dense coriaceum; pileus (pars reflexa) ad 5(–10) mm lat. Superficies pilei tomento vestita, mellea, deinde subglabra, radiato-striata, fuscescens, ultimo fusco-nigra. Hymenophorum impar, sparse et irregulariter aculeatum (hydnoideum) vel processibus digitiformibus,

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fulvo-ochraceum, posterius (in statu sicco) profunde rimosum. Denticuli 0.5–2 mm alt., 0.2–1 mm diam.

Systema hypharum dimiticum. Hyphae generatoriae tunicis tenuibus vel incrassatis, septis numerosis, efibulatae, 4–5.5 μm diam. Hyphae skeleticae crasse tunicatae vel paene solidae, flavo-brunneae, 4.5–6 μm diam.: apices hypharum deorsum revoluti in hymenio pseudocystidia immersa clavata apice rotunda 6–8 μm diam. vel digitis acanthophysoideis praedita constituentes. Scetocystidia pauca immersa, obpyriformia, crasse tunicata, 25–50 × 10–17 μm. Acanthohyphidia multa 30–100 × 3.5–7(–10) μm in parte superiore cum processibus 2.5–7 μm longis. Sporae cylindraceae, leviter arcuatae, parietibus laevibus amyloideis, (9–)10–12.8(–14,2) × (2.5–)3(–4) μm.

Typus: U.R.S.S., in regione Primorskij, distr. Kavalerovskij, Gornoretshensk, ad ramum Quercus mongolicae dejectum, 9.X.1977, legit *E. Parmasto* (TAA no. 101 895).

Basidiocarps effused or with narrowly reflexed pilei, annual (?), adnate or with almost free margins, densely coriaceous, pliable, arising as small patches 0.3–3 cm in diam. which soon become confluent and may become effused up to 20 cm long, 0.3–1 mm thick in section; the initial points distinct.

Pileus narrow or rarely almost semicircular, up to 5(–10) mm wide, 0.5–2(–3) mm thick. Upper surface covered with thick tomentum, faintly concentrically zonate, greyish apricot (Munsell 10 YR 7/6 or 8/6; Methuen 5C6) with somewhat darker indistinct zones; tomentum disappearing soon and surface subglabrous, radially striate, almost silky smoke grey (Munsell 10 YR 7/1 or 7/2; Methuen 5B2–5C2) with narrow whitish edge, darkening with age, almost fuscous black (Munsell 10 YR 3/1 or 3/2; Methuen 5F5). Margin of the resupinate part determinate, thinning out, a narrow band (up to 0.3 mm, rarely 0.5 mm) white or whitish, becoming concolorous with hymenium with age. Hymenial surface uneven, tuberculate, with rare or scattered irregular finger-like outgrowths or toothed, rarely almost smooth, golden brown or fulvous ochraceous (Munsell 10 YR 5/8 – 6/8 or 7.5 YR 5/7; Methuen 5D6–5D7), old specimens becoming deeply radially cracked on drying. Teeth 0.5–2 mm long, 0.2–1 mm broad at the base, broadly conical or irregularly cylindrical, obtuse, sometimes flattened, often confluent at their bases, sometimes forming toothed ridges. Context distinctly layered, composed of loose cottony tomentum (basal zone of resupinate specimens) concolorous with young upper surface, and almost suberose buff (Munsell 10 YR 9/4) main layer separated by a narrow dark line.

Hyphal system dimitic. Tomentum thick in young specimens, very thin in old ones, composed of loosely woven, olive brown, thick-walled, sparsely branched hyphae with rare septa, 4–5.5 μm in diam. Cuticular layer distinct, 40–100 μm thick, of densely arranged, almost parallel, brown, thick-walled hyphae, agglutinated with resinous matter. Context layer composed of compactly radiately arranged parallel hyphae, curved into the subhymenium. Generative hyphae abundant, with thin or thickened walls, frequently septate (without clamps), slightly yellowish or almost yellow, 4–5.5 μm in diam. Skeletal hyphae usually small in number except in the upper part of the context or at the bottom of the 'processes', thick-walled or almost solid, with rare septa, dark honey-yellow or yellow-brown, 4.5–6 μm in diam; some skeletal hyphae curve into the subhymenium and hymenium as immersed indistinct 'pseudocystidia' having rounded, slightly or sometimes distinctly clavate tips, 6–8 μm in diam. Mostly they end obliquely in the subhymenium as acanthophyses with rough diverticules. Subhymenium thin, composed of almost perpendicularly arranged, thin-walled, branched, dark yellow generative hyphae 4–5.5 μm in diam.; gloeocystidia rare (more frequent in Indian specimen), immersed in subhymenium and hymenium, obpyriform, moderately thick-walled (up to 2 μm), sometimes with thin-walled rostrate upper part, 25–50 × 10–17 μm, rarely with 1–2 secondary septa, contents negative with sulfo-aldehyde. Hymenium composed of very abundant acanthohyphidia, basidioles (hyphidia?) and scattered basidia. Acanthohyphidia subclavate, subfusiform or subcylindrical, some rather irregular, with a basal septum, sometimes with secondary septa, thin-walled, in old hymenium thick-walled, and brownish, 30–100 × 3.5–7(–10) μm, covered with naked spines or digitate processes in the apical third; spines densely arranged, 2.5–7 μm long. Basidioles few, thin-walled, with rounded apex, 2–3.5 μm in diam. Basidia rarely seen,

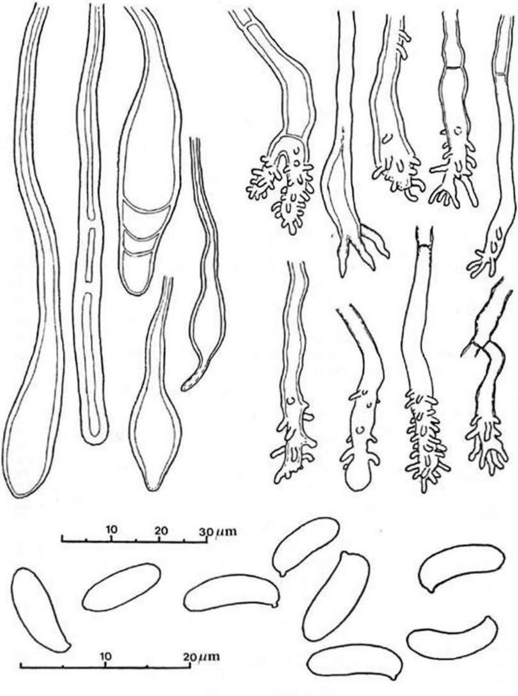

Fig. 1. *Stereum peculiare:* pseudocystidia, acanthohyphydia, and spores.

clavate, somewhat sinuate, 30–40 × 7–8 μm, with 4 conical sterigmata, 4–5 μm long. Spore print white. Spores cylindrical, slightly curved, smooth, with thin, amyloid walls, (9–)10–12.8(–14.2) × (2.5–)3(–4) μm.

All microscopical elements acyanophilous and not markedly coloured by sulfovanilline; all elements except spores non-amyloid and non-dextrinoid.

Associated with an intensive white rot; decayed wood fibrillose.

Type: U.S.S.R., Primorskij Terr., Kavalerovo Distr., Gornoretshensk, on fallen branch of *Quercus mongolica*, *E. Parmasto* 9 Oct. 1977 (holotype: TAA 101 895; isotype: LY 8630).

SPECIMENS EXAMINED. – U.S.S.R., near the holotype's locality, *E. Parmasto* 9 Oct. 1977 (TAA 101 891 and LY 8629); Primorskij Terr., Hasanskij Distr., near the lake 'Karasj', *L. N. Vassilyeva* 2 Oct. 1963 (TAA 97 398 and LY 4828); Primorskij Terr., Lazo Distr., Lazo Nature Reserve Area, *E. Parmasto* 6 Sept. 1961 (TAA 15 326 and LY 4338); India: in a forest with *Michelia champaka* dominating, Sirohi, Ukhrul, Manipur, Chandigarh herbarium, 2 Sept. 1978, PAN 190093 and LY 9250.

The new species microscopically is somewhat similar to *Stereum acanthophysatum* Rehill & Bakshi which, according to the description given in Rattan's paper (*1977*: 158), has a smooth to finely tuberculate hymenial surface, conducting hyphae containing orange coloured contents, acanthophyses, 15–20 × 3–4.5 μm, and ellipsoid spores 6–9 × 3.5–4.5 μm.[1]

The 'pseudocystidia' of *Stereum peculiare* arise from the skeletal hyphae; their contents are neither markedly coloured nor changing colour in sulfovanilline. There are transitions from these cystidia to the obpyriform gloeocystidia.

The spore print was obtained from the type specimen in room conditions during the night after collecting; during the microscopical study of the herbarium specimens (including the type) only few basidia and spores were seen. The average measurements of 50 spores from the spore print, were $10.60 \pm 0.74 \times 3.39 \pm 0.25$ μm for the type. For the paratypes we found the following values.

	N	$\bar{x} \pm s$	extremes
TAA 101.891	30	$10.17 \pm 1.08 \times 2.87 \pm 0.21$ μm	8–13.5 × 2.5–3.5 μm
TAA 97.398	30	$11.70 \pm 0.75 \times 2.96 \pm 0.15$ μm	10.5–14 × 2.5–3.2 μm
TAA 15.326	40	$12.75 \pm 0.99 \times 2.73 \pm 0.14$ μm	10–14 × 2.2–3 μm

It is worth while noticing here the great resistance of this fungus: the specimen TAA 97.398 collected 2 Oct. 1963 gave a good spore print upon its arrival in Lyon in June 1964.

All East Asian specimens mentioned above were collected in broad-leaved forests of tertiary relict type in the southern part of the Soviet Union Far East region, which has a very rich fungal flora with many species in common with Japan[1] and North America.

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[1] Before publishing this new species, we would have liked to obtain the loan of *Stereum kurilense* Yasuda. Unfortunately our requests remained unanswered. These specimens might have been destroyed during World War II.

According to the description reported by Ito (*1955*), *S. kurilense* differs from *S. peculiare* by its smooth, white or wood-coloured hymenium and by the more dumpy aspect of its spores.

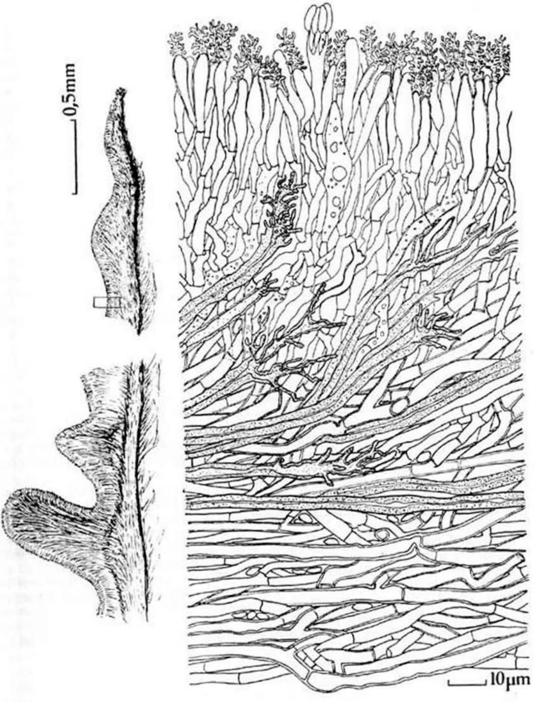

Fig. 2. *Stereum peculiare* (type): schematic section through fruit-body and detail of a part.

CULTURAL CHARACTERS OF STEREUM PECULIARE

LY 4338 and 4828, paratypes.

Spores.—Binucleate.

Germinations.—The LY 4338 specimen, received at Lyon in October 1962, gave a spore print from which we were able to isolate a very small number of monosporous cultures. In December 1964, from the same spore print kept at 4 °C since 1962, we obtained germinations and several new monosporous cultures. In June 1964, upon arrival at Lyon, basidiocarp LY 4828 produced a spore print from which many germinations were obtained; unfortunately none of the 56 isolated germinations grew, but 4 months later, new germinations were obtained, 48 hours after sowing under collodion-films. Young germinations are cenocytic and show no septa at the 7 to 13 nuclei stage.

Monosporous cultures.—LY 4338: 6 monosporous mycelia out of 17 show very rare clamps, simple or opposite on the bigger hyphae, after patient research in cultures on agar slides or in Petri-dishes filled with sawdust medium. Their hyphae are composed of multinucleate articles, the terminal article contains 17 to 30 nuclei, following articles, 10 to 12, and near the centre of the culture, articles have 3 to 7 nuclei.

LY 4828.—All of the 33 monosporous cultures, sowed on a medium of sawdust, show rare clamps, they are single on 3.5–4 μm wide hyphae, opposite on hyphae 4 μm wide, verticillate in threes on hyphae 5 μm wide and verticillate in whorls of four on hyphae 6 μm wide. Their hyphae are composed of multinucleate articles, containing 7–18(–22) nuclei near the centre, while terminal articles contain 110–250 nuclei. Simple or opposite clamps have been observed in culture under the collodion-film.

Polysporous cultures.—LY 4338, 4828.

Growth.—Moderately rapid (petri-dishes covered in 4 weeks). Rate of growth was the same both in 1978 and in 1964.

Aspect.—Margin regular, slightly elevated. Young aerial mycelium cottony, more or less woolly, loose. After 6 weeks white aerial mycelium low, felted or on the contrary formig big white cottony masses tinged very pale alutaceous (Munsell 10 YR 9/2). To the side of the petri-dishes a roll-like zone was observed (Munsell 7.5 YR 4/3). Reverse unchanged. Fruity odour. A four months old culture shows a peripheral zone coloured M 7.5 YR 6/4, with M 7.5 YR 5/4 patches.

Microscopical characters.—Aerial mycelium: numerous fine branches 1–2 μm wide, axial hyphae 3–6 μm wide with thin walls and rare single clamps in LY 4338; more frequent, opposite or verticillate by 3 in LY 4828. A few axial hyphae with thickened walls, 0.5–1 μm in hyphae 5–6 μm wide.

Some broad hyphae 5–8 μm wide with homogeneous, yellowish, faintly refringent contents. These hyphae also have rare, single, opposite or verticillate clamps in LY 4828.

Submerged mycelium.—Hyphae 2.5–5 μm wide with thin or clearly thickened walls in certain axial hyphae. Whereas LY 4338 has no clamps on hyphae deeper in the medium, submerged hyphae of LY 4828 possess single, rare, or verticillate clamps like those of the aerial mycelium.

Cytology.—Hyphae with rare clamps are composed of articles containing (2–)4–10(–15) nuclei, except the terminal one which is generally longer and contains 28–70(–94) nuclei.

Oxidases.—

gallic acid: + + + + +, 15 mm
p.-crésol: —
gaiacol: + + + +, 0
tyrosine: – ou + (LY 4828)
: + + (+ +) (LY 4338)

Code.—2(a) – 5 – 32 – 36 – 38 – 44 – 53 – 54 – 57 – 66.[2]

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[2] Nobles (*1965*) completed by Boidin (*1966*).

In contrast to mycelia of *Xylobolus* species which we studied earlier (*X. frustulatus*, LY 4420, U.S.S.R., Transcaucasia, leg. *Parmasto*, *X. subpileatus*, LY 4421, U.S.S.R., Transcaucasia, leg. *Parmasto*, *X. princeps*, LY 4393, India, leg. *Bakshi*, and *X. sepium*, LY 6333, Tennessee (U.S.A.), leg. *Boidin*), the mycelium of *S. peculiare* has a strong positive reaction with guaiacol and does not blacken in sulphuric acid.

STEREUM REFLEXULUM Reid—Fig. 3

Stereum reflexulum Reid *in* Rev. Mycol. (Paris) **33**: 262. 1969 ['1968'].

Reid's original description was based on a hardly reflexed specimen whereas M. Tortić (*1975*) published a photograph of a Yugoslavian 'fan-shaped' specimen. Approximately fifteen collections were made in the Park of Port-Cros, France, which show that forms of such extreme habit as mentioned above are connected by many intermediates. This interesting and long mistaken fungus is described below.

Habitus very variable, either completely effused on large horizontal supports or on the contrary reflexed, the reflexed parts 1.5–2 cm in diam., imbricate or still umbonate-affixed when attached to vertical or oblique substrata especially small branches. Upper surface of the concentrically furrowed reflexed parts hirsute by greyish tufts through which shows the dark cortex which is M. 5 YR 4/4, chocolate (M. 5 YR 3/3), havane (M. 7.5 YR 5/6) but becomes chestnut-brown with age (M. 2.5 YR 3/6, 3/4 and even 2/2); margin narrow, pale alutaceous (M. 10 YR 9/5). Hymenial surface with a narrow whitish margin which darkens after bruising without reddening, smooth, somewhat zonate, beige (M. 10 YR 7/3), chamois beige (M. 10 YR 7/4), light yellowish brown (M. 10 YR 6/4) or beige reaching isabellinus (M. 7.5 YR 7/2, 7/4), then cinnamon (M. 7.5 YR 6.5/4–6/4), near the centre, light reddish brown (M. 5 YR 6/3 and even 5.5/3.5). Reflexed parts in dried specimens hard, appressed parts densely cracked; hymenium pale, extreme margin pale alutaceous (M. 10 YR 8/4, 7.8/4, 8/3) with beige zones (M. 10 YR 7/3); the slits showing a chamois coloured substance (M. 10 YR 7.5/6); upper surface of reflexed parts sterile, bristled with whitish tufts on the sides, then furrowed with hirsute strigose bands reaching 'pale shadow' (M. 10 YR 6/4) but becoming greyish with age, disappearing and finally showing a black crust.

Basidiocarp 220–380 μm thick, tomentum up to 300 μm thick. Cortex very dark, 40–50 μm thick, composed of brown generative and skeletal hyphae stuck together. Tomental hyphae brown at their base, rapidly becoming hyaline terminally, regular, thick-walled with narrow lumen, 3–4–4.5 μm wide, rarely branched, agglomerated into acute tufts. Context developed in both the appressed and reflexed parts, subhyaline or slightly yellowish, composed of generative and skeletal hyphae. Generative hyphae 3–3.8 μm wide, thin- to distinctly thick-walled, branched and septate, without clamps. Skeletal hyphae numerous, subhyaline, 3.5–6 μm wide, very thick-walled, with narrow lumen (observed in ammoniacal Congo).

Hymenial zone 40–80 μm high, likewise composed of generative and the tips of numerous skeletal hyphae. Generative hyphae at first oblique, later becoming vertical, 2.8–3.2 μm wide, often slightly thick-walled. Skeletal hyphae curved to form pseudocystidia which are of various lengths, 50–180 μm, cylindrical, slightly widened at their end, 5–6 μm wide, the tip often rounded, rarely mucronate, with the wall generally very thick almost up to the tip where it suddenly becomes thin; cytoplasm granular with oil drops sometimes slightly brown, turning green in sulphuric acid but giving no reaction in sulpho-aldehyde reagent. Short cystidia 24–40 × 4.5–5.5 μm vertically borne on branching subhymenial generative hyphae which bear also basidia and acanthophyses. Actually, these short cystidia are only much shortened skeletals with

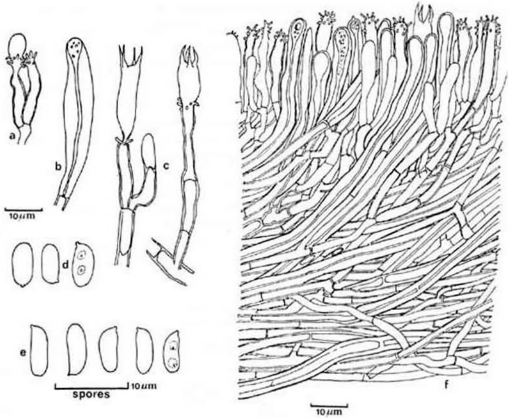

Fig. 3. *Stereum reflexulum*. — a. Acanthophyses. — b. Short hymenial cystidia. — c. Acanthobasidia (a, b, and c from LY 8342). — d. Spores (LY 8486, on *Myrtus communis*). — e. Spores (LY 8450, on *Arbutus unedo*). — f. Detail of section through fruit-body, showing the hymenium (LY 8478).

the same kind of wall becoming suddenly thinner at the tip, and the same contents. Acanthophyses numerous, cylindrical, 18–25–40 × 3–4–5.5 µm, of hymenial origin, with slightly thickening walls, apically with abundant (8–30) hyaline outgrowths up to 3 × 0.75 µm.

Basidia usually rare, 28–40 × 5–5.5 µm, not or only little protruding (3–5 µm), bearing 4 sterigmata; they often are acanthobasidia which originate terminally as a renewed growth of the acanthophyses.

Spores cylindrical, sometimes slightly depressed, smooth, amyloid, binucleate, 5.25–7 × 2.2–2.7 µm (N = 30, $\bar{x} = 6.28 \pm 0.4 \times 2.35 \pm 0.16$) (collected on *Arbutus*); oblong, 5–6.2 × 2.2–3 µm ($\bar{x} = 5.50 \pm 0.38 \times 2.77 \pm 0.15$) (collected on *Myrtus communis*, LY 8486). Frequently collected on the island of Port-Cros (Var, France) on dead or living *Arbutus unedo* but also on *Quercus ilex*, *Cistus monspeliensis*, *Myrtus communis*, *Erica arborea* (LY 8341 and 8342, leg. *J. Beller* ; LY 8442, 8446–8450, 8457, 8462, 8470, 8478, 8486... leg. *J. Boidin*, December 1977).

This species, first described from a collection on *Cistus monspeliensis* in Corsica and reported in Tanger by Reid (*1969*) was found again in Tenerife (Canary Islands) and in Portugal according to Ryvarden (*1974*), and also reported from Yugoslavia by M. Tortić (*1975*). This species was compared by Reid to *Peniophora incarnata* on account of the waxy appearance, and considered to be microscopically related to *Stereum insignitum*, while Ryvarden compared it to *Stereum* *hirsutum*. Although it probably is frequent around the Mediterranean, it is commonly mistaken in the field for *Stereum ochroleucum* sensu Bourd. & Galz. by French mycologists (according to Donadini, viva voce) or for *S. fasciatum* sensu auct. Europ. (= *S. subtomentosum* Pouzar) or even for *S. hirsutum*, to judge from the successive determinations of a Yugoslavian specimen in the herbarium at Vienna (Austria); this species after microscopic investigation was also mistaken for *Xylobolus subpileatus* first by Reid (*1957*), then by Ryvarden (*1972*). *Stereum reflexulum* is easily distinguished from *S. hirsutum* by its colours, from *S. insignitum* by its smaller size and less contrasting colours, from *Xylobolus subpileatus* by its thinness, flexibility, and sterile pale surface. Under the microscope, it cannot be mistaken either for *S. rameale* (= *S. ochroleucum* sensu Bourd. & Galz.) or for *S. subtomentosum*, both of which have no acanthophysis-like elements, while it differs from *S. insignitum* which possesses only pseudoacanthophyses.

Although the habit is extremely variable (resupinate, narrowly reflexed or broadly reflexed), the crevices appearing during dessiccation, especially in the non-reflexed parts, are very characteristic. These were moreover also reported both by Reid and Tortić.

CULTURAL CHARACTERS OF STEREUM REFLEXULUM

SPORES.—Binucleate.

POLYSPOROUS CULTURES.—(LY 8341–8342).

GROWTH.—Growth moderately rapid, plates covered in three weeks. Advancing zone even and appressed.

ASPECT.—Aerial mycelium whitish (M. 2.5 Y 9.25/2), loosely arachnoid, becoming woolly with erect tufts, reaching the cover or becoming flattened. Mycelium more upright in young parts than around inoculum and tinged (M. 2.5 Y 9.25/4). Reverse unchanged. Odour fruity or none.

MICROSCOPICAL CHARACTERS.—Aerial mycelium consisting of numerous slender branches without clamps, 1–1.2(–2) μm wide, frequently branched, forming a fine mesh between wide axial hyphae, 5–7(–9) μm in diam., which show single clamps on hyphae 3 μm wide, opposite or verticillate in threes on hyphae 5–6 μm wide, and verticillate in whorls of 4 to 5 on hyphae 6–8 μm wide and even verticillate in whorls of 6 on hyphae 9 μm wide. Hyphae are regular with homogeneous content, with a thin wall except in axial hyphae where the wall often reaches 1 μm. Sulpho-aldehyde reagent gives no reaction on this mycelium.

SUBMERGED MYCELIUM.—Branches less dense, less slender, 1.5–3 μm wide, less frequently branched, regular, without clamps. Axial hyphae 4–6(–10) μm wide, frequently bearing single, opposite or verticillate clamps in whorls of 2 to 6, often thick-walled, 0.5–2 μm, with very long articles, (100–)380–880 μm.

CYTOLOGY.—Hyphae composed of multinucleate articles, containing 2–6 nuclei in secondary hyphae and 4–10(–20) nuclei in axial hyphae. Terminal articles containing 14–30 nuclei in secondary hyphae, 49–92 nuclei in axial hyphae. Single or opposite clamps are not rare even when mycelium is growing under collodion film.

OXYDASES.—
gallic acid: + + + + +, 8–10 mm
guaiacol: + + + + +, 12 mm
p.-cresol: –
tyrosine: –, 0

CODE.—2 – 5 – 32 – 36 – 38 – 43 – 53 – 54 – (57) – 66.

The very conspicuous aspect of *Stereum peculiare*, notably with its irregularly ornate hymenium, might have in the past justified the creation of a monospecific genus. Its anatomy, life-cycle, and nuclear behaviour, however, agree perfectly with those of *Stereum* sensu stricto from which it is distinguished by its (1) acanthophyses; (2) skeletal hyphae often terminating into acanthophyses; (3) irregular hymenial outgrowths which are fertile up to the apex.

Stereum reflexulum Reid itself is closer to classical *Stereum* sect. *Luteola* with which it has long been confused and from which it can be distinguished only by its acanthophyses. It forms the transition between species of *Stereum* with pseudo-acanthophyses such as *S. ostrea, insignitum, rugosum*, and *S. peculiare*. It does appear preferable to include *S. peculiare* into *Stereum*, attaching the greatest importance to the presence or lack of acanthophyses on the one hand and of pseudo-acanthophyses on the other in the subdivision of the genus.

We therefore no longer use the subdivision based on the reddening of the hymenium (sect. *Cruentata* Bourd. & Galz. 1921 = genus *Haematostereum* Pouzar). In this section the reddening is brought about by the great amount of phenolic substances and phenoloxydases, released on rupturing of the extremely brittle tips of pseudocystidia. These substances turn quickly green when brought into contact with iron salts. The non-bleeding Stereums, such as *Stereum* sect. *Luteola*, seem to possess the same substances but undoubtedly in appreciably smaller quantity, which results in these species turning green much more slowly with iron salts. Moreover Léger (*1968*), using the vegetative anastomosis method, proved that *S. insignitum*, a member of section *Luteola* with pseudo-acanthophyses, failed to make anastomoses with other species of the *Luteola* group characterized by the absence of pseudo-acanthophyses such as *S. complicatum, subtomentosum, striatum*, and *rameale*, whereas it did make anastomoses with *S. rugosum* which is a species with pseudo-acanthophyses of the section *Cruentata*. The conclusion to be drawn from this is that the presence of pseudoacanthophyses is a more significant characteristic than is reddening.

Stereum subgen. **Acanthostereum** Boidin, Parmasto, Dhingra & Lanquetin, *subgen. nov.*

A subgeneribus Stereo et Aculeatostereo acanthophysibus praesentibus differt. Typus: *Stereum peculiare* Parmasto, Boidin & Dhingra.

The species of this subgenus have all the characters of the genus *Stereum*, such as dimitism, pseudocystidia with sulpho-aldehyde negative-contents, smooth and amyloid spores, opposite or verticillate clamps on the bigger axial hyphae of the mycelium. This subgenus is characterized by the presence of acanthophyses, type: *Stereum* (*Acanthostereum*) *peculiare*, Parmasto, Boidin & Dhingra; other species are *Sterum* (*Ac.*) *reflexulum* Reid 1969 and probably, to be confirmed by the study of the mycelial characters: *S.* (*Ac.*) *acanthophysatum* Rehill & Bakshi 1966, *S.* (*Ac.*) *spectabile* Klotzsch 1843 (= *S. radiato-fissum* Berk. & Br. 1883), and *S.* (*Ac.*) *illudens* Berk. 1845; it is important to note, however, that Refshauge & Proctor (*1936*) described the culture of *S. illudens* as bearing single sparse clamps whereas one culture kept in Baarn showed opposite and verticillate clamps.

Stereum subg. **Aculeatostereum** Boidin, Parmasto, Dhingra & Lanquetin, *subgen. nov.*

A subgeneribus Stereo et Acanthostereo pseudoacanthophysibus vel basidiolis aculeatis praesentibus differt. Typus: *Stereum insignitum* Quélet.

The species of this subgenus possess all characters of the genus *Stereum* but, in addition, have pseudoacanthophyses (or aculeolate basidioles); type: *Stereum* (*Aculeatostereum*) *insignitum* Quélet 1889; other species are *Stereum* (*Aculeatostereum*) *australe* Lloyd 1913, *S. durbanense* van der Byl 1922, *S. lobatum* (Kunze ex Fr. 1830) Fr., *S. macrocystidiatum* Welden 1967, *S. obscurans* Burt 1924, *S. ostrea* (Blume & Nees ex Fr. 1828) Fr., *S. rugosum* (Pers. ex Fr. 1831) Fr., *S. sanguinolentum* (Alb. & Schw. ex Fr. 1821) Fr., *S. versicolor* (Swartz ex Fr. 1821) Fr., *S. zonarium* Lloyd 1917, etc.; *Thelephora concolor* Jungh. 1838, *Kneiffia coriacea* Berk. & Br. 1875, *Stereum traplianum* Velen. 1920 also belong to this group. Nearly all of these members of *Aculeatostereum* formerly belonged to section *Cruentata* Bourd. & Galz.

STEREUM SUBG. STEREUM

Species of this subgenus have neither acanthophyses nor pseudoacanthophyses. Type: *Stereum hirsutum* (Willd. ex Fr.) S. F. Gray.

Other species: *S. complicatum* Fr., *S. ochraceo-flavum* (Schw.) Ell., *S. rameale* (Schw.) Burt [sensu auct. europ., = *S. ochroleucum* Bres., = *S. hirsutum* subsp. *sulphuratum* (Berk. & Rav.) Bourd. & Galz.], *S. rimosum* var. *africanum* Talbot, *S. scutellatum* Cunn., *S. striatum* (Fr.) Fr. [= *S. sericeum* (Schw.) Sacc.], *S. styracifluum* (Schw. ex Fr.) Fr., *S. subtomentosum* Pouz., *S. vellereum* Berk., *S. zebra* Heim & Malençon.

We would like to present a comparative table of genera and subgenera containing species with acanthophyses:

(1) Genera or subgenera whose species have true acanthophyses: genus *Xylobolus*, *Stereum* subg. *Acanthostereum*, *Aleurodiscus* subg. *Aleurobolus* Boid. & Coll. 1968 (with small and smooth spores).

(2) Subgenera whose species may possess acanthophyses: *Aleurodiscus* subg. *Aleurodiscus* (with big, pink and ornamented spores), *Aleurodiscus* subg. *Acanthophysium* (with white ornamented spores); in these two subgenera, acanthophyses have a much more irregular shape. We would like to add *Aleurodiscus delicatus* Wakef. which Oberwinkler (*1965*) indicated as the type of the monotypic genus *Acanthobasidium*, placing it in the family of Xenasmataceae on account of its pleurobasidia; these basidia at a young stage look like small acanthophyses but will develop aculeolate basidia (acanthobasidia). Without opening the debate on the systematic value of the pleurobasidium, it should be noted that non-pleurobasidial acanthobasidia can be seen to develop more or less numerously from acanthophyses in various species of *Stereum* subg. *Acanthostereum* as demonstrated by Jülich (*1978*: 472, fig. 13) in *S. illudens*, in *S. reflexulum* in this paper or in some *Aleurodiscus* as shown by Lemke (*1964*: 263, fig. 16) in *A. penicillatus* or again in *A. mirabilis* as seen by one of us (J. B. unpublished).

Examination of Table I reveals the relative importance of the different characters.

(1) Characters common to all species studied thus far: amyloid and binucleate spores.

(2) Characters useful to distinguish genera.—

For *Aleurodiscus*: monomitism.

TABLE I

Comparative table of genera having acanthophyse-like elements

	Acanthobasidium	*Aleurodiscus* subgen.			*Xylobolus*	*Stereum* subgen.		
		Aleurodiscus	*Acanthophysium*	*Aleurobolus*		*Acanthostereum*	*Aculeatostereum*	*Stereum*
Spores:								
amyloid	+	+	+	+	+	+	+	+
pinkish	?	+	−	−	−	−	−	−
ornamented	+	+	±	−	−	−	−	−
binucleate (1)	?	+	+	+	+	+	+	+
Sulfocystidia	−	−	+	+	(2)	−	−	−
Acanthohyphidia	(3)	±	±	+	+	+	(4)	−
Mitism (5)	I	I	I	I	II	II	II	II
Verticillate								
clamps (6)	−	−	−	−	−	+	+	+
Laccase	?	+	+ (7)	+	−	+	+	+

(1) for all species studied up to now

(2) the species of *Xylobolus* sensu stricto should be re-examined on fresh material. Weak reactions have moreover been noticed in specimens collected several months ago.

(3) acanthobasidia

(4) pseudoacanthophyses

(5) mitism: I = monomitic, II = dimitic

(6) in culture

(7) except *Aleurodiscus apricans*.

For *Xylobolus:* alveolar rotting, absence of laccase, absence of verticillate clamps in cultures, and presence, as well in the carpophore as in culture, of an orange-yellow substance turning black in sulphuric acid.

For *Stereum:* verticillate clamps in cultures and absence of reactions with sulphuric acid or sulpho-aldehydes.

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Résumé

Les carpophores et cultures de deux *Stereum* à acanthophyses vraies sont décrits: *S. peculiare nov. sp.* de Sibérie et des Indes à l'hyménium ornementé, et *S. reflexulum* Reid retrouvé en abondance à Port-Cros (France). Le genre *Stereum* est découpé en 3 sous-genres: subg. *Stereum*, *Aculeatostereum* subg. nov. et *Acanthostereum* subg. nov., qui sont comparés aux autres ensembles pouvant posséder des acanthophyses (*Acanthobasidium*, *Aleurodiscus*, *Xylobolus*) et les caractères distinctifs de ces différents groupements sont soulignés.

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STUDIES IN RESUPINATE BASIDIOMYCETES—VI

On some new taxa

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Resupinate Basidiomycetes from various parts of the world have been studied, all belonging to the Corticiaceae sensu lato. Eleven new genera and two new species are described, forty-three new combinations proposed. Two new families are described, viz. Corneromycetaceae (resupinate) and Heteroscyphaceae (cyphelloid).

A number of resupinate Basidiomycetes from temperate and tropical areas have been studied. Several new genera, based on microscopical characters, are described. All are placed in the Corticiaceae sensu lato, at least for the moment and in spite of the fact that some of them are characterized by a dimitic hyphal system, brown spores, or pleurobasidia, features which are typical for some closely related families.

SOME NEW GENERA AND SPECIES

CORTICIACEAE sensu lato

Adustomyces Jülich, *gen. nov.*

Carposomata perennia, resupinata, effusa, adnata, 1–5 mm crassa, trama in KOH solutione nigra, firme membranacea vel crustacea, margine abrupta, adnata vel paulum reflexa. Systema hypharum monomiticum. Hyphae hyaline vel brunneae, cylindraceae, dense intertextae, distinctae, tenui- vel incrassate tunicatae, circa 2–4 μm latae, fibulatae. Cystidia desunt sed hyphidia adsunt, nonnulla vel multa, hyalina, cylindriacea, tenui-tunicata. Basidia hyalina, clavata, circa 50 × 8 μm, fibulata, tetraspora. Sporae hyalinae, late ellipsoideae, tenui- vel paulum incrassate tunicatae, laeves, circa 9 × 7 μm, inamyloideae.

Typus: *Stereum repandum* var. *lusitanicum* Torrend 1913.

Basidiocarp perennial, resupinate, effused, adnate, 1–5 mm thick, the trama blackening in KOH, firm-membranaceous to crustaceous, the margin abrupt, adnate or slightly reflexed. Hyphal system monomitic. Hyphae hyaline or brown in the trama, cylindrical, densely arranged, distinct, thin- to slightly thick-walled, about 2–4 μm wide, with clamps. Cystidia absent but hyphidia present, few or abundant, hyaline, cylindrical, thin-walled. Basidia hyaline, clavate, about 50 × 8 μm, four-spored, with a basal clamp. Spores hyaline, broadly ellipsoid, thin- to slightly thick-walled, smooth, about 9 × 7 μm, not amyloid.

Type locality: Portugal

The genus *Adustomyces* is close to *Radulomyces*, but differs from that genus in its crustaceous, up to 5 mm thick basidiocarp, brown hyphae and a blackening trama (in KOH).

Adustomyces lusitanicus (Torrend) Jülich, *comb. nov.* (basionym: *Stereum repandum* var. *lusitanicum* Torrend *in* Broteria (Bot.) **11**: 76. 1913).

Aphanobasidium Jülich, *gen. nov.*

Carposomata resupinata, effusa, tenuia, ceracea, pallide colorata. Hymenophorum laeve. Systema hypharum monomiticum. Hyphae hyalinae, tenui-tunicatae, fibulatae. Cystidia desunt. Basidia (pleurobasidia) hyalina, parva, tenui-tunicata, tetraspora, fibulata. Sporae hyalinae, ellipsoideae, laeves, tenuitunicatae, inamyloideae vel amyloideae.

Typus: *Corticium subnitens* Bourd. & Galz. 1928.

Basidiocarp resupinate, effused, thin, ceraceous, light coloured. Hymenial surface even. Hyphal system monomitic. Hyphae hyaline, thin-walled, with clamps. Cystidia lacking. Basidia (pleurobasidia) hyaline, small, thin-walled, four-spored, with a basal clamp. Spores hyaline, ellipsoid, smooth, thin-walled, not amyloid or amyloid.

Type locality: France.

The genus *Xenasma* sensu lato was composed of a number of not closely related groups held together by only one character, the more or less typically developed pleurobasidia. In the meantime it became clear that this genus had to be split up in smaller genera, containing now species with warted spores (the warts soluble in KOH or not) and species with thin-walled, smooth and amyloid or inamyloid spores. It is for this last group of species that the new genus is described.

Aphanobasidium allantosporum (Oberw.) Jülich, *comb. nov.* (basionym: *Xenasmatella allantospora* Oberw. *in* Sydowia **19**: 35. 1965).

Aphanobasidium filicinum (Bourd.) Jülich, *comb. nov.* (basionym: *Corticium filicinum* Bourd. *in* Revue scient. Bourbonn. **23**: 12. 1910).

Aphanobasidium gaspesicum (Liberta) Jülich, *comb. nov.* (basionym: *Xenasma gaspesicum* Liberta *in* Mycologia **58**: 932. '1966', publ. 1967).

Aphanobasidium grisellum (Bourd.) Jülich, *comb. nov.* (basionym: *Corticium grisellum* Bourd. *in* Revue scient. Bourbonn. **35**: 17. 1922).

Aphanobasidium lloydii (Liberta) Jülich, *comb. nov.* (basionym: *Xenasma lloydii* Liberta *in* Mycologia **52**: 906. '1960', publ. 1962).

Aphanobasidium ralla (H. S. Jacks.) Jülich, *comb. nov.* (basionym: *Corticium rallum* H. S. Jackson *in* Canad. J. Res. (C) **28**: 889. 1950).

Aphanobasidium subnitens (Bourd. & Galz.) Jülich, *comb. nov.* (basionym: *Corticium subnitens* Bourd. & Galz., Hyménomycètes de France 224. 1928).

Columnodontia Jülich, *gen. nov.*

Carposoma resupinatum, effusum, membranaceum vel crustaceum. Hymenophorum odontioideum ad hydnoideum. Systema hypharum monomiticum. Hyphae hyalinae vel luteo-brunneae, cylindricaceae, incrassate tunicatae, cum vel sine fibulis. Cystidia desunt vel adsunt. Spinae cylindraceae ad conicae,

constans ex columellis crystallorum procurrentibus. Basidia hyalina, anguste clavata, tetraspora. Sporae hyalinae, cylindraceae vel ellipsoideae, tenui-tunicatae, laeves, inamyloideae.
Typus: *Columnodontia resupinata* Jülich

Basidiocarp resupinate, effused, membranaceous or crustaceous. Hymenial surface odontioid to hydnoid. Hyphal system monomitic. Hyphae hyaline to yellowish-brown, cylindrical, somewhat thick-walled, with or without clamps. Cystidia present or lacking. Spines cylindrical to conical, consisting of small, projecting columns of crystals. Basidia hyaline, narrowly clavate, four-spored. Spores hyaline, cylindrical or ellipsoid, thin-walled, smooth, not amyloid.
Type locality: Borneo.

Columnodontia resupinata Jülich, *spec. nov.*

Carposomata resupinata, effusa, circa 300 μm crassa, adnata, ceraceo-crustacea. Hymenophorum odontioideum. Systema hypharum monomiticum. Hyphae hyalinae vel basales luteo-brunneae, incrassate tunicatae, 3–4 μm latae, sine fibulis. Cystidia desunt. Columellae crystallorum plus minusve cylindraceae, 150–250 × 40–80 μm. Basidia hyalina, anguste clavata, 16–22 × 3.5–4.5 μm, tetraspora. Sporae hyalinae, ellipsoideae, tenui-tunicatae, leaves, 3–4 × 2–2.2 μm, inamyloideae.

Basidiocarp resupinate, effused, about 300 μm thick, adnate, ceraceous-membranaceous. Hymenial surface odontioid. Hyphal system monomitic. Hyphae hyaline or yellowish-brown at the base, somewhat thick-walled, 3–4 μm wide, without clamps. Cystidia lacking. Columns of crystals more or less cylindrical, 150–250 × 40–80 μm. Basidia hyaline, narrowly clavate, 16–22 × 3.5–4.5 μm, four-spored. Spores hyaline, ellipsoid, thin-walled, smooth, 3–4 × 2–2.2 μm, not amyloid.
Type: Borneo, Sarawak, Gunong Mulu National Park, N. of Base Camp, *c.* 65 m alt., 10.III.1978, *W. Jülich 78–1564* (L).

The genus *Columnodontia* is easily identified because of the glistening, projecting columns of crystals. Three more species, all from South East Asia or Australia, belong to this genus.

Columnodontia columellifera (Cunn.) Jülich, *comb. nov.* (basionym: *Odontia columellifera* Cunn. *in* Trans. R. Soc. N. Zeal. **86**: 84. 1959).

Columnodontia lutea (Cunn.) Jülich, *comb. nov.* (basionym: *Odontia lutea* Cunn. *in* Trans. R. Soc. N. Zeal. **86**: 82–83. 1959).

Columnodontia subfascicularia (Wakef.) Jülich, *comb. nov.* (basionym: *Acia subfascicularis* Wakef. *in* Trans. Proc. R. Soc. S. Austr. 1930: 155–156. 1930).

Cyanobasidium Jülich, *gen. nov.*

Carposomata resupinata, effusa, hypochnoidea vel membranacea. Hymenophorum laeve. Systema hypharum monomiticum. Hyphae hyalinae vel luteae, cum vel sine fibulis, in parte basali grandes et crasse tunicatae, cyanophileae. Basidia hyalina, cylindracea vel clavata, tetraspora, cyanophilea. Sporae hyalinae vel pallide luteae, tenui vel leviter incrassate tunicatae, subglobosae vel late ellipsoideae, verrucosae, cyanophileae, inamyloideae.
Typus: *Pellicularia chordulata* D. P. Rogers 1943.

Basidiocarp resupinate, effused, hypochnoid or membranaceous. Hymenial surface even. Hyphal system monomitic. Hyphae hyaline or yellowish, with or without clamps, the basal ones

large and thick-walled, cyanophilous. Basidia hyaline, cylindrical or clavate, four-spored cyanophilous. Spores hyaline or pale yellowish, thin-walled to slightly thick-walled, subglobose to broadly ellipsoid, warty, cyanophilous, not amyloid.
Type locality: U.S.A.

The wide, thick-walled basal hyphae in the genus *Cyanobasidium* indicate a relationship with *Botryobasidium* or *Botryohypochnus*. *Botryobasidium* deviates because of its smooth spores, *Botryohypochnus* because of its larger spores with long spines. The spores of *Cyanobasidium* have an ornamentation of low warts more or less resembling that of the conidia in *Aspergillus* or *Penicillium*. Two species can be placed in the new genus.

Cyanobasidium asperulum (D. P. Rogers) Jülich, *comb. nov.* (basionym: *Pellicularia asperula* D. P. Rogers *in* Farlowia **1**: 100. 1943).

Cyanobasidium chordulatum (D. P. Rogers) Jülich, *comb. nov.* (basionym: *Pellicularia chordulata* D. P. Rogers *in* Farlowia **1**: 98. 1943).

Granulobasidium Jülich, *gen. nov.*

Carposomata resupinata, effusa, adnata, membranacea. Hymenophorum laeve vel leviter tuberculatum. Systema hypharum monomiticum. Hyphae hyalinae, angustae, fibulatae, saepe guttulatae. Cystidia desunt. Basidia hyalina, cylindracea vel anguste clavata, 40–60 μm longa, granulosa vel guttulata, tetraspora, fibulata. Sporae hyalinae, crasse tunicatae, asperae, guttulatae, cyanophileae, inamyloideae. Plerumque cum chlamydosporis ellipsoideis, crasse tunicatis, cyanophileis et dextrinoideis.
Typus: *Corticium vellereum* Ell. & Cragin apud Cragin 1885.

Basidiocarp resupinate, effused, adnate, membranaceous. Hymenial surface even or slightly tuberculate. Hyphal system monomitic. Hyphae hyaline, narrow, with clamps, often guttulate. Cystidia absent. Basidia hyaline, cylindrical to narrowly clavate, 40–60 μm long, with granular or guttulate contents, four-spored, with a basal clamp. Spores hyaline, thick-walled, with uneven surface, guttulate, cyanophilous, not amyloid. Often with ellipsoid, thick-walled, cyanophilous and dextrinoid chlamydospores.
Type locality: U.S.A.

The type species has been placed in the genus *Hypochnicium* by Parmasto (*1968*). It differs, however, from that genus in its long and slender basidia with remarkably short sterigmata and granular contents, lack of cystidia, uneven spore surface, presence of usually large numbers of chlamydospores; reaction on laccase weak or absent (laccase present in typical species of *Hypochnicium*).

Granulobasidium vellereum (Ellis & Cragin apud Cragin) Jülich, *comb. nov.* (basionym: *Corticium vellereum* Ellis & Cragin apud Cragin *in* Bull. Washburn Coll. Lab. Nat. Hist. **1**: 66. 1885).

Gyrophanopsis Jülich, *gen. nov.*

Carposomata resupinata, effusa, membranacea. Hymenophorum laeve. Systema hypharum monomiticum. Hyphae hyalinae vel basales luteo-brunneae, incrassate tunicatae, fibulatae. Lamprocystidia adsunt, luteo-brunnea, conica, incrustata, septata, cum fibulis. Basidia hyalina, clavata, tetraspora. Sporae hyalinae vel pallide luteae, leviter incrassate tunicatae, laeves, ellipsoideae, inamyloideae.
Typus: *Pellicularia zealandica* Cunn. 1953.

Basidiocarp resupinate, effused, membranaceous. Hymenial surface even. Hyphal system monomitic. Hyphae hyaline of yellowish brown in the trama, thick-walled, with clamps. Lamprocystidia present, yellowish-brown, conical, incrusted, septate, with clamps. Basidia hyaline, clavate, four-spored. Spores hyaline of slightly yellowish, slightly thick-walled, smooth, ellipsoid, not amyloid.
Type locality: New Zealand.

The genus *Gyrophanopsis* differs from all other genera with resupinate basidiocarp in its slightly thick-walled spores, yellowish-brown lamprocystidia and rather large yellowish-brown, thick-walled basal hyphae. The genus is up to now monotypic.

Gyrophanopsis zealandica (Cunn.) Jülich, *comb. nov.* (basionym: *Pellicularia zealandica* Cunn. *in* Trans. R. Soc. N. Zeal. **81**: 169. 1953).

Jacksonomyces Jülich, *gen. nov.*

Carposomata resupinata, effusa, adnata, ceracea, absque rhizomorphis. Hymenium laeve vel rugosum. Systema hypharum monomiticum. Hyphae hyalinae, cylindraceae vel torulosae, basales crasse-tunicatae, fibulatae. Cystidia hyalina, plus minusve tenui-tunicatae, fibulatae. Basidia hyalina, stipitate clavata, fibulata, tenui-tunicata, tetraspora, circa 10–20 μm longa. Sporae hyalinae, cylindraceae, laeves, tenuitunicatae, circa 5 μm longae.
Typus: *Peniophora phlebioides* Jackson & Dearden 1949.

Basidiocarp resupinate, effused, adnate, ceraceous, without rhizomorphs. Hymenial surface even or somewhat folded. Hyphal system monomitic. Hyphae hyaline, cylindrical to torulose, thick-walled in the trama, with clamps. Cystidia (leptocystidia) hyaline, more or less thin-walled, with a basal clamp. Basidia hyaline, stalked-clavate, thin-walled, about 10–20 μm long, with a basal clamp, four-spored. Spores hyaline, cylindrical, smooth, thin-walled, about 5 μm long.
Type locality: Canada.

The type species of *Jacksonomyces* has the typical ceraceous basidiocarp of a *Phlebia* but deviates from that genus in its stalked-clavate, partly pleurobasidioid, and rather small basidia. It is named after H. S. Jackson who contributed much to our knowledge of Canadian Corticiaceae.

Jacksonomyces phlebioides (Jackson & Dearden) Jülich, *comb. nov.* (basionym: *Peniophora phlebioides* Jackson & Dearden *in* Canad. J. Res. (C) **27**: 150–151. 1949).

Lepidomyces Jülich, *gen. nov.*

Carposomata resupinata, effusa, ceraceo-crustacea, adnata. Hymenophorum laeve. Systema hypharum monomiticum. Hyphae hyalinae, tenui-tunicatae, indistinctae, torulosae, fibulatae. Leptocystidia adsunt,

hyalina, tenui-tunicata, fibulata, plus minusve incrustata. Basidia variabilia, cylindricacea, suburniformia vel clavata, nonnumquam pleurobasidioidea, circa 20 × 5 μm, hyalina, fibulata, tetraspora. Sporae hyalinae, cylindricaceae vel anguste ellipsoideae, tenui-tunicatae, laeves, 6–8 μm longae, inamyloideae.
Typus: *Peniophora subcalcea* Litsch. 1939.

Basidiocarp resupinate, effused, ceraceous-crustaceous, adnate. Hymenial surface even. Hyphal system monomitic. Hyphae hyaline, thin-walled, indistinct, torulose, with clamps. Leptocystidia present, hyaline, thin-walled, clamped, more or less incrusted. Basidia variable, cylindrical, suburniform or clavate, sometimes pleurobasidioid, about 20 × 5 μm, hyaline, with a basal clamp, four-spored. Spores hyaline, cylindrical to narrowly ellipsoid, thin-walled, smooth, 6–8 μm long, not amyloid.
Type locality: Austria.

The type species of *Lepidomyces* was formerly placed in *Phlebia* and *Xenasma*. *Phlebia* is characterized by a waxy basidiocarp with elongated and narrowly clavate basidia, *Xenasma* sensu lato is characterized by typical pleurobasidia and (in most species) amyloid or warty spores.

Lepidomyces subcalceus (Litsch.) Jülich, *comb. nov.* (basionym: *Peniophora subcalcea* Litsch. *in* Österr. bot. Z. **88**: 119. 1939).

Pseudomerulius Jülich, *gen. nov.*

Carposomata resupinata, effusa vel effuso-reflexa, ceraceo-membranacea, adnata, rhizomorphae desunt. Hymenophorum distincte merulioideum. Systema hypharum monomiticum. Hyphae hyalinae, distinctae, tenui- vel basales incrassate tunicatae, tumentes in KOH solutione, fibulae adsunt vel in parte desunt. Cystidia desunt. Basidia hyalina, suburniformia vel anguste clavata, fibulata, tetraspora. Sporae pallide luteae, cylindraceae vel leviter curvatae, laeves, leviter incrassate tunicatae, inamyloideae.
Typus: *Merulius aureus* Fr. 1828

Basidiocarp resupinate, effused or effuso-reflexed, ceraceous-membranaceous, adnate, rhizomorphs absent. Hymenial surface distinctly merulioid (also when dry). Hyphal system monomitic. Hyphae hyaline, distinct, thin-walled or the basal ones somewhat thick-walled and distinctly swelling in KOH, clamps present at all or most septa. Cystidia lacking. Basidia hyaline, suburniform or narrowly clavate, four-spored, with a basal clamp. Spores light yellowish (yellowish brown in masses), cylindrical or slightly curved, smooth, slightly thick-walled, not amyloid.
Type locality: Sweden.

The genus *Pseudomerulius* is related to *Leucogyrophana* and *Serpula*, but differs from both genera in its much smaller and narrower spores and basidia; it differs further in its basal hyphae which swell distinctly in KOH.

Pseudomerulius aureus (Fr.) Jülich, *comb. nov.* (basionym: *Merulius aureus* Fr., Elenchus **1**: 62. 1828).

Pseudomerulius elliottii (Massee) Jülich, *comb. nov.* (basionym: *Merulius elliottii* Masse *in* J. Bot., Lond. **30**: 162. 1892).

Pteridomyces Jülich, *gen. nov.*

Carposomata resupinata, effusa, adnata, membranacea. Hymenophorum minute odontioideum. Systema hypharum monomiticum. Hyphae hyalinae, dense aggregatae, tenui-tunicatae, fibulatae. Cystidia desunt. Spinae steriles, conicae, constantes ex hyphis parallelis, fibulatis cum parietibus tenui-tunicatis et hyalinis. Basidia hyalina, clavata, fibulata, tetraspora, 10–15 μm longa. Sporae hyalinae, laeves, tenui-tunicatae, inamyloideae.

Typus: *Epithele galzinii* Bres. apud Bourd. & Galz. 1911.

Basidiocarp resupinate, effused, adnate, membranaceous. Hymenial surface minutely odontioid. Hyphal system monomitic. Hyphae hyaline, densely arranged, thin-walled, with clamps. Cystidia absent. Spines sterile (hyphal pegs), consisting of parallelly arranged, thin-walled, hyaline, clamped hyphae. Basidia hyaline, clavate, with a basal clamp, four-spored, about 10–15 μm long. Spores hyaline, smooth, thin-walled, inamyloid.

Type locality: France.

The type species of *Pteridomyces* is up to now only found on old fronds of ferns (*Arthyrium*, *Dryopteris*). It was originally described as *Epithele*, but the type of that genus has much larger basidia and very large, thick-walled spores. *Epithele galzinii* has been compared with *Athelopsis*, but the basidiocarp is not loosely pellicular, the hyphae are not loosely arranged and the basidia are not podobasidial.

Pteridomyces galzinii (Bres. apud Bourd. & Galz.) Jülich, *comb. nov.* (basionym: *Epithele galzinii* Bres. apud Bourd. & Galz. *in* Bull. trimest. Soc. myc. France **27**: 264. 1911).

Skeletohydnum Jülich, *gen. nov.*

Carposomata resupinata, effusa, adnata, membranacea. Hymenophorum minute hydnoidea cum spinulis sterilibus constans ex hyphis skeleticis hyalinis. Systema hypharum dimiticum cum hyphis skeleticis. Hyphae generativae hyalinae, cylindraceae vel torulosae, tenui-tunicatae, fibulatae. Dendrohyphidia hyalina vel hyphae paraphysoideae torulosae adsunt, cystidia desunt. Basidia in medio distincte constricta, fibulata, tetraspora. Sporae hyalinae, elongatae, ellipsoideae, tenui-tunicatae, laeves, circa 14 × 15 μm, inamyloideae.

Typus: *Epithele nikau* Cunn. 1956.

Basidiocarp resupinate, effused, adnate, membranaceous. Hymenial surface minutely hydnoid with sterile spines (hyphal pegs) consisting of hyaline skeletal hyphae. Hyphal system dimitic with skeletal hyphae. Generative hyphae hyaline, cylindrical to torulose, thin-walled, with clamps. Hyaline dendrohyphidia or torulose paraphysoid hyphae present, cystidia absent. Basidia distinctly constricted in the middle, with a basal clamp, four-spored. Spores hyaline, elongated, ellipsoid, thin-walled, smooth, about 14 × 5 μm, not amyloid.

Type locality: New Zealand.

The type species of *Skeletohydnum* shows the same elongated spores as *Epithele typhae*, but the spores are thin-walled. The genus differs from most other genera with hyphal pegs in that the spines are made up of skeletal hyphae. The genus is up to now monotypic.

Skeletohydnum nikau (Cunn.) Jülich, *comb. nov.* (basionym: *Epithele nikau* Cunn. *in* Trans. R. Soc. N. Zeal. **83**: 629. 1956).

A NEW SPECIES OF TUBULICRINIS DONK 1956

Tubulicrinis corneri Jülich, *spec. nov.* – Fig. 1

Carposomata resupinata, effusa, adnata, membranacea, albida vel cremea, odontioidea vel minute hydnoidea. Spinulae subulatae, 0.5–0.8 × 0.2–0.3 mm. Systema hypharum monomiticum. Hyphae hyalinae, cylindraceae, tenui- vel incrassate tunicatae (0.2–0.4 μm), laeves, fibulatae, 2–4 μm latae. Cystidia (lyocystidia) adsunt, hyalina, parietibus tumentibus in KOH, dimorpha: (a) 40–75 × 4–8.5 μm, subcylindracea vel ventricosa, crasse tunicata (0.5–3.5 μm), apicibus umbraculiformis; (b) 14–22 μm longa, crescentia lateraliter ex hyphis. Basidia hyalina, suburniformia, 20–30 × 5–6.5 μm, tetraspora, fibulata. Sporae hyalinae, late ellipsoideae, tenui-tunicatae, laeves, 5–6 × 4–5 μm, inamyloideae.

Typus: Malaya, Pahang, Fraser's Hill, 1300 m alt., on a rotten trunk in the forest, 3.X.1961, *E. J. H. Corner* (Herb. Corner).

Basidiocarp annual, resupinate, effused, several cm large, adnate, membranaceous, context homogeneous, margin thinning out, byssoid, rhizomorphs or hyphal strand lacking. Hymenial surface odontioid or slightly hydnoid, the spines 0.5–0.8 mm long and 0.2–0.3 mm wide, slender, terete-acicular, mostly simple and entire, scarcely crowded, in places patchily developed, the whole basidiocarp whitish to cream-coloured, not or only slightly cracked when dry. Hyphal system monomitic. Hyphae hyaline, rather distinct, cylindrical, densely arranged in subhymenium and trama, thin-walled and 2–4 μm wide in the subhymenium, slightly thick-walled and 2–4 μm wide in the trama, with smooth surface, clamps present at all septa, contents homogeneous. Cystidia (lyocystidia) present, abundant, of hymenial to subhymenial origin, hyaline, the walls swelling in KOH, dimorphic: (a) large, 40–75 × 4–8.5 μm, ventricose or subcylindric, the base sometimes bi-rooted, the capitate apex 6–8.5 μm wide and set with 6–8(–9) deflexed, up to 4.5 μm long, solid spines (crystals), a basal clamp present, more or less enclosed in the hymenium or projecting up to 30 μm; (b) small, 14–22 μm long, the cylindric stalk 1.5–2.5 μm wide, the head 2.5–4 μm wide and set with 4–6 short, deflexed spines (crystals), the cystidia originating laterally on hyphal cells and not cut off by a septum, the stalk slightly thick-walled, also swelling in KOH. At the base of the spines and in the trama are occasionally thick-walled, spicate processes up to 35 × 6 μm, mostly simple, rarely twinned, acute, not capitate, hyaline, smooth. Basidia hyaline, suburniform when mature, young basidia cylindrical to ellipsoid, 20–30 × 5–6.5 μm, thin-walled, smooth, a basal clamp always present, contents homogeneous, with four subulate sterigmata (4.5 × 0.8 μm). Spores hyaline, broadly ellipsoid, thin-walled, smooth, 5–6 × 4–5 μm, with distinct, about 1 μm long apiculus, contents homogeneous when dry, 1- or 2-guttulate when fresh, neither amyloid, dextrinoid, nor cyanophilous.

This type of lyocystidia with a head of umbrella-like crystals was up to now only known from *Tubulicrinis hamata* (Jackson) Donk (syn.: *Peniophora umbracula* Cunn.). It was a great surprise to find the same situation in a second species, which is microscopically rather similar, but differs in having a distinctly odontioid to somewhat hydnoid basidiocarp with nearly 1 mm long spines, whereas the basidiocarp of *T. hamata* is very thin and smooth. The specimen was sent by Professor E. J. H. Corner together with extensive notes on the macro- and micromorphology of the species. Corner has had the opportunity to study living specimens of this taxon and I made use of his notes to complete my own observations. In a footnote to his notes, Corner expressed exactly what every student of this taxon thinks: 'Why is such a little fungus so complicated?'

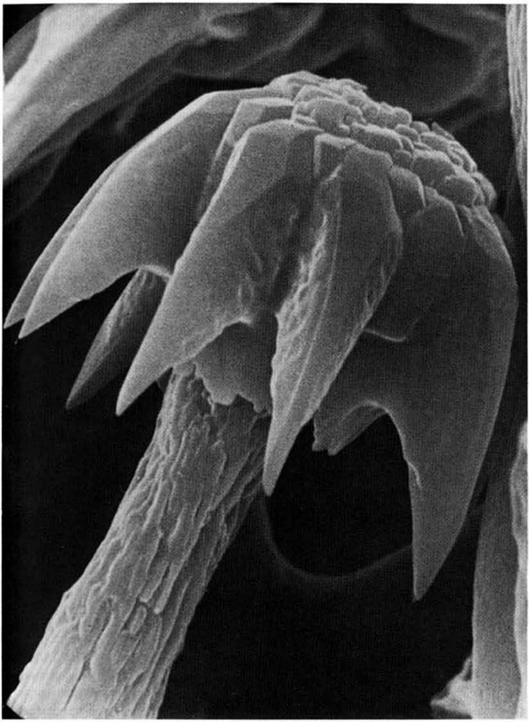

Fig. 1. *Tubulicrinus corneri* (holotype), a lyocystidium × 18,000.

FURTHER NEW COMBINATIONS PROPOSED

Botryobasidium cystidiatum (D. P. Rogers) Jülich, *comb. nov.* (basionym: *Pellicularia cystidiata* D. P. Rogers 1943 *in* Farlowia **1**: 101–102.)

Botryobasidium scabridum (Cunn.) Jülich, *comb. nov.* (basionym: *Pellicularia scabrida* Cunn. *in* Trans. R. Soc. N. Zeal. **81**: 326. 1953).

Botryohypochnus alutaceus (Boidin) Jülich, *comb. nov.* (basionym: *Botryobasidium alutaceum* Boidin *in* Cah. Maboké **8**: 18. 1970).

Lagarobasidium detriticum (Bourd. & Galz.) Jülich, *comb. nov.* (basionym: *Peniophora detritica* Bourd. & Galz. *in* Revue scient. Bourbonn. **23**: 13. 1910).

Megalobasidium humile (Boidin) Jülich, *comb. nov.* (basionym: *Gloeocystidiellum humile* Boidin *in* Cah. Maboké **4**: 9. 1966).

Parvobasidium lundellii (Ryv. & Solheim) Jülich, *comb. nov.* (basionym: *Physodontia lundellii* Ryv. & Solheim *in* Mycotaxon **6**: 376. 1977).

Phanerochaete arenata (Talbot apud Wakef. & Talbot) Jülich, *comb. nov.* (basionym: *Peniophora arenata* Talbot apud Wakef. & Talbot *in* Bothalia **4**: 944. 1948).

Phanerochaete leprosa (Bourd. & Galz.) Jülich, *comb. nov.* (basionym: *Peniophora radicata* subsp. *leprosa* Bourd. & Galz. *in* Bull. Soc. myc. France **28**: 394. 1913).

Phanerochaete pelliculosa (Talbot) Jülich, *comb. nov.* (basionym: *Peniophora pelliculosa* Talbot *in* Bothalia **6**: 63–64. 1951).

Radulomyces pseudomucidus (Petch) Jülich, *comb. nov.* (basionym: *Hydnum pseudomucidum* Petch *in* Ann. Roy. bot. Gdns Peradeniya **6**: 156. 1916. Lectotype: '*Hydnum pseudomucidum* Petch. Hakgala, Ap. 1919, *Petch 5962*' (K).

Radulomyces sulfureo-isabellinus (Litsch. apud Pilát) Jülich, *comb. nov.* (basionym: *Corticium sulfureo-isabellinum* Litsch. apud Pilát *in* Acta Mus. Nat. Pragae **2** B: 43. 1940).

Scotomyces subviolaceus (Peck) Jülich, *comb. nov.* (basionym: *Hypochnus subviolaceus* Peck *in* Ann. Rep. State Bot. for 1893: 25. 1894). The genus *Hydrabasidium* Perker-Rhodes ex Erikss. & Ryv. 1978 (The Corticiaceae of North Europe, 896) is herewith placed in synonymy with *Scotomyces* Jülich 1978.

Xenasmatella insperata (H. S. Jacks.) Jülich, *comb. nov.* (basionym: *Corticium insperatum* H. S. Jackson *in* Canad. J. Res., C **28**: 718. 1950).

SOME NEW COMBINATIONS VALIDATED

In his important article on primitive Basidiomycetes Oberwinkler (*1965*) published a number of new combinations none of which is valid when the rules of the Botanical Code are strictly applied. Article 33 (of the 1978 Code) says: 'A new combination, ..., published on or after 1 Jan. 1953, for a previously and validly published name is not validly published unless its basionym ... is clearly indicated and a full and direct reference given to its author and original publication with page or plate reference and date.' The 1961 Code, which was available when Oberwinkler wrote his article, lays the same emphasis on 'a full and direct reference given to its author and original publication with page or plate reference and date.' In Oberwinklers article, however, the reference is cut down to the citation of the basionym, author and date; no direct reference is given neither to the original publication nor to the page or plate on which the basionym was described. And some of the authors or publications are also not to be found in the bibliography, e.g. Berk. & Br. 1860, Rogers & Liberta 1960, Pat. 1899, Bourd. & Galz. 1913. Some time ago I discussed the problem with Oberwinkler, but he had no inclination to give himself valid publications of the new combinations in question.

In order to make Oberwinkler's article fully available for future use, the new combinations are herewith validly published. It should be noted, however, that some of his combinations have been omitted because the species are either still imperfectly studied, e.g. *Xenasmatella aurora*, or in the meantime placed in another genus, e.g. *Tubulicium clematidis*, or already validly published, *Athelidium aurantiacum* cited with full reference by Jülich (*1972*) and Eriksson & Ryvarden (*1973*).

Acanthobasidium delicatum (Wakef.) Oberw. ex Jülich, *comb. nov.* (basionym: *Aleurodiscus delicatus* Wakef. *in* Trans. Brit. mycol. Soc. **35**: 44. 1952).

Litschauerella abietis (Bourd. & Galz.) Oberw. ex Jülich, *comb. nov.* (basionym: *Peniophora aegerita* subsp. *abietis* Bourd. & Galz. *in* Bull. Soc. mycol. France **28**: 383. 1913).

Paullicorticium niveocremeum (Höhn. & Litsch.) Oberw. ex Jülich, *comb. nov.* (basionym: *Corticium niveocremeum* Höhn. & Litsch. *in* Sber. Akad. Wiss. Wien, Math.-nat. Kl., Abt. I, **117**: 1117.

Sphaerobasidium minutum (J. Erikss.) Oberw. ex Jülich, *comb. nov.* (basionym: *Xenasma minutum* J. Erikss. *in* Symb. bot. upsal. **16** (1): 65. 1958).

Tubulicium dussii (Pat.) Oberw. ex Jülich, *comb. nov.* (basionym: *Hypochnus dussii* Pat. *in* Bull. Soc. mycol. France **15**: 202. 1899).

Tubulicium vermiferum (Bourd.) Oberw. ex Jülich, *comb. nov.* (basionym: *Peniophora vermifera* Bourd. *in* Revue scient. Bourbonn. **23**: 13. 1910).

Xenasmatella subflavidogrisea (Litsch.) Oberw. ex Jülich, *comb. nov.* (basionym: *Corticium subflavidogriseum* Litsch. *in* Annls mycol. **39**: 127. 1941).

Xenasmatella tulasnelloidea (Höhn. & Litsch.) Oberw. ex Jülich, *comb. nov.* (basionym: *Corticium tulasnelloideum* Höhn. & Litsch. *in* Österr. bot. Z. **58**: 330. 1908; also *in* Sber. Akad. Wiss. Wien, Math.-nat. Kl., Abt. I, **117**: 1118. 1908).

Xenosperma ludibundum (D. P. Rogers & Liberta apud Liberta) Oberw. ex Jülich, *comb. nov.* (basionym: *Xenasma ludibundum* D. P. Rogers & Liberta apud Liberta *in* Mycologia **52**: 902. '1960', publ. 1962).

A NEW FAMILY OF APHYLLOPHORALES

In 1976 Ginns described the monotypic genus *Corneromyces* based on a specimen collected by Professor E. J. H. Corner in Sabah. The only species, *Corneromyces kinabalui*, is characterized by a resupinate basidiocarp, monomitic hyphal system, brown hyphae with clamps, clavate basidia, and large, thick-walled, smooth, brown spores with an unusual feature: they are strongly amyloid but not (at least the mature spores) cyanophilous. The species can be compared with species of *Coniophora* which also have brownish basidiocarps and hyphae, clavate basidia and brown, thick-walled spores. But the spores in *Coniophora* are distinctly shorter and wider, not so thick-walled as in *Corneromyces*, never amyloid but practically always strongly cyanophilous. To accomodate this unique genus, a new family is proposed.

CORNEROMYCETACEAE Jülich, *fam. nov.*

Carposomata resupinata, effusa, brunnea. Hymenium laeve vel leviter hydnoideum. Systema hypharum monomiticum. Hyphae distinctae, brunneaea, fibulatae. Basidia stipitate clavata, tetraspora, fibulata. Sporae anguste ellipsoideae, laeves, brunneae, valde crassae et amyloideae.
Typus: *Corneromyces* Ginns *in* Mycologia **68**: 970. 1976.

Basidiocarp resupinate, effused, brownish. Hymenial surface even or slightly hydnoid. Hyphal system monomitic. Hyphae distinct, brown, with clamps. Basidia stalked-clavate, four-spored, with a basal clamp. Spores narrowly ellipsoid, smooth, brown, very thickwalled and strongly amyloid.

A NEW FAMILY OF TREMELLALES

The Tremellales have recently received special attention and several new taxa with unusual features have been described. Nearly all possible basidiocarp types have been found within the Tremellales and one of the missing forms, the cyphelloid ones, has been described recently by Oberwinkler & Agerer. The genus, based on *Cyphella applanata* Talbot (*1956*), has been called *Heteroscypha*. It is a cyphelloid genus with sessile, flat basidiocarps and somewhat curved margins, hyaline and fibulate hyphae and longitudinally septate basidia; the spores are narrowly ellipsoid, thin-walled, smooth, not amyloid and show spore-repetition. The genus was placed in the Tremellaceae, but since it deviates so much from the typical genera of that family, a new family is herewith described. It is not unlikely that the newly described genus *Tremelloscypha* Reid (*1979*) also belongs here.

HETEROSCYPHACEAE Jülich, *fam. nov.*

Carposomata cyphelloidea, sessiles vel stipitata. Systema hypharum monomiticum. Hyphae hyalinae, cum vel sine fibulis. Basidia hyalina, longitudinaliter septata. Sporae hyalinae, tenui-tunicatae, laeves.
Typus: *Heteroscypha* Oberw. & Agerer apud Agerer & Oberw. 1979.

Basidiocarp cyphelloid, sessile or stipitate. Hyphal system monomitic. Hyphae hyaline, with or without clamps. Basidia hyaline, longitudinally septate. Spores hyaline, thin-walled, smooth.

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FLAGELLOSCYPHA SECT. LACHNELLOSCYPHA A LINK BETWEEN THE GENERA LACHNELLA AND FLAGELLOSCYPHA

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A new species is described and a new combination is made in the genus *Flagelloscypha: F. montis-anagae* Agerer and *F. libertiana* (Cooke) Agerer; *Lachnella rosae* W. B. Cooke is recognized as a synonym of *F. libertiana*. — *Flagelloscypha montis-anagae* and *F. libertiana* possess on the fruit-body two different types of surface hairs. — The basidia of these species are bigger and have rather stout sterigmata, the spores are on the average longer than in many typical species of *Flagelloscypha*. Moreover the spores are often subfalcispora-like and the fruit-bodies are cupulate and broadly stipitate as in the species of *Lachnella*.[1] — Because of the similarities of these species and their rather isolated position within the genus *Flagelloscypha* a new section is proposed for this group: *Flagelloscypha* sect. *Lachnelloscypha*.

The genus *Lachnella* Fr. has been emended by Donk some years ago (*1959*). Slightly altered it can shortly be characterized as follows.—

Fruit-bodies cup-shaped with a broad stipe-like base, rarely slightly higher than wide; surface hairs, rounded apex included, finely asperulate with crystals, with rather thick (up to 2–3 μm) walls, from base to apex almost with same diameter; spores rather large, 10–20(–25) μm long, asymmetrically ovoid (in the type species) or subfalcispora-like, smooth and with large apiculus; basidia very large too, generally 40–80 μm long, occasionally longer than 100 μm; sterigmata rather stout, curved, conical.

As an example Fig. 1 depicts *Lachnella tiliae*, a typical species of the genus.

The genus *Flagelloscypha* Donk has recently been emended by myself (*1975*). Briefly summarized the most important characteristics are.—

Fruit-bodies more or less cup-shaped, white; surface hairs with walls mostly thinner than 1 μm, rarely swelling in potassium hydroxide, encrusted with finely acicular or coarsely acicular or rhombical crystals, apically thin-walled, very narrow and mostly not encrusted; basidia on the average mostly shorter than 30 μm with rather thin sterigmata; spores asymmetrically subglobose, ovoid, ellipsoid or naviculate, mostly shorter than 13 μm, smooth, thin-walled, neither amyloid nor dextrinoid.

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[1] Subfalcispora-like means with the same type of spores as *Lachnella subfalcispora*.

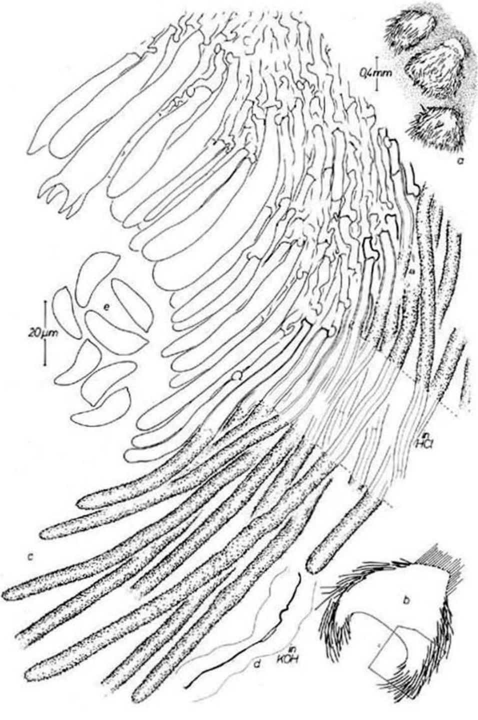

Fig. 1. *Lachnella tiliae*. — a. Habit of fruit-bodies. — b. Section through fruit-body; survey. — c. Section through fruit-body; detail of edge. — d. Surface hair in KOH 10%. — e. Spores. (All figs. from holotype, K.)

Many species are described and illustrated by Agerer (*1975*).

Two species, formerly placed in the genus *Lachnella* (Cooke, *1961*)—*L. libertiana* (Cooke) W. B. Cooke and *L. rosae* W. B. Cooke—and a further species, undoubtedly belong to the genus *Flagelloscypha*, even though all these deviate in the same features from the other species of the genus *Flagelloscypha*.

Flagelloscypha libertiana (Cooke) Agerer, *comb. nov.*—Figs. 2, 3

Cyphella libertiana Cooke *in* Grevillea **8**: 81. 1880. — *Chaetocypha libertiana* (Cooke) O. K. *in* Rev. Gen. **2**: 847. 1891. — *Lachnella libertiana* (Cooke) W. B. Cooke *in* Beih. Sydowia **4**: 73. 1961. — Type: Belgium, near Malmedy, 'in ramis decorticatis Cornis masculae' (= *Cornus mas*) (holotype; K).

Lachnella rosae W. B. Cooke *in* Beih. Sydowia **4**: 78. 1961. — Typus: U.S.A., Idaho, Lewis Co., near Mohler between Nez Perce and Craigmont, 29 Oct. 1949. *H. W. Smith & W. B. Cooke* (holotype; herb. W. B. Cooke 26106).

Fruit-bodies cup-shaped, with more or less distinct stipe, appressed to patently hairy, up to 0.4 mm high, densely crowded. Surface hairs of two types. First type 3–4 μm in diam., slightly thick-walled, with clamps at the base, apically slightly pointed or whip-like with sometimes ramified ends, with minutely acicular, rod- or needle-shaped, up to 4 μm long crystals; this type of hairs particularly present near the 'mouth' of the fruit-body—those quite at the edge of the 'mouth' not flagellate but with tips rounded and finely encrusted. Second type (3.5–)4–5(–6) μm in diam., with somewhat dextrinoid up to 1.5 μm thick walls, clamped at the base, in 10% KOH somewhat irregularly swelling, apically slightly pointed or blunt, with up to 4 μm long, rhombical or amorphous crystals, rarely naked; crystals soluble in HCl, but many granular or acicular structures on the hyphal walls persisting; this second type common on the outside of the fruit-body. Hyphae of trama somewhat agglutinated, (1.5–)2–3.5(–4.5) μm in diam., clamped. Basidia (35–)40–55(–65) × (8–)9–11(–12) μm, suburniform, with 4 sterigmata, clamped at the base.

Spores asymmetrically ellipsoid to asymmetrically ovoid, slightly naviculate or slightly subfalcispora-like, (10–)10.5–12.5(–14) × (5–)5.5–6.5(–7.5) μm, on the average 11.5–12.5 μm long, with sporefactor 1.9–2.1, neither amyloid nor dextrinoid.

SUBSTRATE.—Twigs of *Cornus mas* and *Rosa spauldingii*.

SPECIMENS EXAMINED.—Holotype and isotype of *Cyphella libertiana* and holotype of *Lachnella rosae*.

Flagelloscypha libertiana resembles *Lachnella rosae* very much. The fruit-bodies are alike, although those of *L. rosae* are somewhat larger. The spores as well as the basidia are similarly shaped and of almost the same size. The surface hairs virtually resemble each other, even though the finely encrusted surface hairs in the type of *F. libertiana* seem to lack whip-like ends. However, this specimen is very old and the ends of these surface hairs are difficult to study, but the ends of the younger surface hairs are not as compactly encrusted as their lower parts. Therefore it is well possible that originally whip-like ends were present in the type of *F. libertiana*.

In *F. libertiana* as well as in *L. rosae* young, finely encrusted surface hairs do not have flagella-like ends; instead they have a rounded, encrusted apex. In view of this all I consider *Lachnella rosae* (1961) a younger synonym of *Cyphella libertiana* (1880). Consequently *Flagelloscypha libertiana* is the correct name for this species. For comparison of *F. libertiana* with *F. montis-anagae*, see the discussion under that species (p. 342).

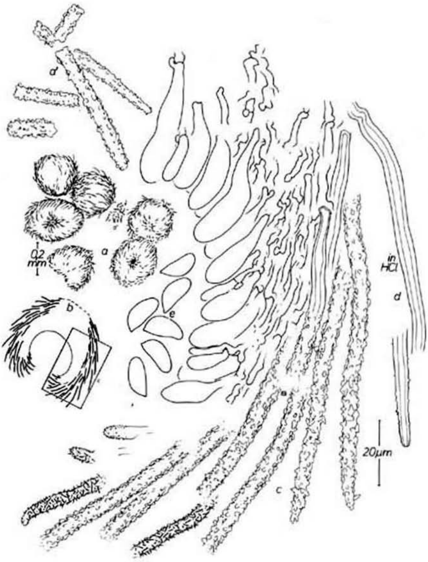

Fig. 2. *Flagelloscypha libertiana*. — a. Habit of fruit-bodies. — a'. Surface hairs of very young fruit-bodies just on the substrate. — b. Section through fruit-body; survey. — c. Section through fruit-body; detail of edge. — d. Surface hairs in HCl. — e. Spores. (All figs. from holotype, K.)

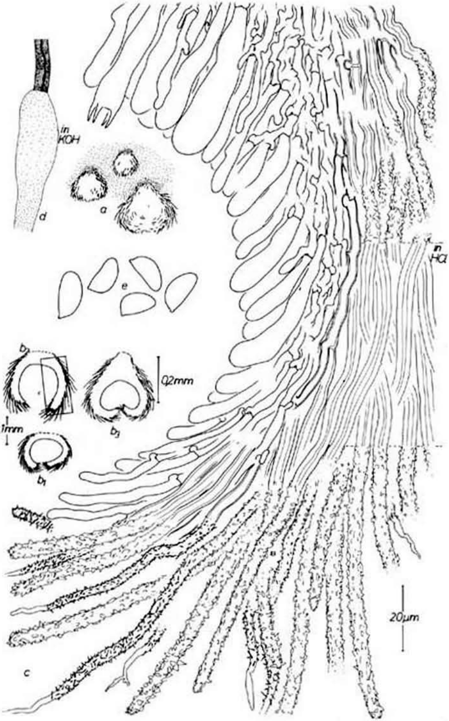

Fig. 3. *Lachnella rosae*. — a. Habit of fruit-bodies. — b_1, b_2, b_3. Sections through fruit-bodies of different age; survey. — c. Section through a fruit-body; detail of edge. — d. Surface hair in KOH 10%. — e. Spores. (All figs. from holotype, herb. W. B. Cooke 26106.)

Flagelloscypha montis-anagae Agerer, *spec. nov.*[2]

MISAPPLIED NAME.—*Lachnella rosae* sensu Agerer *in* Nova Hedwigia **30**: 314. 1978.

Differt ab omnibus speciebus generis pilis crystallis angustis et longe acicularibus, flagellis ramosis in margine cupulae.

Cupulae patinaceae, late stipitatae, hirsutae, albae, ad 200 μm altae, solitariae usque ad gregariae. Pili externi duobus formis: forma una maximam partem in margine cupulae sita, 2.5–3.5 μm crassa, subcrassitunicata, crystallis angustis et longe acicularibus, ad 5 μm longis, flagellis ad 20 μm longis, ramosis. — forma alia non in margine cupulae sed extrinseca sita, 3.5–4.5(–5) μm crassa, ad 2 μm crassitunicata, in 10% KOH irregulariter turgescens; basi tenuitunicata, apicaliter rotundata, subcrassitunicata vel tenuitunicata; crystallis grosse acicularibus vel grosse rhomboideis, ad 4 μm longis. Hyphae tramae subagglutinatae, fibuligerae, 2–3.5(–5) μm crassae. Basidia 28–36 × 8–9 μm suburniformia, 4-sterigmatica, fibuligera. Sporae asymmetrici-ellipticae vel naviculares vel Lachnellae subfalcisporae similes, hyalinae, leves, 8–9.5 × 4.5–5.5(–6.5) μm, *c.* 8.9 μm longae, proportio sporarum *c.* 1.8; nec amyloideae nec dextrinoideae. Ramulis insidens. Typus: Canary Islands, Tenerife, 'Lorbeerwald zwischen Las Mercedes und El Bailadero, ca. 3 km vor El Bailadero, 700–750 m NN', *Agerer & Blanz*, 13 March 1975 (holotypus; in herb. Agerer 5848).

ADDITIONAL SPECIMENS EXAMINED.—Italy, Trentino, Valvestino, 'an der Straße zwischen Turano und Magasa', *R. Agerer & C. Agerer-Kirchhoff*, 16 July 1976 (herb. Agerer 7284, 7285, 7286).

A detailed description with illustrations was given earlier (Agerer, *1978*) under the name *Lachnella rosae*. Therefore, here only a Latin diagnosis is given.

Flagelloscypha montis-anagae differs from *F. libertiana* in the presence of repeatedly ramified, minutely acicularly encrusted surface hairs quite on the rim of the fruit-body—only a few of these hairs occurring on the outside— whereas this type of surface hairs can only be found on the outside of the cup in *F. libertiana*. In the latter species the minutely acicularly encrusted surface hairs on the rim are blunt, not ramified and furnished with crystals up to the very apex.

The spores of *F. montis-anagae* are smaller (averaging 8–10 μm opposed to *c.* 12 μm in *F. libertiana*). Likewise also the bašidia are smaller, viz. 28–36 × 8–9 μm (*F. montis-anagae*) against (35–)40–55(–65) × (8–)9–11 μm (*F. libertiana*). Earlier, Agerer (*1978*: 314) has given the variability in spore size of the whole species, and not only the variability of the cited type specimen.

FLAGELLOSCYPHA SPEC.

Fruit-bodies shallowly cup-shaped, with rather broad stipe-like base, single or in small groups, white, patently hairy, up to 0.2 mm high. Surface hairs of only one type, (3–)3.5–4.5(–5.5) μm in diam., with up to 2.5 μm thick walls, dextrinoid, swelling in KOH 10% (but seldom irregularly), clamped at the base, with coarsely-acicular, rhombical or amorphous crystals; apices sometimes naked, somewhat thick-walled and slightly pointed. Hyphae of the trama (2–)2.5–3.5(–4.5) μm in diam., agglutinate, clamped. Basidia 27–35(–40) × 8–10.5 μm, suburniform, 4-spored, clamped at the base, sometimes transversally septate, with rather stout, horn-like sterigmata.

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[2] ETYMOLOGY.—The type was found in the Anaga Mountains of Tenerife.

Spores asymmetrically ellipsoid, asymmetrically ovoid, slightly naviculate to subfalcispora-like, 9–12.5 × 4–6 µm, on the average 10–10.5 µm long, with sporefactor *c*. 2.1, neither amyloid nor dextrinoid.

SPECIMEN EXAMINED.—Belgium, near Malmedy, 'ad Cornus maris in ramulos emortuos', *Libert* (S).

This specimen, also collected by Libert near Malmedy in Belgium, is very similar to *F. libertiana.* It grew 'ad Cornus maris in ramulos emortuos' and has therefore the same finding data as the type of *F. libertiana*, as the name *Cornus mascula* is a synonym of *C. mas.*

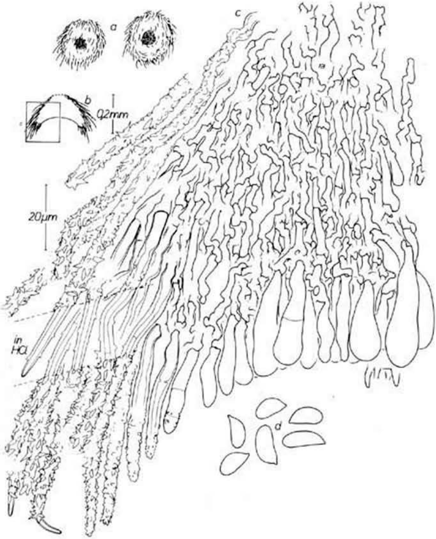

Fig. 4. *Flagelloscypha* spec. — a. Habit of fruit-bodies. — b. Section through fruit-body; survey. — c. Section through fruit-body; detail of edge. — d. Spores. (All figs. from S.)

Flagelloscypha libertiana and this specimen are so different, that they are most probably two distinct species. *Flagelloscypha* spec. exhibits only the coarsely-acicularly to amorphously encrusted type of surface hairs with thick walls, sometimes however possessing naked ends. One could think that this collection represents a young specimen of *F. libertiana*, but already the young fruit-bodies of *F. montis-anagae* and *F. libertiana* have two types of surface hairs. Even though the fruit-bodies of *Flagelloscypha* spec. are small, they are nearly as large as those of *F. libertiana* that at this stage exhibit two types of surface hair, whereas *Flagelloscypha* spec. only exhibits one type.

At first sight it is somewhat astonishing that Libert collected two different but closely related taxa on the same substrate on the same locality, but this is scarcely surprising, if general experience in field-mycology is taken into consideration. Frequently related species grow on the same substrate at the same place (e.g. *F. faginea* and *F. minutissima* on leaves of *Fagus silvatica*).

CHARACTERISTICS COMMON TO FLAGELLOSCYPHA SPEC., F. MONTIS-ANAGAE AND F. LIBERTIANA

The basidia of these species are mostly longer than those of typical species of the genus *Flagelloscypha*, and the sterigmata appear rather stout when compared with those of the other species.

The spores of the species discussed are relatively long. At least some spores are subfalcispora-like contrary to those of typical species of *Flagelloscypha*. (Subfalcispora-like means that in outline the spores have a ventral depression near the middle, combined with a relatively great length.)

The fruit-bodies of the three aberrant species are cup-shaped and have a more or less distinct, broad, stipe-like base. Only two of the species of the genus Flagelloscypha thus far known have such a base, viz. *F. donkii* and *F. dextrinoidea*. However, these two species possess different spores, smaller basidia and other surface hairs (Agerer, *1975*).

The surface hairs of the species described above are very characteristic. In all three there are coarsely-acicularly to rhombically or amorphously encrusted surface hairs with a diameter diminishing only slightly towards the apex. Their apices are more or less blunt and mostly encrusted also. If surface hairs of a second type are present, these have finely-acicular, rod- or needle-like encrustations and are more or less tapering toward the apices, which are naked and ramified in *F. montis-anagae* and *F. libertiana*. In some of the other species of *Flagelloscypha* a few ramified tips of surface hairs occasionally occur, but those species differ considerably in other features. The above described species have relatively thick-walled surface hairs swelling irregularly in a solution of KOH, as in all species of *Lachnella* Fr. emend. Donk and in a few of the other species of *Flagelloscypha* with thick-walled surface hairs.

The coarsely-acicularly and rhombically encrusted surface hairs of *F. montis-anagae* and *F. libertiana* as well as the flagella-like apices of the second type of hairs give reason to put these species into the genus *Flagelloscypha*. On the other hand some characteristics deviate from those of typical species of *Flagelloscypha*.

The relatively big spores of which at least some are subfalcispora-like, the relatively long basidia with their stout sterigmata and the cupulate fruit-bodies with their broad stipe-like base place these species in an extreme position within the genus *Flagelloscypha*. The occurrence of two types of surface hairs on the same fruit-body accentuates this position. *Flagelloscypha* spec. resembles *F. montis-anagae* and *F. libertiana* in many characters. Therefore it seems best to place it together with these two species into one group, even though it does not show two types of surface hairs. For this group of three species a new section is proposed within the genus *Flagelloscypha*.

Flagelloscypha Donk sect. **Lachnelloscypha** Agerer, *sect. nov.*

Cupulae patinaceae, late stipitatae, patentibus pilis, interdum duobus formis pilis vestitae: forma una semper praesens, crystallis maioribus, acicularibus vel rhomboideis obsita, vel amorphe incrustata, apicibus rotundatis vel subcuspidatis, nonnullis flagellis, crassitunicatis, in 10% KOH irregulariter turgescens; forma alia tantum praesens in compluribus speciebus, flagellis instructis; crystallis minoribus, acicularibus vel longe acicularibus. Basidia plerumque longiora quam 30 μm, plus minusve suburniformia, sterigmatibus robustis. Sporae semper quiddam Lachnellae subfalcisporae.

Typus sectionis: *Flagelloscypha montis-anagae* Agerer.

The type-section *Flagelloscypha* Donk sect. *Flagelloscypha* is characterized as the whole genus was characterized by Agerer (*1975*).

THE POSITION OF FLAGELLOSCYPHA SECT. LACHNELLOSCYPHA IN REGARD TO THE GENUS LACHNELLA FR. EMEND. DONK

The species of the genus *Lachnella* as emended by Donk possess apically rounded, finely-acicularly encrusted surface hairs having almost the same diameter from the base to the apex. Though the apices of the surface hairs in *F. montis-anagae* and *F. libertiana* are blunt also and have almost the same diameter from the base to the apex, these species stand nearer to the typical species of *Flagelloscypha* because of the coarsely-acicular and rhombical encrustations. Moreover *F. montis-anagae* and *F. libertiana* feature a further type of surface hair which is flagella-like.

Because of the sometimes subfalcispora-like, rather long spores, the relatively long basidia and the broad stipe-like base of the fruit-bodies, sect. *Lachnelloscypha* is a link between the genera *Flagelloscypha* and *Lachnella*. The gap, however, between *Lachnella* emend. Donk (*1959*) and *Flagelloscypha* emend. Agerer (*1975*) remains sufficiently wide to justify the maintenance of their separation.

Zusammenfassung

In der Gattung *Flagelloscypha* wird eine neue Art beschrieben und eine Neukombination vorgenommen: *F. montis-anagae* Agerer und *F. libertiana* (Cooke) Agerer; *Lachnella rosae* W. B. Cooke wird als Synonym von *F. libertiana* erkannt. — *Flagelloscypha montis-anagae* und *F. libertiana* besitzen am Fruchtkörper zweierlei Randhaartypen. — Die Basidien dieser Arten sind größer und bilden ziemlich kräftige Sterigmen und die Sporen werden durchschnittlich länger als bei typischen Arten der Gattung *Flagelloscypha*; überdies

sind die Sporen oft subfalcispora-ähnlich und die Fruchtkörper schüsselförmig und breit gestielt wie bei den Arten der Gattung *Lachnella*. — Wegen der Ähnlichkeit dieser Arten und der relativ isolierten Stellung innerhalb der Gattung *Flagelloscypha*, wird für diese Gruppe eine eigene Sektion vorgeschlagen: *Flagelloscypha* sect. *Lachnelloscypha*.

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ULTRASTRUCTURE DES HYPHES INCRUSTÉES DANS LE GENRE SKELETOCUTIS

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Les hyphes incrustées de toutes les espèces du genre *Incrustoporia* ont toutes la même ultrastructure à l'exception de *I. carneola* qui doit être replacé, pour cette raison, dans le genre *Poria*. Le même type de cristallisations hyphiques existe par contre chez *Skeletocutis amorpha* nécessitant, vu le caractère prioritaire du genre *Skeletocutis* (1958) sur le genre *Incrustoporia* (1963), les nouvelles combinaisons suivantes: *Skeletocutis alutacea, S. nivea, S. percandida, S. stellae, S. subincarnata* et *S. tschulymica*.

Domański crée en 1963 le genre *Incrustoporia* (espèce type: *Poria stellae* Pilát) pour quelques Polyporacées pourvues d'hyphes incrustées au niveau des dissépiments.

En 1969, Eriksson & Strid ajoutent *Polyporus semipileatus* Peck au genre *Incrustoporia* car 'In our opinion also this species is an Incrustoporia'. Sa position systématique avait d'ailleurs déjà embarassé les mycologues qui l'ont nommé tour à tour *Polyporus semipileatus* Peck (*1881*; Saccardo, *1888*; Lowe, *1966*), *Polyporus chioneus* Fries (*1815*; Bresadola, *1908*), *Polyporus niveus* Jungh. (*1839*), *Leptoporus chioneus* (Fr.) Quél. (*1888*), *Leptoporus semipileatus* (Peck) Pilát (*1938*) et *Tyromyces semipileatus* (Peck) Murr. (*1907*; Jahn, *1963*; Bondarcev, *1971*).

Mais, peu satisfait des genres existants pour y placer *P. semipileatus*, Pouzar (*1966*) propose le genre *Leptotrimitus* Pouz. qui, par son nom, souligne bien le caractère trimitique de la trame (Teston, *1953*; Reid, *1963*; Lowe, *1966*).

Quelque temps après, Donk (*1971*) réunit les genres *Incrustoporia* et *Leptotrimitus*; pour lui, le caractère trimitique n'est pas un critère suffisant pour séparer deux genres et cela d'autant plus que tous les autres éléments (hyménium, spores, hyphes incrustées, caractères culturaux) sont identiques.

Ainsi donc, selon Ryvarden (*1974*, *1976*), le genre *Incrustoporia* comprend 7 espèces, *I. alutacea*, *I. carneola*, *I. nivea*, *I. percandida*, *I. stellae*, *I. subincarnata* et *I. tschulymica*, essentiellement caractérisées par des hyphes incrustées. Et c'est ce point commun particulier qui a éveillé notre curiosité au point d'en faire une analyse au microscope électronique à balayage (M.E.B.) afin de savoir s'il y a unité architecturale dans le genre considéré ou non.

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Sur conseil de Monsieur le Professeur John Eriksson de Göteborg, nous avons également étudié une espèce non rattachée aux *Incrustoporia*, *Skeletocutis amorpha* (Fr.) Kotl. & Pouz., espèce type du genre *Skeletocutis* publié en 1958.

MATÉRIEL ET MÉTHODE

Les espèces étudiées dans le présent article sont d'origine européenne, à l'exception de *I. carneola* récolté en Tanzanie.

Nous avons analysé la matériel suivant. —

Trois exsiccata reçus de J. Eriksson: *Incrustoporia stellae* (Pilát) Dom., Fungi suecici, 12.6.1952 (O 05559). — *I. subincarnata* (Peck) Dom., Fungi suecici, 30.10.1959. — *I. tschulymica* (Pilát) Dom., Fungi suecici, 21.9.1966.

Deux exsiccata reçus de L. Ryvarden: *I. carneola* (Bres.) Ryv. (O 5239). — *I. percandida* (Malenç. & Bert.) Ryv. (O 12471).

Trois espèces en provenance de la région de Neuchâtel: *I. alutacea* (Lowe) Reid, Herbier J. Keller 1883 et 2131 (NEU). — *I. nivea* (Jungh.) Ryv., Herbier J. Keller 2415 et 2440 (NEU). — *Skeletocutis amorpha* (Fr.) Kotl. & Pouz., Herbier J. Keller 1331, 1367 et 1823 (NEU).

Sur les 8 espèces étudiées, 7 ont dû être observées à l'état sec (exsiccata); aucun traitement spécial n'a été nécessaire pour apprêter le matériel et les fragments ont été analysés après simple dorage.

Seul, *I. nivea* a été récolté à l'état frais et immédiatement observé; sa structure a été maintenue en parfait état grâce à la technique du point critique réalisé juste avant le dorage.

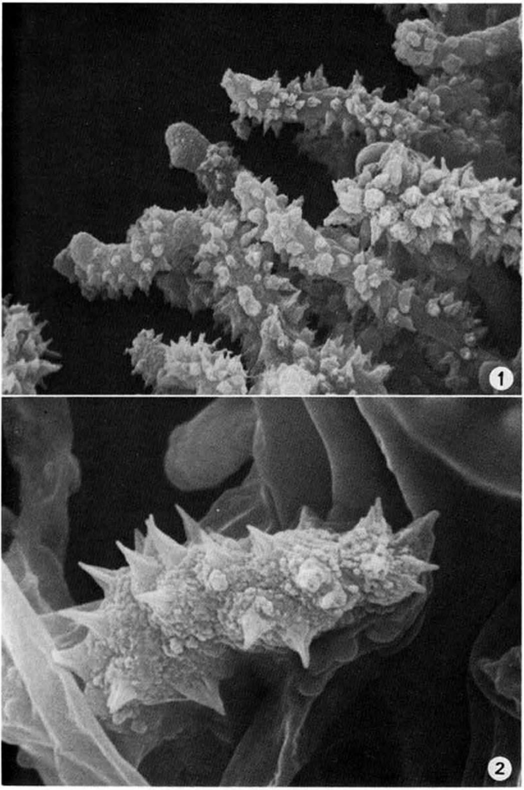
Toutes nos observations ont été réalisées sur un microscope électronique à balayage Jeol JSM 35, à 20 Kv.

REMERCIEMENTS

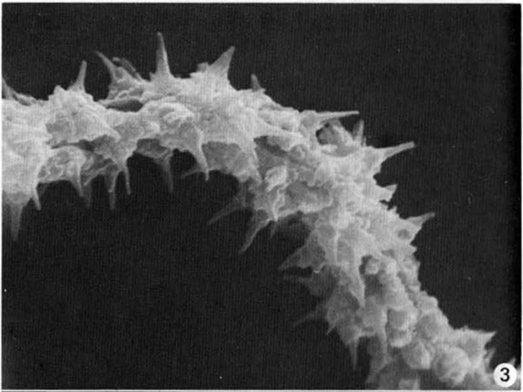
Nous tenons à exprimer notre profonde gratitude à Monsieur le Professeur John Eriksson de Göteborg de ses nombreux conseils judicieux (étude de *S. amorpha*, transfert des différentes espèces du genre *Incrustoporia* dans le genre *Skeletocutis*) et de l'envoi de matériel. Nous tenons à remercier également Monsieur le Professeur Leif Ryvarden d'Oslo de nous avoir fait parvenir divers exsiccata. Nous remercions enfin MM. A. Gauthier (directeur), T. Jalanti et F. Ardizzoni (collaborateurs) du centre de Microscopie Electronique de l'Université de Lausanne pour leur assistance technique.

RÉSULTATS ET DISCUSSION

Tous les *Incrustoporia* étudiés présentent les mêmes hyphes incrustées à l'exception de *I. carneola*. Cependant, contrairement aux cristallisations observées sur les hyphes ou cystides d'autres Aphyllophorales, celles-ci paraissent être bien particulières. En effet, il ne s'agit pas de beaux cristaux en forme de pyramides, de cubes, de plaques ou de paillettes, mais de masses



Figs. 1–2. *Skeletocutis nivea* (Fig. 1, × 4.500; Fig. 2, × 9.000).



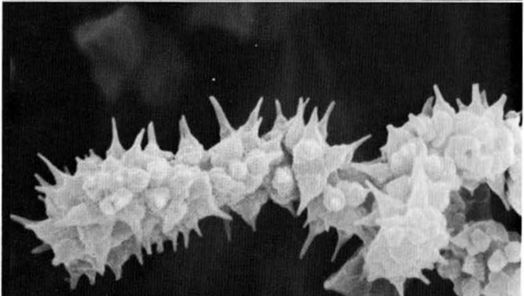
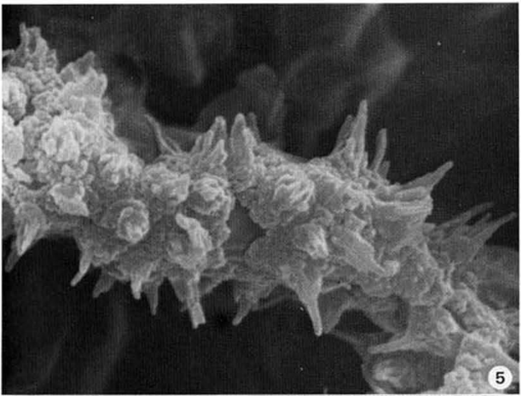


Fig. 3. *Skeletocutis alutacea* × 9.000. — Fig. 4. *Skeletocutis percandida* × 6.000.



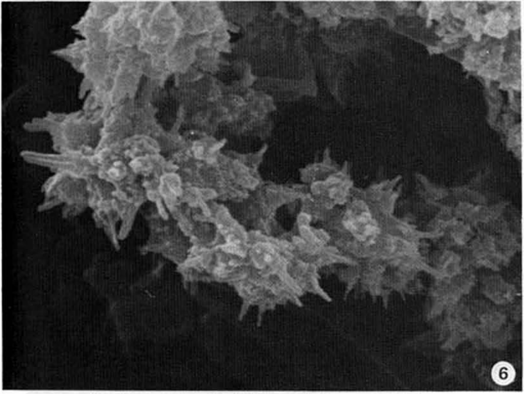
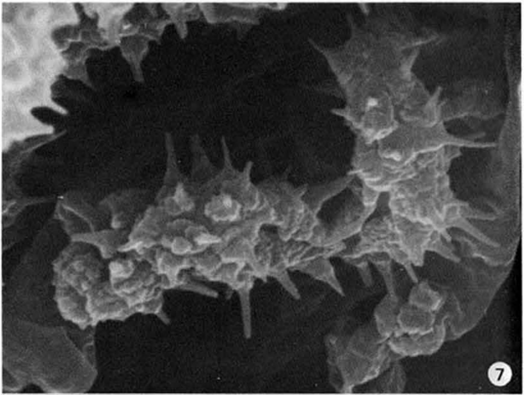


Fig. 5. *Skeletocutis stellae* × 12.900. — Fig. 6. *Skeletocutis subincarnata* × 7.200.



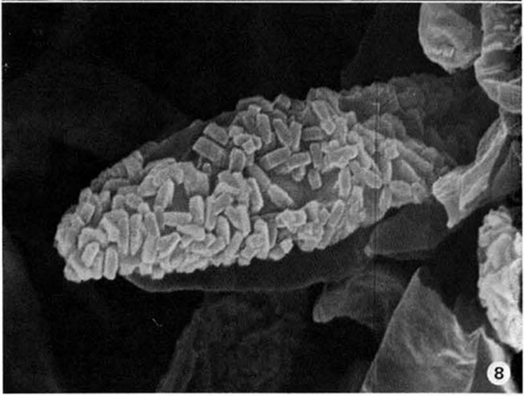


Fig. 7. *Skeletocutis tschulymica* × 10.300. — Fig. 8. *Poria carneola* × 6.600.

amorphes recouvrant plus ou moins intensément les hyphes des pores; ces masses irrégulières présentent toutefois des aiguillons relativement bien développés et souvent composés d'éléments cylindriques disposés perpendiculairement à la surface.

Incrustoporia carneola par contre, révèle une structure très différente car ses cristaux sont de petits parallélépipèdes réguliers (Fig. 8).

En regard de la grande homogénéité de structure des hyphes incrustées du genre *Incrustoporia*, il devient évident que ce caractère peut, sans aucun doute, être utilisé comme critère sûr pour définir le genre. Mais alors, il faut en exclure *I. carneola* et remettre cette espèce dans le genre *Poria* où elle figurait jusqu'ici (Bresadola, *1896*; Lowe, *1966*).

Cette brève révision des hyphes incrustées du genre *Incrustoporia* a donc été complétée, comme nous l'avions mentionné dans l'introduction, par l'examen de *S. amorpha*, espèce type du genre *Skeletocutis*. L'idée de cette étude complémentaire nous a été suggérée par J. Eriksson qui pressentait la proche parenté de cette espèce avec les *Incrustoporia*. Et, conformément aux prévisions du spécialiste suédois, il s'est avéré que les cristaux sont bien identiques à ceux des *Incrustoporia* (Figs. 9, 10).

En résumé, nous sommes en présence de sept espèces voisines possédant un caractère commun évident, des hyphes incrustées à structure particulière. Il est dès lors tout naturel de vouloir les réunier dans un même genre. L'on pourrait être tenté de transférer simplement *S. amorpha* dans le genre *Incrustoporia*, mais le code de nomenclature ne le permet pas car le genre *Skeletocutis* est plus ancien et est, de ce fait, prioritaire. Il devient ainsi nécessaire de transférer les espèces du genre *Incrustoporia* — y compris l'espèce type — dans le genre *Skeletocutis*. Par conséquent, *Incrustoporia* devient synonyme de *Skeletocutis* et les transferts suivants sont nécessaires. —

Skeletocutis alutacea (Lowe) Keller, *comb. nov.* — *Poria alutacea* Lowe. *In* Mycologia **38**: 202. 1946 (basionyme).

Skeletocutis nivea (Jungh.) Keller, *comb. nov.* — *Polyporus niveus* Jungh. *In* Verh. Batav. Genootsch. (Kunst. Wet.) **17**: 48. 1839 (basionyme).

Skeletocutis percandida (Malenç. & Bert.) Keller, *comb. nov.* — *Poria percandida* Malenç. & Bert. *In* Acta Phyt. Barcin. **8**: 35. 1971 (basionyme).

Skeletocutis stellae (Pilát) Keller, *comb. nov.* — *Poria stellae* Pilát. *In* Sb. nár. Mus. Praze (B) **9** (2): 107. 1953 (basionyme).

Skeletocutis subincarnata (Peck) Keller, *comb. nov.* — *Poria attenuata* Peck var. *subincarnata*. *In* A. Rep. NY St. Mus. nat. Hist. **48**: 118. 1895 (basionyme).

Skeletocutis tschulymica (Pilát) Keller, *comb. nov.* — *Poria tschulymica* Pilát. *In* Bull. trimest. Soc. mycol. Fr. **48**: 35. 1932 (basionyme).

Bien entendu, ce transfert n'a été possible que parce qu'il n'y a pas de critère précis permettant de maintenir séparés les deux genres en question.

L'on pourrait à la rigueur nous faire remarquer que *S. amorpha* possède des tubes gélatineux et que ce caractère n'existe pas chez les autres espèces si ce n'est *S. stellae* pourvu de minces zones résineuses entre les couches de tubes. Cette particularité n'est pourtant pas suffisante pour contrebalancer le caractère net et précis des hyphes incrustées.

Par conséquent, le genre *Skeletocutis* s'enrichit de 6 espèces grâce à la mise en évidence d'un caractère nouveau facile à observer: les cristallisations hyphiques.

Summary

The incrusted hyphae of all species of the genus *Incrustoporia* (1963) have the same very typical ultrastructure, with the exception of those of *I. carneola*. Consequently the last-named species is to be re-inserted in *Poria*. The crystallizations on the hyphae of *S. amorpha*, the type species of the earlier generic name *Skeletocutis* (1958), are of the same sort. Therefore *Incrustoporia* has to merge into *Skeletocutis*, and the following new combinations are proposed: *Skeletocutis alutacea*, *S. nivea*, *S. percandida*, *S. stellae*, *S. subincarnata*, and *S. tschulymica*.

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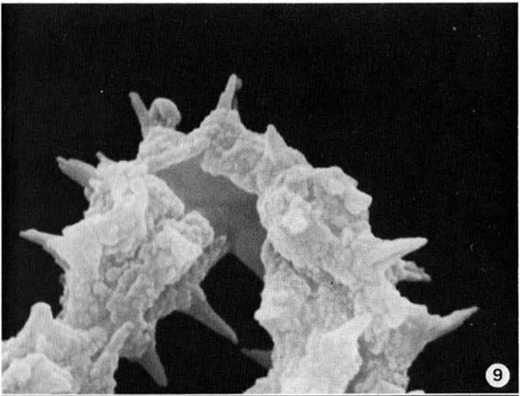

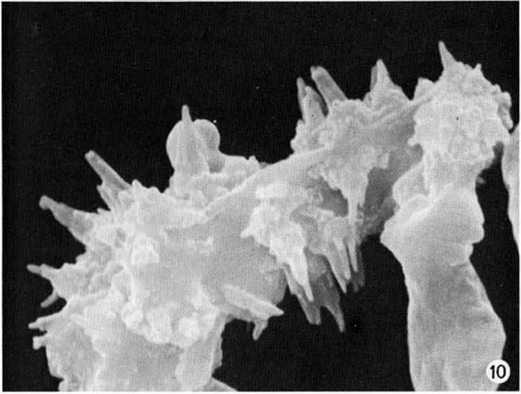

Figs. 9–10. *Skeletocutis amorpha* (Fig. 9, × 11.700; Fig. 10, × 15.000).

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NOTES ON HYGROPHORUS—III

The group of Hygrophorus olivaceoalbus (Hygrophorus subsect. Olivaceoumbrini Bat.) in north-western Europe

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A taxonomical and nomenclatural revision is given of *Hygrophorus* subsect. *Olivaceoumbrini* Bat., as found in western and central Europe, and represented by four species. Extensive descriptions and a key to these species are presented. For nomenclatural reasons one new species is described, viz. *Hygrophorus persoonii*, identical with *H. dichrous* Kühn. & Romagn. (invalidly published) and *H. limacinus* in the concept of some authors. Neotypes are designated for *H. latitabundus* Britz. and *H. olivaceoalbus* (Fr. ex Fr.) Fr. Special attention is paid to the ecology and geographical distribution of the concerning species in the Netherlands and Belgium.

Subsection *Olivaceoumbrini* Bat. seems to be a relatively natural and rather well distinguishable unit within the genus *Hygrophorus*. It comprises species with olivaceous or brownish caps, having a strongly viscid stem due to the presence of a glutinous veil (Singer, *1975*: 200).

While preparing the section on *Hygrophorus* for the Checklist of Agaricales in the Netherlands, I came across the fungus at present generally known as *H. dichrous* Kühn. & Romagn. This name has not been validly published, as noted previously by several authors (see p. 371). To solve the risen nomenclatural and taxonomical questions it has been useful to investigate exsiccata from other countries with emphasis on Belgium.

The very confused situation in this species-complex can be demonstrated by the fact that, from the 14 collections labelled as *H. olivaceoalbus* in Belgian herbaria, five appeared to belong to *H. persoonii* (syn. *H. dichrous* sensu Kühn. & Romagn.) and two to *H. latitabundus* (syn. *H. fuscoalbus* sensu Ricken). Most exsiccata labelled as *H. fuscoalbus* have been identified by me as *H. persoonii*. Yet the species in this group can be distinguished fairly well, mostly even in exsiccata without annotations. Misidentifications are due to the neglect of some microscopic characters, particularly pigmentation of the pileipellis, and especially to the emphasis in keys on

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some macroscopic properties of the stem, namely the absence or presence of brownish belts and spots. In general the clarity of these belts decreases according to the series *H. olivaceoalbus*, *H. persoonii*, *H. latitabundus*, *H. mesotephrus*. However this character depends also largely on the age of the carpophores and weather conditions. Within one group of carpophores of *H. persoonii* I found young specimens with evenly pale ochre stems and mature ones with more or less pronounced olive-brown belts and spots alternating with yellowish parts. The belts become far more distinct on drying out, but usually become almost indistinguishable again in exsiccata. In the same way the stem in moist carpophores of *H. latitabundus* is predominantly white, mostly showing rather few small brownish fibrillose spots. When dry the stem shows distinct grey-brown belts, and sometimes it is almost completely coloured. This phenomenon can be explained by the strong shrinkage of the glutinous layer during the process of drying, which causes the loosely arranged pigmented hyphae to aggregate into a predominantly longitudinal direction.

Bresinsky & Huber (*1967*) have published a key to the exsiccata of *Hygrophorus* sensu stricto. Within *Hygrophorus* sect. *Colorati*, *H. olivaceoalbus* and *H. dichrous* (syn. *H. persoonii*) are distinguished from the other species (among others *H. fuscoalbus*, syn. *H. latitabundus*) on account of their thick pileipellis (180–300 μm thick, in the remaining species less than 180 μm) and the presence of brown spots and belts on the stem. As noted above the pattern on the stem gradually disappears in exsiccata and is often completely invisible after a few years. Moreover *H. latitabundus* can show darker spots in dried specimens. In my opinion neither the thickness of the pileipellis is a good character. The degree to which this ixotrichodermal tissue can be revived, is completely dependent on the methods used for drying. I found the following variation: *H. olivaceoalbus* 150–530 μm; *H. persoonii* 200–800(–1300) μm, and *H. latitabundus* 300–850(–1000) μm. Nevertheless, I think that exsiccata of these species can in most cases be clearly distinguished, employing some of the same characters as used to distinguish fresh fruitbodies. However, I did not find a reliable means of distinguishing small specimens of *H. persoonii* from *H. mesotephrus*, a species not being included in the key of Bresinsky & Huber (l.c.).

It appears that *H. mesotephrus* is the only species of this group of which original material has been preserved (see p. 376). To achieve a clear and reproducible concept of the other species under consideration I have designated neotypes for *H. latitabundus* and *H. olivaceoalbus*, which are responding to the original descriptions and collected in the regions, in which the species were originally recorded. These neotypes can be especially useful for comparison with species from other continents, e.g. the North American taxa described by Hesler & Smith (*1963*). In addition new characters may be tested in the future. It responds to the plea made recently among others by Smith (*1977*: 150).

Next to the morphological characters, special attention has been paid to ecological data and the geographical distribution of the species in the Netherlands and Belgium. On account of the frequent misidentifications in this group I have only indicated those observations on the maps, which are supported by revised collections in an official Herbarium. Hence, the maps do not give a complete picture but, before a sufficient number of collections have been studied, the patterns are probably representative. For the Netherlands I have accepted the 5 × 5 km grid used for the mapping of phanerogams (Mennema *& al.*, *1979*). For Belgium I followed the 'Atlas de la Flore Belge et Luxembourgeoise' (van Rompaey & Delvosalle, *1972*), where squares of 4 × 4 km have been used as basal units.

PRESENTATION OF DATA

The macroscopic characters in the descriptions are based on the rather few collections studied in fresh condition by the author or on exsiccata provided with extensive original annotations. The microscopic characters come from all exsiccata listed after the descriptions. Characters observed in exsiccata are designated with the abbreviation 'exs.'.

The colour codes mentioned are according to Kornerup & Wanscher (*1967*). For the use of some other terms and abbreviations the reader is referred to 'Notes on *Hygrophorus*—I' (Arnolds, *1975*).

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KEY TO THE SPECIES OF HYGROPHORUS SUBSECT. OLIVACEOUMBRINI IN NORTH-WESTERN EUROPE

1a. Spores (9–)10–16(–18) × (6–)6.5–9 μm, on the average 11.5–14.1 × 7.4–8.6 μm. Basidia 61–81 × (9.5–)10–14(–14.5) μm, on the average 64–78 × 10.5–13.6 μm. Hyphae of pileipellis almost exclusively with intracellular pigment, smooth or occasionally very slightly roughened, without extracellular granules, not becoming blue in alkaline solutions. Stem 4–10 mm thick (exs.: 2.5–9 mm), slenderly cylindrical, with distinct dark belts, apex smooth or pubescent. Associated wtih conifers on acid soil
H. olivaceoalbus, p. 376

b. Spores (7.5–)8–12(–13.5) × (4.5–)5–7.5(–8.5) μm, on the average 9.0–10.6 × 5.5–6.8 μm. Basidia (40–)45–71(–80) × 7–11.5(–13) μm, on the average 51–64(–70) × 8–10.5 μm. Hyphae of pileipellis with intracellular pigment, but at least in part rough by encrusting pigment and often with extracellular granules, sometimes becoming blue in alkaline solutions. If stem slenderly cylindrical, then associated with deciduous trees; if associated with conifers then growing on calcareous soil, and stem 10–38 mm thick (exs.: (7–)8–22 mm), fusiform or ventricose. Apex of stem with small whitish pustules, usually turning orange-brown in exsiccata 2

2a. Cap 20–40 mm broad, pale brownish to beige with dark brown centre. Stem slender, 45–65 × 3.5–6.5 mm, in all conditions white or pale brownish without darker belts. Pileipellis with rather faintly encrusting pigment; extracellular granules absent or scarce, never becoming blue in alkaline solutions. Associated with deciduous trees . . . . *H. mesotephrus*, p. 374

b. Cap (27–)30–100 mm broad, rather dark olivaceous to greyish brown with very dark centre. Stem cylindrical to ventricose, (4.5–)6–38 mm thick, mostly with olive to grey-brown belts, at least on drying; if no distinct belts present, then with a very stout stem (10–38 mm thick) and associated with conifers. Encrusting and extracellular pigment in pileipellis often blue in alkaline solutions 3

3a. Cap 50–100 mm broad (exs.: (27–)35–80 mm), brown to grey brown, with at most weak olivaceous tinge. Stem 10–38 mm thick (exs.: (7–)8–22 mm), ventricose or fusiform, when moist almost completely white or with more or less pronounced greyish brown spots, turning more distinct and darker on drying. Flesh compact and firm, in centre of cap *c.* 10–25 mm thick, white. Gills white to pale pinkish cream. Extracellular pigment in pileipellis not blue in alkaline solutions. Associated with conifers
H. latitabundus, p. 360

3b. Cap (27–)30–70(–85) mm broad (exs.: 20–60(–70) mm), brown with more or less distinct olivaceous, ochraceous or pinkish tinge, especially towards the margin. Stem (4.5–)6–15(–17) mm thick (exs.: 3.5–9(–12) mm), cylindrical or slightly fusiform, when moist ochraceous or yellowish, usually with darker olivaceous or brown belts and spots, at least in mature carpophores, turning more distinct and darker on drying. Flesh first firm and white, at centre of cap up to 14 mm thick, becoming softer and greenish yellow with age. Gills first white, often becoming greenish yellow with age. Extracellular pigment in pileipellis well developed, often (but not invariably) turning in part dark green-blue in alkaline solutions, usually only at the most superficial hyphae. Associated with deciduous trees . *H. persoonii*, p. 365

HYGROPHORUS LATITABUNDUS BRITZ.—Figs. 1–8

Hygrophorus latitabundus Britz. *in* Bot. Zentbl. **80**: 118, pl. 437 f. 14. 1899. — Neotype (design. mihi): *R. Gröninger*, 4 Oct. 1962, Augsburg (M).

Hygrophorus olivaceoalbus f. *obesus* Bres., Fungi trid. 92. 1887.

MISAPPLIED NAMES.—*Limacium fuscoalbum* sensu Ricken, Blätterp.: 13, pl. 5, f. 1. 1915. — *Hygrophorus fuscoalbus* sensu Dennis *& al. in* Trans. Br. mycol. Soc. **43**: 74. 1960; sensu Bresinsky & Stangl *in* Z. Pilzk. **32**: 21. 1966; sensu Bresinsky & Huber *in* Nova Hedwigia **14**: 156, 162. 1967; sensu Arnolds *in* Coolia **17** (suppl.): 33. 1974; sensu Moser, Kl. KryptogFl. **2** (b/2): 80. 1978; sensu auct. eur. plur.

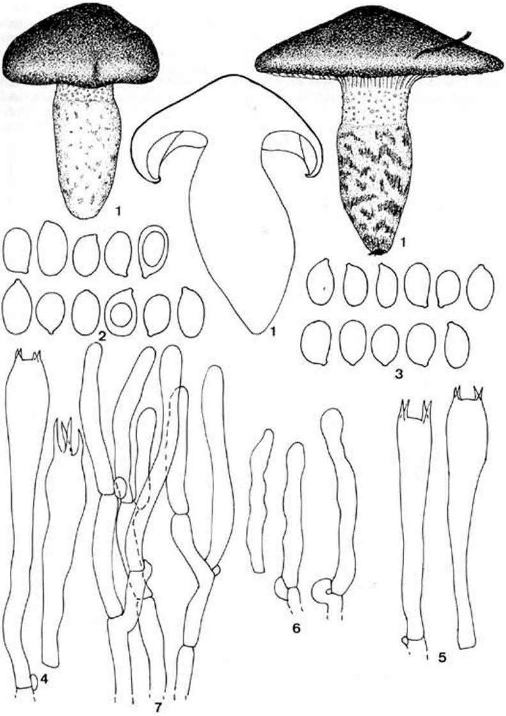
Hygrophorus limacinus sensu Kühn. & Romagn., Flore anal.: 60. 1953; sensu Romagn., Nouv. Atl. Champ. **4**: 259. 1967; sensu Bon, *in* Docums mycol. **7** (27–28): 39. 1977; sensu Moser, Kl. KryptogFl. **2** (b/2): 80. 1978.

COLOURED ILLUSTRATIONS.—Bresadola, l.c.; Ricken, l.c.; Romagnesi, l.c.; Bull. Soc. mycol. France **85**, Atlas 180. 1969; Cetto, I Funghi dal vero **2**: 650. 1976.

SELECTED DESCRIPTIONS.—Bresinsky & Stangl, l.c.; Romagnesi, l.c.; Bon, l.c.; Bull. trimest. Soc. mycol. France, l.c.

Cap [14/4] (50–)65–90(–120) mm broad, first semiglobate or obtusely conical with strongly involute margin, then expanded to almost flat with prominent obtuse umbo, not hygrophanous, first rather dark greyish brown (M 5E6, 6E6) or with faint olivaceous tinge (slightly towards 4E6), with dark fuscous centre (M 5F6, 6F6), then slightly paler, near margin to rather light greyish brown (M 5D4), at extreme margin first whitish tomentose, very strongly glutinous, glabrous or very faintly fibrillose below slime layer. Gills [L = 50–70, l = 1–3] broadly adnate to subdecurrent, thick, distant, not ventricose, up to 9 mm broad, white to pale pinkish cream. Stem 50–115 × (11–)14–38 mm, very stout, fusiform or ventricose, often attenuate downwards, first connected with margin of cap by a glutinous hyaline veil, above veil at apex (15–20 mm) dry, white with small white floccose warts, sometimes with hyaline droplets, downwards strongly glutinous with small grey-brown fibrillose spots scattered to rather dense on whitish background, drying with larger and darker spots and transversal bands to almost evenly grey-brown (M 4D4, E5). Flesh in cap up to 25 mm thick, firm, white; in stem also white or slightly yellowish at base. Smell on cutting agreeable, sweetish; taste none. Macrochemical reactions: KOH on apex of stem light yellow with yellow warts; on base of stem and cap orange; in flesh negative or yellow in base of stem.

Spores [100/10/9] (7.8–)8.1–11.5(–13.4) × 4.7–7.7(–8.1) μm, on the average 9.0–10.6 × 5.7–6.7 μm, Q = (1.25–)1.3–1.9(–2.2), ellipsoid to ellipsoid-oblong, not constricted, with large obtuse apiculus (Figs. 2, 3). Basidia [45/9/8] (45–)47–71(–81) × (7.2–)8.0–11.5(–13.0) μm, on the average 53–63(–70) × 8.2–10.5 μm, Q = (4.6–)5.0–7.3(–8.2), slenderly clavate, 4-spored, sometimes a few 2- or 3-spored (Figs. 4, 5); in some carpophores intermixed with scattered cylindrical basidiolae, *c.* 29–41 × 4–5.5 μm (Fig. 6). Hymenophoral cystidia none. Trama of gills divergent, composed of long chains consisting of short to moderately long, cylindrical or somewhat inflated elements, measuring [35/6/5] 20–125(–192) × 3.8–14.0 μm. Pileipellis a well developed ixotrichodermium,



Figs. 1–7. *Hygrophorus latitabundus*. — 1. Carpophores, × 0.5. — 2, 3. Spores, × 1000. — 4, 5. Basidia, × 1000. — 6. Basidiola, × 1000. — 7. Section of warts on apex of stem, × 1000. (Figs. 1, 2, 4, 6, 7 from *Arnolds 3878*; Figs. 3, 5 from *Gröninger*, 4 Oct. 1962, neotype.)

up to 1100 μm thick, (in exsiccata reviving variably, mostly to 300–850 μm thick), consisting of irregularly branched erect hyphae, loosely interwoven in the upper part, more compactly downwards, with cylindrical elements 1.5–4.8(–6.0) μm broad; hyaline or with intracellular dispersed light brown pigment and a variable part of the hyphae with encrusting pigment, also commonly with more or less intercellular granules not changing colour in alcaline solutions (Fig. 8). Stipitepellis an ixotrichodermium like pileipellis but thinner, up to 400 μm thick. Warts at apex of stem consisting of compact fascicles of branched hyphae with cylindrical or slenderly clavate terminal cells, *c.* 38–65 × 4.3–5.8 μm, smooth with greenish intracellular pigment and some intercellular granules (Fig. 7). Stipitetrama regular with rather long cylindrical elements, *c.* 4.5–10.5 μm broad. Clamps numerous in most tissues of the carpophores.

EXSICCATA.—Cap (27–)35–70(–80) mm broad, often with thick involute margin, fleshy, greyish ochre brown to rather dark greyish brown with fuscous to almost black centre, dull or moderately shining, often slightly radially fibrillose. Gills cream to orange- or brownish ochre. Stem (43–)50–90 × (7–)8–22 mm, fusiform, apical part distinct, cream to ochraceous with many small orange brown to dark brown pustules, downwards mostly ochre brown to light orange brown, darker at base, sometimes with grey brown tinge, mostly almost evenly coloured but in some carpophores with pronounced darker spots and belts.

NOTES ON THE NEOTYPE (*R. Gröninger s.No.*, 4 Oct. 1962, M).—Exsiccata or three halves of rather young carpophores in good condition. Spores [10/1] 8.6–10.5 × 6.2–7.2(–7.5) μm, ellipsoid (Fig. 3). Basidia [5/1] *c.* 53–69 × 8.6–9.6 μm, slenderly clavate, 4-spored (Fig. 5). Gill trama bilateral with narrow cylindrical elements, *c.* 23–105 × 4.3–6.2 μm. Pileipellis an ixotrichodermium reviving in KOH 5% to up to 850–1100 μm thick; hyphae 1.8–4.8 μm broad, hyaline or with pale olivaceous intracellular pigment, moreover with encrusting pigment and rather numerous extracellular granules, not becoming green blue in alcaline solutions.

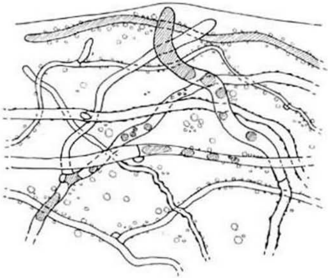


Fig. 8. *Hygrophorus latitabundus*, radial section of pileipellis, × 1000 (from *Arnolds 3878*).

ECOLOGY.—*Hygrophorus latitabundus* has been reported by all authors from natural or planted forests of *Pinus* (e.g. Ricken, *1915*: 13; Romagnesi, *1967*: 259; Bresinsky & Stangl, *1966*: 21). From the eleven collections studied, eight were reported from the neighbourhood of *Pinus sylvestris*, but two collections from Belgium are reported to have been found near *Picea*. From one collection (*Damblon*, 21 Oct. 1952) no details about the habitat are known.

Near Augsburg the species grows in *Pinus* woods with a herb layer dominated by *Molinia* on calcareous soil (Bresinsky & Stangl, *1966*: 22). A preference for limestone has also been reported by almost all other authors (e.g. Ricken, l.c.; Romagnesi, l.c.; Bon, *1977*: 39). The distribution pattern in Belgium confirms these observations (see below). Probably *H. latitabundus* occurs optimally in open grassy woodland and at wood edges. Near Ave-et-Auffe it has been observed for several years growing in the direct surroundings of one isolated pine at the margin of a dry limestone grassland (Mesobrometum) on stony soil with low humus content. This clearly indicates a mycorrhizal relationship with trees (in this case with conifers), as is supposed for all members of *Hygrophorus* sensu stricto (e.g. Singer, *1975*: 198), although no direct proof has yet been given. Fructification occurs in western Europe in October and November. In more southern regions carpophores have been observed until December.

DISTRIBUTION.—*Hygrophorus latitabundus* seems to be widespread in the temperate and warm regions of central Europe, especially in hilly and mountainous districts. It has not been reported in Scandinavia and seems to be also absent from the Netherlands. A probable record of *H. fuscoalbus* sensu Ricken from the Netherlands by Arnolds (*1974*: 33) relates most likely to *H. persoonii* (syn. *H. dichrous* sensu Kühn. & Romagn.).

In Belgium the species has only been observed in the calcareous hills in the southern part of the phytogeographical 'Meuse-district', characterized by the occurrence of numerous calciphytic and thermophytic phanerogams (de Langhe *& al.*, *1973*).

COLLECTIONS EXAMINED.—Belgium: prov. Namur: Ave-et-Auffe, Le Roptai, Tiène del Côre, 6 Oct. 1977, E. Arnolds & J. Frencken, *Arnolds 3878* (WAG-W); *s.loc.*, 2 Nov. 1975, *J. Frencken s.No.* (L); Biron S. of Barvaux, 21 Sept. 1952, *J. Damblon s.No.* (LG); Barvaux, 19 Nov. 1970, *P. Heinemann 4962* (BR, GEMBL); between Vierves and Treignes, 9 Nov. 1970, *A. Marchal 70.219* (GEMBL).

FRANCE: Provence, Carqueiranne near Toulon, Dec. 1959, *A. W. Koopman & A. C. Veth s.No.* (L).

GERMANY: Bavaria, Augsburg, Siebentischwald, 4 Oct. 1962, *R. Gröninger s.No.* (neotype, M); *s.loc.*, *s.dat.*, *C. Bas 2791* (L); Augsburg, Hainstetterwald, 3 Oct. 1969, *R. Gröninger s.No.* (M); *s.loc.*, Oct. 1958, *A. Bresinsky s.No.* (M).

Hygrophorus latitabundus is the most robust representative of *Hygrophorus* subsect. *Olivaceoumbrini* and can even be distinguished in the field on account of its thick and heavy flesh and its stout stem. Like *H. olivaceoalbus*, it is associated with coniferous trees, but the latter species grows on poor acid soils, whereas *H. latitabundus* seems to be restricted to calcareous soils. As a consequence, these two species occur in different phytogeographical districts in Belgium (Fig. 9). Moreover numerous macoscopic and microscopic characters exist: in *H. olivaceoalbus* the cap is smaller and the stem much more slender without a floccose apex and with distinct darker belts also when moist, the flesh under the pileipellis is usually yellow; spores and basidia are significantly larger (Figs. 33, 34) and encrusting pigment in the pileipellis is lacking.

For the differences between *H. latitabundus* and *H. persoonii* the reader is referred to the key on page 359. These species, too, appear to be well separated in morphological and ecological respects. However completely reliable microscopic differences have not been found, although *H. persoonii* generally possesses more pronounced encrusting pigment and intercellular granules

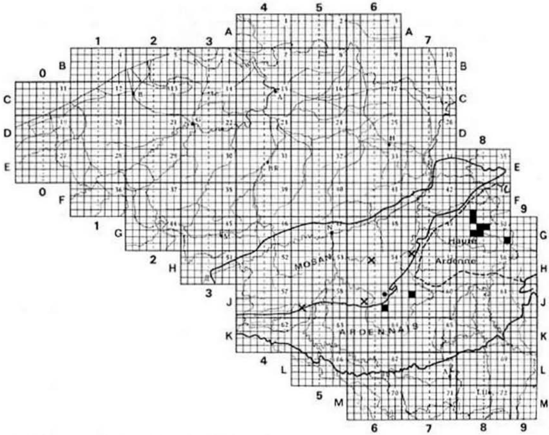


Fig. 9. Geographical distribution of *Hygrophorus latitabundus* (×), *H. mesotephrus* (●) and *H. olivaceoalbus* (■) in Belgium. The relevant phytogeographical districts have been indicated according to de Langhe & al. (*1973*).

often turning blue in alkaline solutions. Exsiccata without annotations cannot always be distinguished with certainty.

Hygrophorus latitabundus is best known in Europe under the name of *Hygrophorus fuscoalbus*, especially since the interpretation of that name given by Ricken (*1915*). However the original description of *Agaricus fuscoalbus* by Lasch (*1829*: 520) shows large discrepancies with the species above: it should be a fungus with a stature near *Agaricus olivaceoalbus* with the cap 39–65 mm broad and the stem 52–78 × 6.3–12.6 mm, hence considerably smaller than *H. latitabundus*. Moreover the stem should be not viscid, without spots or belts, but on the contrary white and floccose-squamulose ('Stipes floccoso-squamulosus, neque maculatus nec viscosus'). This description suggests a species near *H. agathosmus* (Fr. ex Fr.) Fr. and *H. pustulatus* (Pers. ex Fr.) Fr. in *Hygrophorus* subsect. *Tephroleuci* Bat. A fungus which meets this description is not known to me.

In the 'Flore analytique' Kühner & Romagnesi (*1953*: 60) have described this species as '*H. limacinus* Fr. ex Scop.' Scopoli (*1772*: 422) described *Agaricus limacinus* as a slender fungus with a stature completely different from that of *H. latitabundus*. According to Orton (*1960*: 258) it might represent *H. mesotephrus* Berk. & Br. Also Fries used the name always for a much more slender species. In my opinion the epithet 'limacinus' has to be rejected as a 'nomen ambiguum et confusum', which will be argued in the discussion on *H. persoonii* (p. 373).

Kühner & Romagnesi (l.c.) were followed mainly by French authors. Moser (*1978*: 80) distinguishes *H. limacinus* sensu Romagnesi from *H. fuscoalbus* sensu Ricken mainly on account of the grey brown belts and spots on the stem of the first compared to the white stem in the latter species. Bresinsky & Stangl (*1966*: 22) have established that in the surroundings of Augsburg the clothing of the stem varied from indistinct to very pronounced belts. I observed in the collection *Arnolds 3878*, that fresh and moist carpophores had almost completely white stems, but that striking grey brown girdles developed during the process of desiccation. Consequently in my opinion both taxa are synonymous, which coincides with the idea of Bon (*1977*: 39).

In a publication of Bresinsky & Stangl (*1966*) dealing with a revision of Britzelmayr's 'Hymenomyceten aus Südbayern' I came across the name *Hygrophorus latitabundus* Britz., which is identical with *H. fuscoalbus* according to these authors. Indeed Britzelmayr's plate (*1899*: 437, f. 14) shows the characteristic stature of our fungus and his description fits also well. Moreover Bresinsky & Stangl were able to study a collection of this mushroom from the type locality in the Siebentischwald near Augsburg. It seems self-evident to choose this collection, which is in perfect condition, as the neotype of *H. latitabundus*. To my knowledge this is the oldest acceptable name for the fungus described above, although it is not impossible that an older name will be discovered in future.

Hygrophorus persoonii Arnolds, *spec. nov.*—Figs. 10–16

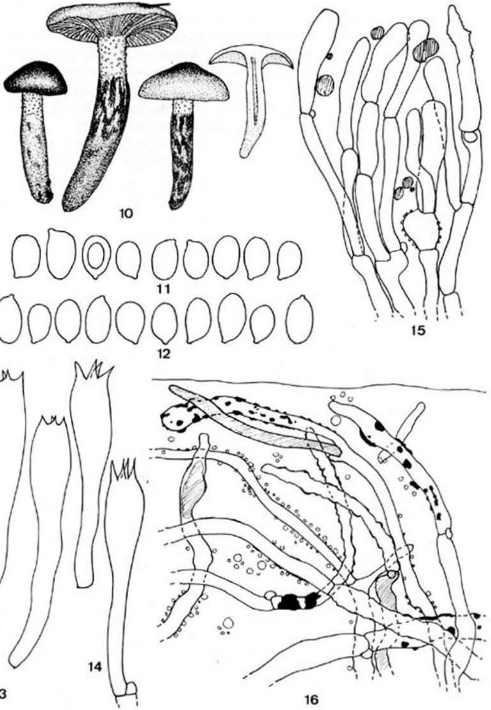
Agaricus limacinus Schaeff., Fung. Bav. **4** (Index primus): 74. 1774 (pl. 312, 1771); ex Pers., Mycol. europ. **2**: 94. 1828 [non *Hygrophorus limacinus* (Scop. 1772) ex Fr. 1838 = ? *H. mesotephrus*].

Hygrophorus dichrous Kühn. & Romagn., Flore anal.: 60. 1953 (not validly published); Orton *in* Trans. Br. mycol. Soc. **43**: 258. 1960 (n.v.p.); Bresinsky & Huber *in* Nova Hedwigia **14**: 156, 162. 1967 (n.v.p.); Malençon & Bertault, Champ. sup. Maroc **2**: 496. 1975 (n.v.p.); Moser *in* Gams, Kl. KryptogFl. 4. Aufl. **2** (b/2): 80. 1978 (n.v.p.); non *Hygrophorus dichrous* Hongo *in* J. Jap. Bot. **33**: 101. 1958 (= species of subgenus *Hygrocybe*).

COLOURED ILLUSTRATIONS.—Cooke, Ill. Brit. Fungi **6**: 881 (897). 1888; Lange, Fl. agar. dan. **5**: 162A. 1940; Marchand, Champ. Nord Midi **2**: 112. 1973.

SELECTED DESCRIPTIONS.—Kühner & Romagnesi, l.c.; Trans. Br. mycol. Soc. **43**: 258. 1960; Westfäl. Pilzbr. **9**: 36. 1972; Coolia **17** (suppl.): 31. 1974; Malençon & Bertault, l.c.; Docums mycol. **7** (27–28): 39. 1977.

Pileus (27–)30–70(–85) mm latus, primo obtuso-conicus vel semiglobatus margine involutus, dein convexus vel expansus, umbonatus, non hygrophanus, olivaceo- vel griseo-brunneus, margine pallidior ochraceo-brunneus vel isabellinus, glutinosissimus. Lamellae [L = 28–52, l = 1–7] late adnatae vel subdecurrentes, subdistantes, latae, frequenter intervenosae, primo albae dein pallide virido-luteae. Stipes 43–85(–105) × (4.5–)6–15(–17) mm, aequalis vel subfusiformis, deorsum attenuatus, apice siccus, albus, albo-flocculosus, deorsum velo universali glutinoso, primo ochraceus vel pallide brunneus, mox olivaceo-brunneo-maculatus. Caro in pileo usque ad 12 mm lata, primo compacta, alba, dein mollis, frequenter pallide viridis, odore saporeque indistinctis vel leviter fructio-odoris. Sporae (7.7–)8.0–11.5(–12.0) × (4.3–) 4.8–6.7(–7.2) μm, ellipsoideae, ovoideae vel oblongae. Basidia 45–68 × (7.2–)8.0–12.0 μm, vulgo 4-sporigera, raro pro parte minore 2-sporigera. Cystidia nulla. Lamellarum trama divergens, cellulis (29–)33–



Figs. 10–16. *Hygrophorus persoonii.* — 10. Carpophores, × 0.5. — 11, 12. Spores, × 1000. — 13, 14. Basidia, × 1000. — 15. Section of warts on apex of stem, × 1000. — 16. Radial section of pileipellis, × 1000. (Figs. 10, 11, 13 from *Arnolds 3892*, holotype; Figs. 12, 14, 15 from *Bas 955*; Fig. 16 from *Bas & Swanenburgh de Veije*, 21 Oct. 1954.)

148 × (3.8–)5.4–25 μm. Pileipellis ixotrichodermiformis, 500–1200 μm latus, exsiccata (200–)250–800(–1300) μm, hyphis tenuibus ramosis, (1.5–)2.0–5.8(–8.5) μm latis, cylindricis, pigmento intracelluloso olivaceo cum pigmento incrustante et granulis extracellularibus frequenter pro parte obscure caeruleoviride in NH_4OH et KOH. Verrucae ad apicem stipitis hyphis compactis, cellulis terminalibus clavatis vel cylindricis, (17–)25–62 × 4.3–7.2 μm. Stipitipellis ixotrichodermiformis ut pileipellis sed tenuior. Fibulae frequentes. Ad terram in silvis deciduis, sub *Quercus*.

HOLOTYPUS.—Belgium, Prov. of Namur, Tiène aux Pauquis near Nismes, 10 km S. of Philippeville, 3 Oct. 1977, *Arnolds 3892* (L; isotypus WAG-W, BR).

ETYMOLOGY.—Named in honour of C. H. Persoon (1761–1836).

Cap [26/8] (27–)30–70(–85) mm broad, first obtusely conical or semiglobate with involute margin, then convex to expanded with weak to large obtuse umbo, not hygrophanous, first rather dark greyish or olivaceous brown (M 4E7/8, 6E7 or more olivaceous towards 4E7) with dark greyish to blackish brown centre (M 5F7, 6E7/F7, 6F7), then paler especially in marginal zone towards light greyish or olivaceous brown, ochre brown to pale orange ochre, incarnate or isabella (M 6C4, 6D5, 5C4, 5C4/4C4, 5B3, 5B3/4), mostly with olivaceous tinge, centre always much darker, sometimes slightly fibrillose near centre, very strongly glutinous. Gills [L = 28–52, l = 1–7] broadly adnate to shortly decurrent, rather thick, subdistant to distant, often interveined, up to 9 mm broad, first white, discolouring gradually light greenish yellow (M 1A3, 3B3, 3B4, 3B4/C4). Stem 43–85(–105) × (4.5–)6–15(–17) mm, Q = 3.8–8.5, rather firm to rather slender, cylindrical to slightly fusiform, gradually attenuate towards base, at apex (*c.* 8–15 mm) dry, first white then pale greyish or greenish, with many small white floccose warts, downwards glutinous, first evenly ochraceous to light brown (M 4B4, 4B4/C5, 5C6), gradually more or less breaking up into irregular olivaceous to greyish brown fibrillose bands and spots (M 5D6, 5C5, 5D5 or more olivaceous towards 4D5, C5) on whitish background; this pattern becoming more prominent in dry condition. Flesh in cap up to 12 mm thick, first firm and white, then softer and often with pale greenish tinge, especially below pileipellis; in stem becoming fibrillose, white; smell and taste variable: almost neutral to fruity or disagreeable sweetish, always weak. Spore-print white.

Macrochemical reactions: NH_4OH on cap negative or exceptionally blue-green (not observed by me, mentioned by Kühner & Romagnesi *1953*: 59); KOH 10% on cap yellow brown to orange, on base of stem orange-red.

Spores [115/12/12] (7.7–)8.0–11.5(–12.0) × (4.3–)4.8–6.7(–7.2) μm, on the average per mount 9.1–10.3 × 5.4–6.4 μm, Q = 1.4–1.8(–1.9), ellipsoid or ellipsoid-oblong to ovoid with rather large obtuse apiculus (Figs. 11, 12). Basidia [45/9/9] 45–68 × (7.2–)8.0–12.0 μm, on the average per mount 52–64 × 8.0–10.6 μm, Q = (4.6–)4.8–7.6(–8.5), slenderly clavate, 4-spored or sometimes a few 2-spored (Figs. 13, 14). Cylindrical basidiolae sometimes present. Hymenial cystidia absent. Trama of gills with rather short cylindrical to strongly inflated elements, [40/7/7] (29–)33–148 × (3.8–)5.4–25 μm.

Pileipellis a well developed ixotrichodermium, in fresh carpophores *c.* 500–1200 μm thick, in exsiccata variably re-inflating to (200–)250–800(–1300) μm thick, consisting of slender erect branched hyphae, above the trama rather compact but towards the surface very loosely interwoven, (1.5–)2.0–5.8(–8.5) μm broad, hyaline or with olive green intracellular pigment, but also a variable part of the hyphae with irregularly encrusting pigment, moreover with numerous hyaline or pale green granules on and in between the hyphae; often (but not constantly) some extracellular pigment turning dark blue green in alkaline solutions, especially on the most superficial layers (Fig. 16). Warts on apex of stem consisting of closely packed erect hyphae, frequently forked and with slenderly clavate or cylindrical terminal elements, *c.* (17–)25–62 × 4.3–7.2 μm, colourless or with olive yellow or green contents, in between with greenish granules and clods, up to 25 μm broad, not discolouring in alkaline solutions (Fig. 15). Stipitepellis downwards an ixotrichodermium like the pileipellis but slightly thinner, hyphae with vacuolar and encrusting pigments, also extracellular granules, which turn sometimes in part blue green in alkaline solutions. Stipitetrama with rather long elements, *c.* 4.0–12.5 µm broad. Clamps numerous in all parts of the carpophore.

EXSICCATA.—Cap 20–60(–75) mm broad, with thin flesh, strongly wrinkled near margin, dull to very much shining, strongly variable in colour: greyish, orange, olivaceous, ochraceous to rather dark reddish brown, darker at centre. Gills cream, greenish to orange ochre. Stem 40–85 (–90) × 3.5–8(–12) mm, cylindrical; apical part distinct, whitish, cream to ochraceous or light orange brown with small orange or brown pustules; downwards greyish, ochraceous or orangy brown, frequently slightly darker towards base, evenly coloured or with mostly inconspicuous darker spots and belts.

NOTES ON THE HOLOTYPE (*E. Arnolds 3892*, L).—Exsiccata of nine carpophores in good condition with extensive notes on fresh specimens and water-colour drawing (originals preserved at the Biological Station, Wijster).

Spores [10/1] 8.1–10.8(–11.3) × (5.3–)5.5–6.5(–6.7) µm (Fig. 11). Basidia [6/1] *c.* 50–64 × 8.6–10.5 µm, 4-spored (Fig. 13). Pileipellis an ixotrichodermium up to 800 µm thick; hyphae 2–5 (–6.5) µm broad with greenish intracellular pigment, moreover with numerous irregular encrustations and extracellular granules, in most carpophores in part turning dark greenish blue in NH_4OH. Collected under one oak (*Quercus robur*) at the transition from deciduous wood towards poor grassland (Mesobrometum) on dry calcareous soil.

ECOLOGY.—In the Netherlands *Hygrophorus persoonii* has only been found in the neighbourhood of oaks (*Quercus robur*) in deciduous forests on mesotrophic and subneutral sandy or loamy soils, often with a high lime content, varying from rather moist to dry, All these vegetations belong to the suballiance Ulmion carpinifoliae (see e.g. Westhoff & den Held, *1969*: 266). In Belgium most collections have been made in deciduous forests on dry loamy calcareous soils, belonging to the alliance Carpinion betuli. In north-western Europe *H. persoonii* can be regarded a character species of the order Fagetalia sylvaticae.

The species has also been observed at margins of woods or near isolated oaks in grasslands on limestone. Some Belgian collections are reported from pine woods, but we have some doubts as to whether no deciduous trees were present. All detailed accounts on the habitat of *H. persoonii* (e.g. Michael-Hennig, *1964*: 222; Jahn, *1972*: 36) mention the presence of *Quercus* as a mycorrhiza partner. It is not certain whether it can also grow amongst other (deciduous) trees.

DISTRIBUTION.—It is difficult to establish the precise area in Europe as a result of the high degree of confusion around this species. On the basis of the present data it is very probable that its distribution coincides with the area of the oak, viz. from the Mediterranean area (e.g. in Maroc; Malencon & Bertault, *1975*: 496) to southern Scandinavia.

In the Netherlands *H. persoonii* is a rare fungus; it has a characteristic distribution along the big rivers (the 'Fluviatiel' phytogeographical district, see van Soest in Heukels-van Ooststroom, *1973*) and on the inner side of coastal dunes rich in lime (the 'Duin' district; Fig. 17). In Belgium the species seems to be restricted to the calcareous hills of the Meuse-district (de Langhe *& al.*, *1973*), where it is rather common (Fig. 18). It has never been observed in the western part of that country, as confirmed in a letter by Imler (Antwerpen). On the basis of its habitat *H. persoonii* would also be expected to occur in the southern-most part of the Netherlands, which forms part of the Meuse-district. However it seems to be absent there and also in the adjacent part of northern Belgium.

COLLECTIONS EXAMINED.—NETHERLANDS: prov. Gelderland, Wilp, estate 'de Poll', 29 Oct. 1978, *G. & H. Piepenbroek 68* (WAG-W); prov. Utrecht, Breukelen, estate 'Gunterstein', 22 Oct. 1955, *H. v. d. Laan s.No.* (L); Driebergen, Sept. 1862, Anon. *s.No.* (L); Utrecht, Sept. 1862, *Hartig s.No.* (L); prov. Noord-Holland, Castricum, 'Geversduin', 21 Oct. 1954, *C. Bas s.No.* (L); *s.loc.* 31 Oct. 1964, *E. Kits van Waveren s.No.* (L); Castricum, 1 Nov. 1964, *J. van Brummelen 1879* (L); Santpoort, 'Neethof', Nov. 1911, *C. Cool s.No.* (L); Velzen, 'Duin en Kruidberg', 13 Nov. 1962, *E. Kits van Waveren s.No.* (L); *s. loc.*, *s. dat.*, *C. Bas 2904* (L); IJmuiden, 'Heerenduinen', 6 Nov. 1976, *C. Bas s.No.* (WAG-W); prov. Zuid-Holland, Wassenaar,

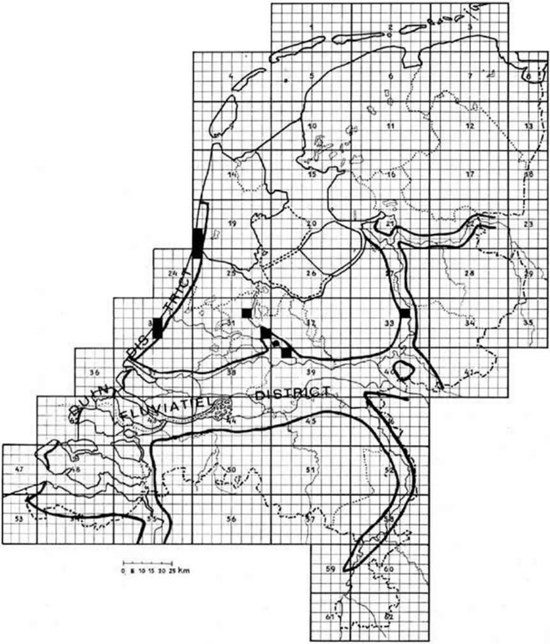


Fig. 17. Geographical distribution of *Hygrophorus persoonii* (■) and *H. mesotephrus* (●) in the Netherlands. The relevant phytogeographical districts have been indicated according to van Soest *in* Heukels & van Ooststroom (*1973*).

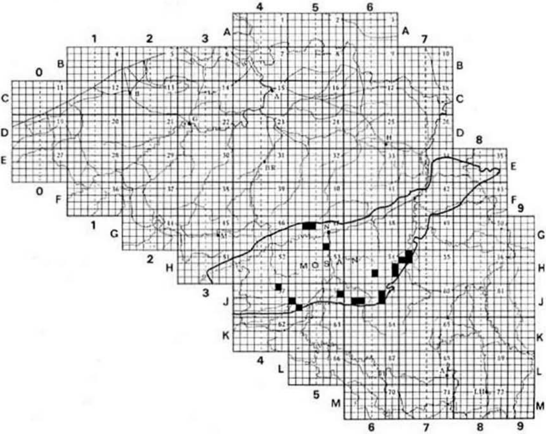


Fig. 18. Geographical distribution of *Hygrophorus persoonii* in Belgium. The Mosan phytogeographical district has been indicated according to de Langhe *& al.* (*1973*).

'Meyendel', 30 Oct. 1955, *C. Bas 955* (L); Wassenaar, 'Raaphorst', Sept. 1923, Anon. *s.No.* (L); *s.loc.*, 6 Oct. 1974, *C. Bas 6423* (L).

BELGIUM: prov. Namur, Wavreille, 'Champs Spalaux', 24 Sept. 1950, *F. Darimont s.No.* (LG); Beaumont (Etneux), 7 Nov. 1944, *F. Darimont s.No.* (LG); Hogne, 20 Oct. 1974, *V. Damblon s.No.* (LG); Onoz-Spy, 28 Oct. 1943, *P. Heinemann s.No.* (GEMBL); Profondeville, 15 Oct. 1952, *P. Heinemann 1918* (BR, GEMBL); Senzeille, 1951, *P. Heinemann s.No.* (GEMBL); Olloy, 17 Sept. 1967, *P. Heinemann 4170* (GEMBL); *s.loc.*, 22 Oct. 1948, *P. Heinemann 1522* (BR); Ave-et-Auffe, 22 Oct. 1967, Anon. *s.No.* (GEMBL); Grupont, 26 Sept. 1969, *Thoen 4166* (BR); Balâtre, 1942, *P. Heinemann 1220*^{bis} (BR); Nismes, 'Tiène aux Pauquis', 3 Oct. 1977, *E. Arnolds 3892* (holotype: L; isotypes: WAG-W, BR); Lavaux-S^{te} Anne, 5 Oct. 1977, *E. Arnolds 3866* (WAG-W); prov. Luxembourg, Wéris, Bouchaimont, 4 Nov. 1973, *J. Lambinon s.No.* (LG); Warenne, near 'Château de Verdène', 5 Oct. 1969, *J. Lambinon s.No.* (LG); Wéris, E. of the road Barvaux-Erezée, 15 Oct. 1967, *J. Lambinon s.No.* (LG); Hotton, 'Tier de Tine', 5 Oct. 1969, *J. Lambinon s.No.* (LG); Grandhan, 'Bois de Grandhan', 17 Oct. 1969, *V. Demoulin s.No.* (LG).

GERMANY: Bavaria, Kaltenberg S. of Augsburg, 20 Oct. 1973, *A. Bresinsky & J. Stangl 699/73* (M); Riederau, Nature-reserve 'Seeholz', 7 Oct. 1978. *A. Einhellinger 51/78* (M).

Without locality and date: '*Agaricus limacinus* Schaeff.' in Herbarium Persoon (L).

Hygrophorus persoonii can be clearly distinguished from the related species, as demonstrated in the key (p. 360).

Kühner & Romagnesi (*1953*: 59) used as the most important key character of this fungus, described under the name *H. dichrous*, the discolouring of extracellular pigment in the pileipellis to dark greenish blue in KOH and NH_4OH. In some collections this reaction would be visible even macroscopically. Also Bon (*1977*: 39) regards this as a constant feature. However, Orton (*1960*: 258) mentioned the occurrence of one collection that did not turn blue at all. In the collections studied by me, only about 70 per cent showed the characteristic reaction with alkaline solutions under the microscope. Often only part of the granular bodies on the most superficial hyphae turned blue, sometimes even very locally. Moreover two collections showed the bluing only in fresh condition. I never observed a bluish discolouring on the cap macroscopically. On account of the large variation in this reaction I do not regard it as a constant property of *H. persoonii*; if present, however, it remains a good differentiating character, because it has never been demonstrated in other species.

The blue reaction with alkalis mainly occurs on the dark irregular crustlike encrustations on the hyphae, which can perhaps be better regarded as excretions than as true pigments. Moreover a variable amount of hyaline or greenish granules are present, which do not discolour at all and often occur in between the hyphae. Also these granules or perhaps droplets of unknown composition are perhaps excretions of the hyphae. Such an origin might explain the great variation in this character.

In a few collections I observed the bluing of extracellular pigment also in granular encrustations on the hyphae of the stipitepellis. This is regarded by Bon (*1977*: 39) as a possible character of his var. *fuscovinosus* of *H. dichrous*, which would be characteristic of evergreen deciduous forests in southern Europe. Another difference should be the size of the fruitbodies: cap 2–5(–6) cm in the typical variety, (4–)5–8(–10) cm in var. *fuscovinosus;* stem 5–8(–10) mm and 10–15 mm thick respectively. From the description above it is clear that such large forms also occur in cool-temperate regions. There is no hiatus between small and large carpophores. A possibly persisting difference is the constant occurrence of pink or reddish tinge in old carpophores of var. *fuscovinosus.*

It is obvious that the nomenclature of this species is rather confused. I shall try to explain why in my opinion it is necessary to introduce a new name to replace the epithets used in the past.

The fungus is usually called *Hygrophorus dichrous* in European literature since the introduction and clear definition of that name by Kühner & Romagnesi (*1953*: 60). Before that it had often been confused, especially with *H. olivaceoalbus*. Probably this is also the case in North America as the description and photograph of *H. olivaceoalbus* by Hesler & Smith (*1963*: 291, fig. 88) show a strong resemblance to *H. persoonii*. The former differs, however, in the more blackish brown colour of cap and stem and its habitat in woods of redwood and spruce.

Unfortunately Kühner & Romagnesi (l.c.) published their description of *H. dichrous* without a Latin diagnosis or a direct reference to a validly published name, as noted earlier among others by Orton (*1960*: 258), Moser (*1967*: 60), and Arnolds (*1974*: 32). However the authors of the Index of Fungi (Commonwealth mycological Intitute, *1959*: 474) considered *H. dichrous*, 'Validly published by reference to the Latin diagnosis of *H. olivaceoalbus* forma *obesa*

Bresadola'. In my opinion this statement is not correct for nomenclatural (1) and taxonomical (2) reasons. (1) Kühner & Romagnesi (l.c.) only mentioned the plate of Bresadola incidentally, while article 33.2 of the 'Code' (Stafleu *& al.*, *1978*: 31) states, that a nomen novum is published validly after 1 Jan. 1953 only if '.... its basionym or the replaced synonym is clearly indicated and a full and direct reference given to its author and original publication with page or plate reference and date.' (2) The quoted plate of Bresadola (*1887*: 92) shows important differences with the original description of *H. dichrous*, e.g. in the ventricose stem and the habitat in coniferous forests. Doubt about the correctness of the reference of Kühner & Romagnesi has already been expressed by Orton (*1960*: 258). I agree with Bon (*1977*: 39) and Cetto (*1976*: 650), who regard *H. olivaceoalbus* f. *obesus* Bres. identical with *H. limacinus* sensu Romagnesi, i.e. *H. latitabundus*. For the sake of nomenclatural stability it is regrettable, that it is no longer possible to validate the name *Hygrophorus dichrous* as Hongo (*1958*: 101) used it for quite a different species from Japan belonging to the (sub-)genus *Hygrocybe*.

Another name, earlier in use for *H. persoonii*, is *Hygrophorus limacinus*. Orton (*1960* : 258) has pointed out that in this case already before the nomenclatural starting point there existed two homonyms, viz. *Agaricus limacinus* of Scopoli (*1772*; later validated by Fries in 1838) and *A. limacinus* of Schaeffer (*1774*; later validated by Persoon in 1828). Scopoli (*1772*: 422) described a rather slender fungus with a white stem and a cap without olivaceous tinge, most probably different from the species described above. Orton (l.c.) thinks, that the original plate of Scopoli might represent *H. mesotephrus* Berk. & Br. I have not seen that plate myself, so I cannot judge this statement. According to the view of Donk and other European mycologists, including the present author, the description and plate by Scopoli should be regarded the nomenclatural type of *Agaricus limacinus* Scop. ex Fr. since Fries obviously wanted to redescribe Scopoli's species. In that case this name cannot be used for the present species.

Generally the validation of *A. limacinus* Scop. has been assigned to Fries (*1821*: 36). This author lists *A. limacinus* Scop. under the heading 'Species inquirendae', which means that these species have still to be investigated. From this it is clear, that Fries did not accept Scopoli's species at that point and consequently did not then validate Scopoli's name for it (article 34.1.a of the 'Code', Stafleu *& al.*, *1978*: 32). This is also the opinion of C. Bas (Leiden), R. A. Maas Geesteranus (Leiden), and V. Demoulin (Liège). It is true that Fries published *Hygrophorus limacinus* (Scop.) validly in the 'Epicrisis' (*1838*: 324), but this validation is antedated by others. To my knowledge Persoon (*1828*: 94) was the first author to validate the name *Agaricus limacinus*, based however on the description (*1774*: 74) and plate (*1771*: 312) by Schaeffer. The latter might be regarded the lectotype. It shows a fungus, which might be very well the species under consideration: the cap is about 40 mm broad, umbonate, brown with yellowish tinge near the margin; the stem has been depicted about 60 × 11 mm, yellowish, and would be spotted according to the description. Unfortunately no exact habitat has been indicated. Orton (*1960*: 258) also regards *Agaricus limacinus* Schaeff. ex Pers. identical with *H. dichrous* Kühn. & Romagn.

Persoon certainly used the name *H. limacinus* in this sense, as can be concluded from an investigation of material present in Persoon's Herbarium at Leiden. Singer (*1961*) published a study on types present in the Herbarium of Persoon, but he did not focus on *Agaricus limacinus*.

Therefore it seems useful to give a short description of this material (labelled: L 910.255–678). Persoon has written in the corner the names *Agaricus limacinus* Schaeff. and *A. olivaceoalbus* Fr.

The collection consists of one carpophore cut lengthwise, superficially affected by a mould, but revived relatively well in NH_4OH 10%. Cap 38 mm broad, orange brown beneath mould. Stem 47 × 7.5 mm, subfusiform, dirty orange ochre. Spores [10/1] (8.1–)8.7–9.8(–10.5) × (5.2–) 5.6–6.3(–6.7) µm, ellipsoid or oblong with obtuse apiculus, frequently collapsed. Basidia [5/1] *c.* 48–56 × 9.5–10.2 µm, almost all more or less collapsed, probably 4-spored. Pileipellis amazingly well reviving; an ixotrichodermium up to more than 1000 µm thick, in the upper part very loosely interwoven; hyphae *c.* 2.1–5.6 µm broad with olive green vacuolar pigment and moreover densely covered with irregular and granular encrustations, not discolouring blue in alkaline solutions. Stipitepellis of the same structure, but thinner. Clamps present.

From the above deliberations it is clear, that it would be appropriate to identify the species under consideration with *A. limacinus* Schaeff. ex Pers. Unfortunately that epithet is preoccupied in the genus *Hygrophorus* by Fries, who made first the combination *Hygrophorus limacinus* in 1838 (: 324), based however upon Scopoli's name. Fries' description at that point of time is difficult to interpret. It is not impossible, that he had the same fungus in mind as Persoon, but he referred to Scopoli and did not mention Schaeffer's platé. Moreover he regarded only var. *β* of *A. limacinus* Schaeff. ex Pers. in Mycologia europaea identical. It is not clear, whether Fries had already seen the species himself.

A more detailed, new description has been published by Fries in 1852 (: 129). At that occasion he reports *H. limacinus* from frondose woods in the surroundings of Stockholm and for the first time he mentions dimensions of the carpophores, which together with other characters point in the direction of *H. persoonii*. However, he explicitly considers Scopoli as the only original source. Fries probably handled the same concept in 'Hymenomycetes' (*1874*: 409). In the latter book he cites a plate of Saunders & Smith (*1872*: 28 fig. 1) with the designation 'optime'. This plate shows a fungus with the typical habitus of *H. persoonii* with a dark brown cap and ochraceous stem, which would be 'fibroso-striated' according to the description. It is reported in 'leafy woods'.

According to M. Moser (Innsbruck; in letter) Fries' plate of *H. limacinus* in Stockholm shows a fungus with a coloured stem (contrary to the description by Scopoli) which could 'eventually suggest *H. dichrous*'. Because Fries knew *H. olivaceoalbus* very well from the surroundings of Femsjö (see p. 380) this seems quite probable.

In my opinion the final conclusion must be, that the name *Hygrophorus limacinus* has to be rejected as a 'nomen ambiguum et confusum' for the following reasons:—

(1) The existence of two early homonyms, viz. *Agaricus limacinus* Schaeff. and *A. limacinus* Scop. The first name belongs to the present species and has been validated (in the genus *Agaricus*) by Persoon (*1828*). The second name relating to another species has been validated somewhat later by Fries in 1838, but was the first to be transferred to *Hygrophorus* also by Fries in 1838.

(2) On behalf of this complex situation typification can be done in different conflicting ways.

(3) Fries' early concept of *A. limacinus* before 1852 remains uncleared. Since 1852 it seems to cover the present species, although Fries never changed the original reference to Scopoli's description.

(4) Great confusion exists in the applications of the name *Hygrophorus limacinus* by later authors.

(5) A new but nomenclaturally invalid name has already been proposed for this species and has been generally accepted, viz. *Hygrophorus dichrous* Kühn. & Romagn. Unfortunately this name cannot be validly published on account of a validly published earlier homonym, viz. *H. dichrous* Hongo.

HYGROPHORUS MESOTEPHRUS Berk. & Br.—Figs. 19–25

Hygrophorus mesotephrus Berk. & Br. *in* Ann. Mag. nat. Hist. II **13**: 402. 1854. — *Limacium mesotephrus* (Berk. & Br.) P. Henn. *in* Natürl. PflFam. **1** (1): 213. 1898.
MISAPPLICATIONS.—*Hygrophorus mesotephrus* sensu Cooke, Ill. Brit. Fungi: 293. 1889 (= *H. leucophaeus* (Scop. ex Fr.) Gill.); sensu Boudier, Icon. mycol. **1**: 34. 1905–10 (= *H. leucophaeus*).

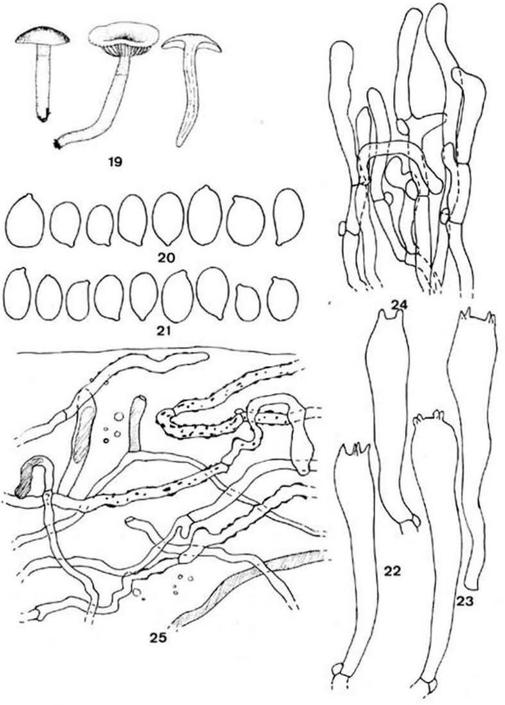
COLOURED ILLUSTRATIONS.—Lange, Fl. agar. dan. **5**: 162 B. 1940 (but cap depicted too green).
SELECTED DESCRIPTIONS.—Trans. Br. mycol. Soc. **43**: 258. 1960; Coolia **17** (suppl.): 35. 1974; Docums mycol. **7** (27–28): 39. 1977.

Cap [5/1] 19–32 mm broad, first conico-convex, then expanded with weakly crenulate, sometimes ascending margin, not hygrophanous, pale greyish brown or beige, towards centre much darker greyish sepia with slight olivaceous tinge, strongly glutinous. Gills [L = *c.* 25–35, l = 1–3] shortly decurrent, rather distant, thick, becoming slightly ventricose with age, white to creamy. Stem 43–63 × 3.5–6.5 mm Q = 9–15, slightly fusiform, apex white, pruinose to minutely white floccose, dry, sometimes guttulate, sharply separated from remaining viscid part which is white or pale ochre-orange ('isabella'), becoming yellowish at base, without darker spots or belts, also on drying. Flesh white, in base of stem yellowish. Smell and taste absent.

Spores [50/4/3] (8.4–)8.6–12.0(–12.2) × (5.3–)5.5–7.4(–8.6) μm, on the average 9.6–10.4 × 6.1–6.8 μm, Q = (1.3–)1.4–1.8, ellipsoid to ellipsoid- or ovoid-oblong with short obtuse apiculus (Figs. 20, 21). Basidia [25/4/3] (40–)44–60(–63) × (7.2–)7.7–10.0(–11.0) μm, on the average 51.6–54.2 × 8.0–9.4 μm, Q = (4.7–)5.1–7.7(–8.2), slenderly clavate, 4-spored or 4- and 2(–1)-spored intermingled (Figs. 22, 23). Hymenial cystidia absent. Hymenophoral trama bilateral, composed of short to moderately long cylindrical to strongly inflated elements, measuring [22/4/3] 28–131 × 3.8–21(–26) μm. Pileipellis a well developed ixotrichodermium, in exsiccata variably reinflatable to *c.* 120–870 μm thick, consisting of slender erect branched hyphae, 1.4–4.8 μm broad, hyaline or mostly with greenish intracellular pigment and intracellular granules, hyphae mostly smooth, but in some fruit-bodies a small percentage faintly rough by encrusting pigment; extracellular granules absent or few, pale greenish in alkaline solutions (Fig. 25). Warts on apex of stem consisting of fasciculate close hyphae *c.* 1.2–3.5 μm broad with cylindrical to slenderly clavate terminal elements, *c.* 2.5–6 μm broad, colourless (Fig. 24). Stipitepellis downwards an ixotrichodermium like the pileipellis but thinner. Stipitetrama with rather long elements, *c.* 3.8–14.5 μm broad. Clamps numerous in all parts of the carpophore.

EXSICCATA.—Cap 13–32 mm broad, with thin flesh, concentrically wrinkled, shining at centre, pale ochre yellow or brownish ochre to rather bright brown-orange with sharply delimited dark reddish brown centre. Gills creamy to orange ochre. Stem 36–85(–105) × 2–6 mm, cylindrical; apex whitish or pale ochre with obscure to striking small ochre to orange brown pustules; downwards shining, ochre orange to orange-brown, often red-brown at base, without darker spots.

ECOLOGY.—In the Netherlands *H. mesotephrus* is known from one locality in an old frondose wood with *Fagus* and *Quercus* on rather rich subneutral river clay. According to Bon (*1977*: 39) this species would occur in mixed frondose woods on silicate soils. The material from Belgium has been stated from a Fagetum with *Luzula*, so probably more in accordance with the data of Bon (l.c.). Fructification occurs in October.



Figs. 19–25. *Hygrophorus mesotephrus.* — 19. Carpophores, × 0.5. — 20, 21. Spores, × 1000. — 22, 23. Basidia, × 1000. — 24. Section of warts on apex of stem, × 1000. — 25. Radial section of pileipellis, × 1000. (Figs. 19, 20, 23, 24 *from Bas 1323*; Figs. 21, 22, 25 from *Heinemann 4277*.)

DISTRIBUTION.—In the Netherlands and Belgium *H. mesotephrus* is very rare (Figs. 9, 17). This seems to be the case in other countries of western Europe too. Only Lange (*1940*: 12) mentions it as being 'not uncommon' in Denmark.

COLLECTIONS EXAMINED.—NETHERLANDS: prov. Utrecht, Zeist, near 'Wulperhorst', 20 Oct. 1957, *C. Bas 1323* (L).

BELGIUM: prov. Namur, Wavreille, 16 Oct. 1967, *P. Heinemann 4277* (GEMBL). Probably also belonging to this species (or perhaps *H. persoonii*): prov. Liège, Basse-Bodeux, 22 Oct. 1955, *J. Lambinon s.No.* (LG).

GERMANY: Bavaria, Landskreis Landsberg am Lech, Geltendorf, 20 Oct. 1973, *A. Bresinsky s.No.* (M, 2 wrappers).

Hygrophorus mesotephrus is the most slender species in the group of *H. persoonii* and can be recognized fairly easily by its pale cap and whitish stem without spots. Orton has studied the type of *H. mesotephrus* and published some details (*1960*: 258), so it seemed not necessary to repeat this investigation.

Hygrophorus mesotephrus sensu J. Lange has been regarded a misapplication by most authors. According to Orton (l.c.) Lange's plate is doubtfully distinct from *H. dichrous*, while Bon (*1977*: 38) regards it identical with *H. olivaceoalbus* f. *gracilis* Maire. Moser (*1978*: 80) also quotes this plate under *H. olivaceoalbus*, although between brackets. In my opinion and that of Bas (Leiden; priv. comm.) however Lange's plate depicts *H. mesotephrus* fairly well, although in the material from the Netherlands the cap centre is slightly more brownish and less olivaceous. Lange (*1940*: 11) describes the cap being 'olive-fuscous' at the centre. Certainly *H. mesotephrus* sensu Lange is totally unrelated to *H. olivaceoalbus* since colours of the stem, size of spores and habitat are quite different.

HYGROPHORUS OLIVACEOALBUS (Fr. ex Fr.) Fr.—Figs. 26–32

Agaricus olivaceoalbus Fr., Obs. mycol. **1**: 5. 1815. — *Agaricus olivaceoalbus* Fr. ex Fr., Syst. mycol. **1**: 35. 1821. — *Hygrophorus olivaceoalbus* (Fr. ex Fr.) Fr., Epicr.: 324. 1838. — *Limacium olivaceoalbum* (Fr. ex Fr.) Kummer, Führ. Pilzk.: 119. 1871. — Neotype (design. mihi): *M. Moser 72/190*, 6 Aug. 1972, Femsjö (**IB**).

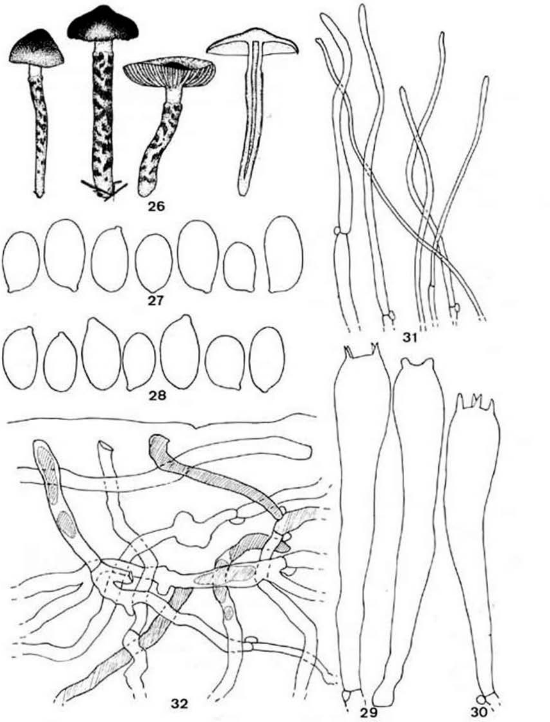
MISAPPLICATIONS.—*Limacium olivaceoalbum* sensu Ricken, Blätterp. **1**: 13. 1915 (= *H. persoonii*); sensu J. Lange, Fl. agar. dan. **5**: 162 A. 1940 (= *H. persoonii*). — *Hygrophorus olivaceoalbus* sensu Hesler & Smith, North American species of *Hygrophorus*: 291. 1963 (= *H.* spec.); sensu auct. eur. p.p. (= *H. persoonii*).

COLOURED ILLUSTRATIONS.—Bresadola, Icon. mycol. **7**: 316. 1928; Michael-Hennig, Handb. Pilzfr. **3**: No. 238. 1964; Marchand, Champ. Nord Midi **2**: 154. 1973.

SELECTED DESCRIPTIONS.—Kühner & Romagnesi, Flore anal.: 60. 1953; Michael-Hennig, l.c.; Docums mycol. **7** (27–28): 38. 1977.

Cap [22/4] 19–55(–60) mm broad, first semiglobate to conical, then expanding with prominent subacute to obtuse umbo with convex sometimes crenulate margin, not hygrophanous, first grey- to olive-brown with dark brown to almost black centre, slightly paler when old. Gills [L = 22–35, l = 1–3(–5)] broadly adnate with tooth or decurrent, rather distant to distant, thick, up to 6 mm broad, white to creamy white. Stem 40–85(–100) × 4–10(–12) mm, Q = *c*. 8–14, rather slender, cylindrical or slightly fusiform, first with slimy-fibrillose veil between stem and margin of cap, apex dry, white, whitish pubescent to pruinose, below veil in young carpophores entirely olive-brown, but soon with olive or grey-brown transverse bands and spots on white background, most conspicuously so on drying, completely slimy when moist. Flesh in cap rather thin, up to 7 mm thick, rather firm, white but usually lemon yellow at centre below pileipellis; in stem fibrillose, white. Smell and taste not remarkable.

Spores [95/10/10] (9.1–)10.2–15.8(–18.2) × (6.2–)6.7–8.8(–9.1) μm, on the average 11.5–14.1 × 7.4–8.6 μm, Q = 1.4–1.9(–2.0), ellipsoid to ellipsoid-oblong with large obtuse apiculus (Figs.



Figs. 26–32. *Hygrophorus olivaceoalbus.* — 26. Carpophores, × 0.5. — 27, 28. Spores, × 1000. — 29, 30. Basidia, × 1000. — 31. Hairs on apex of stem, × 1000. — 32. Radial section of pileipellis, × 1000. (Figs. 26, 27, 29, 31 from *Arnolds 804*; Figs. 28, 30 from *Moser 72/190*, neotype; Fig. 32 from *Roucart*, 5 Oct. 1951.)

27, 28). Basidia [42/9/9] 61–79(–83) × (9.6–)10.1–14.4 μm, on the average 64–77 × 10.5–13.6 μm, Q = (4.3–)4.8–7.5, rather slenderly to slenderly clavate, 4-spored, in some collections a few 2-spored (Figs. 29, 30). Hymenophoral trama bilateral, composed of rather short cylindrical to inflated elements, [27/5/5] 43–148 × 4.8–22 μm.

Pileipellis a well developed ixotrichodermium, in exsiccata reinflating to *c.* 150–530 μm thick, in the upper layers loosely interwoven, consisting of branched slender cylindrical hyphae *c.* 2.2–6.7 μm broad, hyaline or with olivaceous vacuolar pigment, smooth or, exceptionally, a few can be slightly roughened, commonly completely without encrusting pigment and extracellular granules (Fig. 32). Stipitepellis at apex of stem a dry irregular cutis of thin hyaline hyphae with scattered long free ends, projecting up to *c.* 500 μm, cylindrical and hyaline, *c.* 2.8–5.8(–7.2) μm broad; fascicles of compact hyphae absent (Fig. 31). Stipitepellis below apex an ixotrichodermium like the pileipellis but thinner, up to 200 μm in exsiccata; hyphae 1.5–5 μm broad, sometimes on some hyphae with very fine encrustations. Stipitetrama regular with rather long cylindrical elements, *c.* 2.5–12.0 μm broad. Clamps numerous in all parts of the carpophore.

EXSICCATA.—Cap 16–48(–60) mm broad, with thin flesh, mostly strongly concentrically wrinkled, dull to weakly shining, rather dark brown, often with greyish, reddish or orange tinge, with very dark brown centre. Gills creamy ochre to orange ochre. Stem 30–95 × 2.5–9(–11) mm, cylindrical, apex whitish to ochraceous, pubescent or pruinose without pustules, often sharply delimited from the remaining part, which is ochre to rather dark brown, with or without conspicuous darker belts and spots.

NOTES ON THE NEOTYPE (*M. Moser 72/190*, 6 Aug. 1972, IB).—Exsiccata of 3 mature carpophores. Spores [10/1] (10.5–)12.0–14.5(–17.2) × (7.2–)7.4–8.8(–9.1) μm, ellipsoid or ellipsoid-oblong (Fig. 28). Basidia [5/1] *c.* 64–79 × 12.9–14.4 μm, slenderly clavate, 4-spored (Fig. 30). Pileipellis an ixotrichodermium reviving in KOH 5% to up to 200–390 μm thick; hyphae *c.* 2.2–5.8 μm broad, hyaline or with olivaceous vacuolar pigment, smooth, without granular elements.

ECOLOGY.—Mentioned by all authors from coniferous forests with preference for spruce (*Picea abies*). In Belgium *H. olivaceoalbus* occurs only in spruce plantations on acid peaty soil. Also other authors mention a preference for moss-rich forests on moist acid soils (e.g. Favre, *1960*: 393; Michael-Hennig, *1964*: 220; Bon, *1977*: 38). Fructificating from August until November.

DISTRIBUTION.—In Europe *H. olivaceoalbus* seems to have a mainly boreo-montane distribution: it is widespread in Scandinavia as well as in the montane and subalpine belts of the central European mountains. It is far more rare in the western European lowland and has never been found in the extensive spruce plantations of the Netherlands. However, it has been found several times in the adjacent part of northern Germany.

In Belgium *H. olivaceoalbus* has a characteristic distribution pattern: it seems to be confined to the phytogeographical district of the Ardennes, which is the highest part of Belgium mainly consisting of Devonian, Silurian and Cambrian silicate rocks, giving rise to acid soils poor in lime (de Langhe *& al.*, *1973*). The species is especially common in the subdistrict of the high Ardennes ('Haute Ardennais'), which is situated for the greater part higher than 500 meter above sea level. This region was covered mainly with extensive peat moors ('Hauts Fagnes'), but large areas have now been planted with *Picea* (Fig. 9).

COLLECTIONS EXAMINED.—BELGIUM: prov. Liège, S. of Eupen, 'Herzogenwald' (alt. 500 m), 16 Sept. 1970, *E. Arnolds 804* (WAG-W); Robertville, 'Pessière de Drello', 2 Aug. 1950, *F. Darimont s.No.* (LG); *s. loc.*, 5 Oct. 1951, *R. Roucart s.No.* (LG); Robertville, Mont Rigi, 23 Aug. 1936, *P. Heinemann 468* (BR); Robertville, near Sourbrodt, 12 Sept. 1937, *P. Heinemann 595* (BR); Robertville, near Sourbrodt, 'Pont de la Roer', 23 Oct. 1955, *J. Lambinon s.No.* (LG); Malmédy, near Bevercé, 15 Aug. 1957, *C. Bas 1332* (L); Rockerath, 'Drei Herrn Wald', 14 Oct. 1956, *J. Lambinon s.No.* (LG); prov. Luxembourg, Champlon, 'La Converserie' (alt. 550 m), 17 Oct. 1961, *P. Heinemann 3167* (BR, GEMBL); Awenne, 17 Oct. 1958, *P. Heinemann 2614* (BR).

SWEDEN: Smoland, Femsjö, E. of Dullaberget, 6 Aug. 1972, *M. Moser 72/190* (neotype, IB).

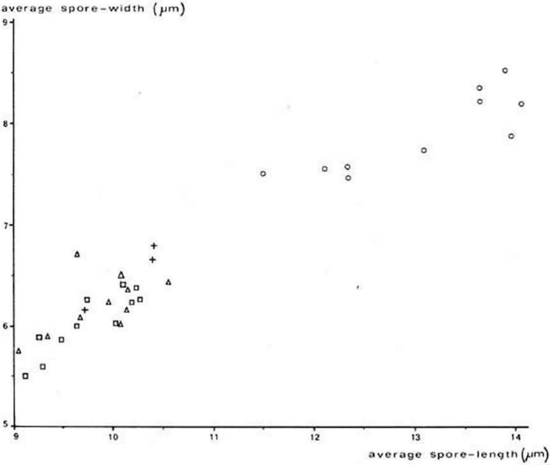


Fig. 33. Scatter diagram of average length and width of basidiospores of *Hygrophorus latitabundus* (△), *H. persoonii* (□), *H. mesotephrus* (+) and *H. olivaceoalbus* (○).

GERMANY: Westfalen, SW of Ibbenbüren, 18 Oct. 1961, *J. Barkman 7148* (WAG-W); Niedersachsen, Oldenburg, 'Neuenburger Urwald' near Zetel, 24 Oct. 1961, *J. Barkman 7207* (WAG-W).

The name *H. olivaceoalbus* has been frequently misapplied in the past, especially as a consequence of confusion with *H. persoonii*. As indicated in the key (p. 359) important macroscopic as well as microscopic and ecological differences exist between the two species. The significant difference in spore size is demonstrated in the scatter diagram of Fig. 33. However, in a single specimen the variation of spore measurements can be considerable and may show some overlap with those of other species in this group. Also basidia in *H. olivaceoalbus* are larger than in other species treated here (Fig. 34). However, the difference in length can be obscured by strong reinflation of the basidia in alkaline solutions, resulting in a relatively broadly clavate shape. Differences in reinflating of exsiccata are probably due to differences in the process of drying.

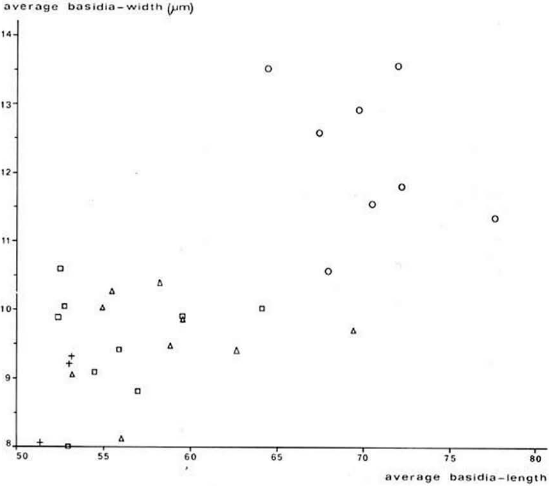


Fig. 34. Scatter diagram of average length and width of basidia of *Hygrophorus latitabundus* (△), *H. persoonii* (□), *H. mesotephrus* (+) and *H. olivaceoalbus* (○).

It is beyond any doubt, that Fries meant the fungus described above when introducing the name *Agaricus olivaceoalbus* in his Observationes (*1815*: 5). In Systema (*1821*: 35) he mentions, that this species should be frequent in coniferous forsts. According to Moser (in letter) this is still true for the surroundings of Femsjö, where Fries collected during that period of his life. Moser kindly sent me one collection from this region on loan, which is proposed here as neotype.

Hygrophorus olivaceoalbus forma *obesa*, described by Bresadola (*1887*: 92) is identical with the species described here under the name *H. latitabundus*. *Hygrophorus olivaceoalbus* var. *gracilis* Maire (*1933*: 53), described in contrast to var. *obesus* (Bres.) Maire, is in my opinion the same as typical *H. olivaceoalbus*, like described above.

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DEVELOPMENTAL ANATOMY OF COPRINUS

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The aim of this study has been to compare the ontogenetic structures of as many species of *Coprinus* as possible in order to obtain a better insight into their mutual relationships. The sequence of development of the parts in the first phases of primordium development has been traced with greater precision here; several degrees of rupthymenial hymenophore development have been distinguished; the veil and pileipellis structures and the corresponding terminology have been critically discussed. Finally, an attempt has been made to establish phylogenetic relationships between about 27 species, but to acheive a higher degreę of accuracy in this field, ontogenetic information concerning still more species is required.

INTRODUCTION

The genus *Coprinus* is one of the most intensively studied genera of the higher Basidiomycetes. As early as the time of Brefeld (*1877*) and de Bary, the anatomy of the fruit bodies was well known. Brefeld also laid the basis for a series of investigations about the influence of external factors, such as light, on the fructification and morphogenesis of *Coprinus*. Very well known are the observations of Buller (*1909, 1924, 1931*) concerning the finer anatomy and sporulation of a series of species of *Coprinus*. Since the discovery of incompatibility by Bensaude (*1918*) with *Coprinus fimetarius*, species of this genus have played a very important role in the genetic research of the Basidiomycetes. Moreover, new research about speciation has usually been done on species of *Coprinus*: well known are the crossings of species of the Setulosi group by M. Lange (*1952*), by which it was possible to delimit these species much better. Also, the experiments of Kemp (*1977*) concerning sympatric speciation (homing of oidea, etc.) were done with species of *Coprinus*.

The fact that many species of *Coprinus* can be easily cultivated and also that they fructify in cultures is probably the main reason for the preference shown by research workers for this genus. It was also Brefeld (*1877*) who gave a good account of the development of the fruit bodies of several species, illustrating it with several splendid lithographs. Since then, a rather large number of species has been studied in this respect (Reijnders, *1963*: 190–197).

When we had the opportunity several years ago to collect the primordia of some not previously examined species (mainly in cucumber hothouses, through the kind intervention of my friend, J. Daams), we decided to continue the research in order to be able to compare as many species as possible from all sections and sub-sections. In this way, we have now acquired a general knowledge, as far as the development is concerned, of 27 species which belong to this heteromorphous genus.

Classification within the genus is now based mainly on the properties of the veil and the pileipellis, and they have lead, for example, Kühner & Romagnesi (*1953*) and Singer (*1975*) to discern very nearly the same sections and sub-sections, although there is a slight difference in the order of these groups and in the names. We will investigate the degree to which the characteristics of the development agree with this classification and the degree to which they can improve or supplement it. Fries (e.g. *1874*) made use of the presence or absence of a veil and some of its characteristics to a great degree in his classification. However, it was J. E. Lange (*1938*) who emphasized the importance of the structure of the pileipellis. In the 'Flore analytique', the system that is now commonly used appeared.

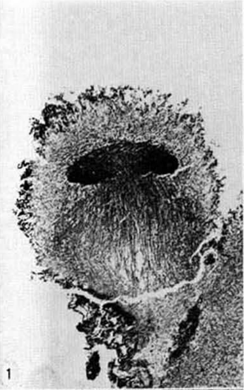
The question of why this big, polymorphous genus has not been split up can be asked. Attempts to do this have probably been made, but there are two main objections: First, the whole group is bound together by one characteristic which is unique in the system of the Agaricales: the deliquescence of the gills (pileus), although this characteristic does not appear in all cases. And second, there are many intermediate forms. It is clear that the structure of the veil and the pileipellis should receive a great deal of attention in this study. In general, we see that the dermium is strongly developed when the veil is reduced, and vice versa. But in reality, the situation is more complicated. There does not yet exist unanimity in the terminology concerning the pileipellis, and this can cause confusion. It will not, however, be difficult to arrive at an adequate nomenclature.

Apart from the development of the velum and the pileipellis, there are two other ontogenetic structures of extreme importance during the primordial condition of Agaricales. The sequence of development of the most important parts of the carpophore (stem, cap, hymenophore) is not the same; we discussed this not-yet-fully-conceived topic of ontogeny of agaric fruit bodies several times (Reijnders *1963*: 235–245; *1979*a). Moreover, it is precisely the case with *Coprinus* that the development of the hymenophore is remarkable, for here a different structure was discovered as compared with other Agricales (Levine, *1914*). This problem became controversial after Atkinson (*1916*) thought that he had to dispute the results of Levine (Reijnders *1948*: 266–267; *1963*: 245). In connection with the deviating initial structure of the gills, attention should be paid to their open edge during a great part of the primordial condition. This edge is turned toward the stem. The problem is now whether the young gills are attached to the tissue below (lipsanenchyma). This comparative research on *Coprinus* can therefore serve to facilitate some taxonomic conclusions and can also produce some precision concerning some ill-defined ontogenetic structures.

We would prefer to postpone a treatment of these questions until the discussion below. We can then draw our conclusions on the basis of what was already known.

As for materials and methods used, there are no novelties. The fixative was Bouin's liquid. The stains were Mayer's haemalum or saffranin – gentian violet.

Figs. 1–5. *Coprinus phaeosporus*. — 1. Isocarpous young stage with wide protenchymatic zone around the base of cap and stem between which the lipsanenchyma is perceptible. The universal veil consists of radiating dichophysoid hyphae × 80. — 2. A tangential section of an intermediate developmental stage with open edge of the primary gills × 80. — 3. The universal veil and the protenchyma under it at an intermediate stage × 200. — 4. The pileus-trama and the veil in the lateral part of a primordium at a more advanced stage × 200. — 5. Tangential section of a young primordium showing three groups of palisade-hyphae × 320.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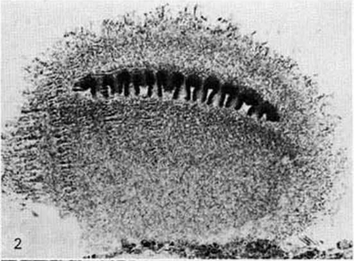
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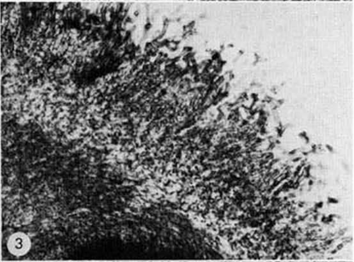
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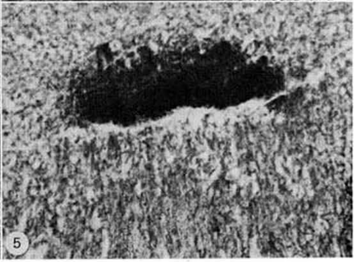
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DESCRIPTIVE PART

COPRINUS PHAEOSPORUS AND COPRINUS BRASSICAE

Dealing with these closely related species together may have some advantages. The ontogenetic structures are slightly different in some respects, but on the whole, they are congruent and deviate somewhat from those of other Coprini, as does the group to which they bellong: the section *Impexi* Romagn. apud Kühn. & Romagn. (=subsection *Alachuani* Sing.)

(1) The youngest stage studied (Fig. 1, height 567 μm, width 529 μm) of *C. phaeosporus* has an isocarpous structure. The longitudinal hyphae of the stem, the chromophilous cap, and the still darker stained, downward-growing hyphae of the hymenophore and pileusmargin show up clearly. Remarkable is a broad zone of protenchyma enveloping these parts; at the outside of this, the universal veil arises through the appearance of radiating hyphae which widen somewhat and have thicker walls toward the periphery, while the small branches at the extremity are already present, giving this veil what Singer (*1975*: 63, 493) calls a dichophysoid structure. The lipsanenchyma between stem-surface and pileus margin is made up of longitudinal, protenchymatic hyphae.

It would be inaccurate to consider the whole protenchymatic peripheral layer as belonging to the universal veil. Certainly, it represents in part a matrix-layer of the veil, the radiating hyphae of the latter originating from this tissue. Though the demarcation between cap and surrounding tissue seems to be quite conspicuous, there is no real segregation of the hyphae at the centre of the cap-surface where the hyphae remain interwoven, and this continues to be the case in later stages. It is quite possible that during the extension of the cap, this tissue is partly absorbed into the rapidly growing hyphae of the cap-trama. We have met with this not very well-defined position of cap and veil in several other species (e.g. *Coprinus*), and Atkinson (*1914*) observed this for *Lepiota clypeolaria*.

Coprinus brassicae seems to be more strictly pileocarpous. The youngest primordium we can represent (Fig. 8, height 378 μm, width 592 μm) shows a deeply stained area in the centre, surrounded by a wide zone of protenchyma. Here the veil is far less differentiated than in the preceding species, as it is in mature specimens. Beneath the chromophilous dome, there is a zone where the tissue also has a dark colour, and this may be the rudiment of the stem (cf., e.g. very young stages of *Amanita*, etc.). But the longitudinal direction of the hyphae in this zone is hardly noticeable, and no inflation has as yet taken place.

It is possible that in still younger primordia, the pileus also arises first in *C. phaeoporus*, but in

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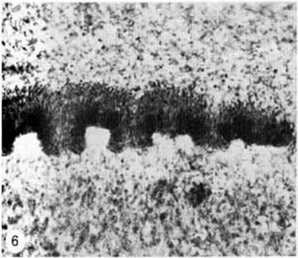
Figs. 6–7. *Coprinus phaeosporus*. — 6. Tangential section of an intermediate stage showing the young gills × 320. — 7. Tangential section of a somewhat more advanced stage showing the open gill-edges and hyphae which pass into the lipsanenchyma × 200.

Figs. 8–11. *Coprinus brassicae*. — 8. Median section of a young stage showing the pileocarpous origin × 125. — 9. Intermediate stage with wide protenchymatic zone around the primordium (universal veil) × 63. — 10. Pileus-margin and lipsanenchyma at an advanced stage × 125. — 11. Upper portion of the pileus-trama with hyphae merging into the universal veil and peripheral zone of the latter with somewhat altered hyphae × 125.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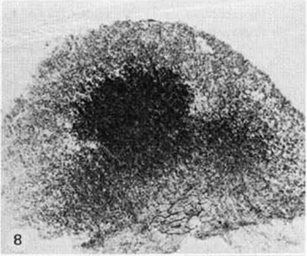
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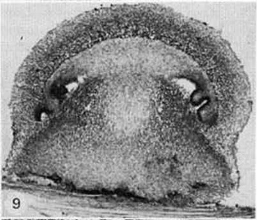
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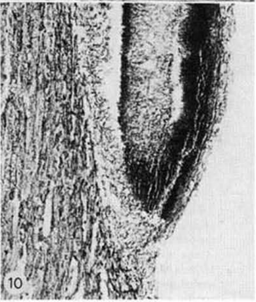
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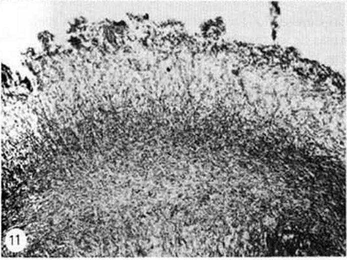
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the section of the minute primordium of Fig. 1, the stipe is already so well-marked that an isocarpous or even a pileo-stipitocarpous mode may be present as well.

(2) In both cases, the shape of older primordia is striking and somewhat characteristic, the primordia being very wide and less high. To demonstrate this, we inserted Fig. 9, which represents an approximately median section of a stage of *C. brassicae* with a height of 807 μm and a width of 1 mm, and Fig. 2, a tangential section of *C. phaeosporus* (height 630 μm, width 857 μm; cf., here the open edge of the lamellae and the continuous palisade-layer over the lamellulae).

A section of a very advanced stage, representing the pileus-margin and what is for Coprini a rather abundant lipsanenchyma along the elongated stem is given in Fig. 10 (width of the glandiform cap 1.4 mm) for *C. brassicae*.

During the course of the entire development, the layer of interwoven protenchyma between the pileus-trama and the veil (new branches of the latter continue to appear between the older ones) merged into the pileus-trama, at least in the centre of the cap. This phenomenon is obvious in Fig. 3, a photomicrograph of a somewhat older stage of *C. phaeosporus* (width 1 mm) and in Fig. 11 for *C. brassicae* (width of cap about 1.5 mm). This connection is of course less evident at the side of the cap in older specimens, where the hyphae of the pileus-trama are parallel and directed downward for the purpose of cap-growth. A pileipellis is missing in these two species as it is in *C. macrocephalus* and *C. macrorhizus*, but in contrast to these species, there is no meristemoid at the contour of the pileus to produce the radiating hyphae of the veil (the latter arises from the layer of protenchyma at the outside of the cap. Fig. 4, width of the unexpanded cap of *C. phaeosporus* about 1.8 mm). The nature of the universal veil in *C. phaeosporus* has been described above. In more advanced stages there are no important transformations in this respect. The hyphae of the veil are initially radiating, slightly widening toward the tip, metachromatic with rather thick walls, and provided with short, spine-like branches (dichophysoid structure). In older primordia, these peripheral hyphae are more interwoven, resulting in a rather coherent cover.

The veil in *C. brassicae* has a much more simple structure. The peripheral hyphae are still interwoven, and the protenchyma underneath is slightly altered and somewhat more inflated and metachromatic.

(3) Here again we find a similar development of the hymenophore in these two species. Initially, the layer of palisade-hyphae may be interrupted here and there (Fig. 5, width of the primordium 491 μm, *C. phaeosporus*; Fig. 12, width 882 μm, *C. brassicae*), and no regular arched structure can be observed or arches alternating with sterile bands. Very soon after this initial stage, however, the rupthymenial structure becomes apparent through the activity of the downward-growing hyphae of the gill-trama in horizontal stripes radiating outward from the centre toward the periphery (Fig. 6, width 724 μm, *C. phaeosporus*). From the beginning, the edge

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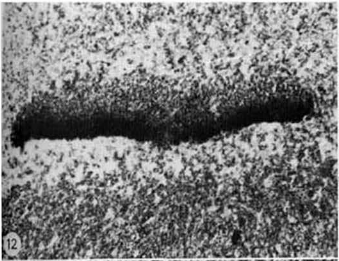
Figs. 12–13. *Coprinus brassicae*. — 12. Tangential section of a young stage showing the uninterupted layer of palisade-hyphae of the hymenophore × 320. — 13. Tangential section of an intermediate stage showing the open gill-edges × 200.

Figs. 14–16. *Coprinus patouillardii*. — 14. Nearly median section of young primordium × 200. — 15. Median section of an intermediate stage with universal veil consisting of an inner layer of protenchyma and serried sperocysts × 125. — 16. Upper portion of the cap of a more advanced stage. Nearly the whole weil consists of spherocysts × 80.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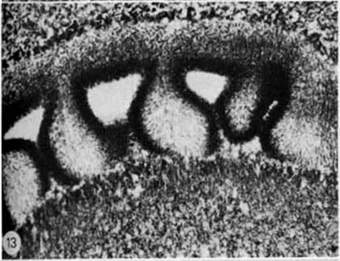
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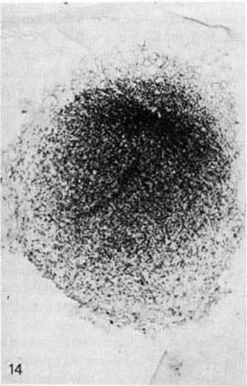
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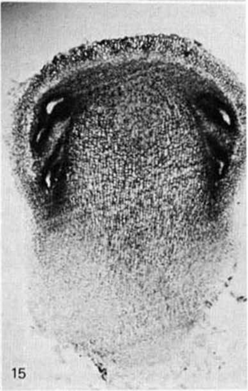
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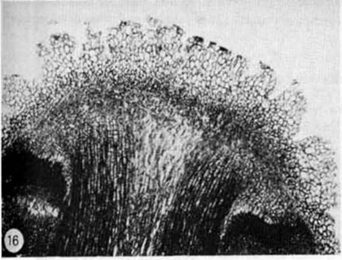
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of the gill is open and there is, especially in these two species, a larger number of hyphae passing from the gill-trama into the underlying lipsanenchyma (Fig. 7, width of the primordium at the level of the hymenophore 945 μm, *C. phaeosporus*. Note the loose texture of the divergent gill-trama). The hyphae at the demarcation between lamellae and lipsanenchyma are not in any way crowded together; on the contrary, the hyphae appear to be drawn out in that region. (Cf., Fig. 13, *Coprinus brassicae*, and 'Development of the hymenophore').

COPRINUS PATOUILLARDII

(1) The youngest stage (Fig. 14, largest diameter 277 μm) shows the structure typical of the initial phase in *Coprinus*. In the centre, the thin protenchymatic hyphae, which extend mainly in a longitudinal direction, and over this part a darker staining zone with miniscule cells, can be observed where this orientation of the hyphae is less evident. Immediately over this darker spot is the universal veil, consisting of cells with very thin walls, of which the diameter increases toward the periphery. The cells of the basal plectenchyma are already strongly inflated, and their walls are equally thin. It is clear that the dark-staining part of the section represents the rudiment of the cap, and soon thereafter the hymenophore appears in the usual manner (cf., e.g. *C. macrophizus*: Fig. 33).

(2) A median stage is represented by Fig. 15. As there are no deviations here from the ordinary mode of development in *Coprinus*, we shall pay attention to the universal veil only, and to its relationship to the pileus-trama. The entire universal veil has a cellular structure. At the outside of the stem and the pileus-margin, the ascending hyphae are divided into short cells, acquiring the character of the veil to an increasing degree toward the exterior. Over the cap, there are rows of oblong cells (or spherocysts, somehow reminiscent of the radiating hyphae in *C. microrhizus*, etc.; width of the veil *c.* 64 μm). Immediately over the cap, the hyphae are divided into short cells. There is no sharp boundary between veil and pileus trama, and this is also the case in older stages. Figure 16 represents the top of a young carpophore (the pileus is not yet spread out). We observe the cells of the veil and beneath the repent hyphae of the thin pileus-trama (Fig. 17).

(3) The development of the hymenophore is rupthymenial. At first, there are isolated arched groups of palisade hyphae. The lipsanenchyma is scanty and not subject to further development (Fig. 18).

COPRINUS POLIOMALLUS

This species and the preceding one belong to the same section, called by Singer (*1975*) *Cycloidei* Fr. and by Kühner & Romagnesi, *Vestiti* (Lange) Kühn. & Romagn. It is to be

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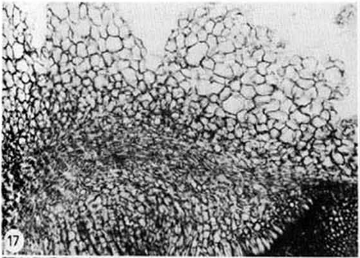
Figs. 17–18. *Coprinus patouillardii*. — 17. Detail of the section shown in Fig. 16 demonstrating the narrow pileus-trama of repent hyphae between the spherocysts of the veil and the pseudoparenchyma of the stipe × 200. — 18. Tangential section of a young stage showing the tendency towards the rupthymenial mode of hymenophore formation × 320.

Figs. 19–22. *Coprinus poliomallus*. — 19. Very young stage: the pileo-stipitocarpous primordium and the veil × 160. — 20. Young isocarpous primordium × 160. — 21. Intermediate stage × 100. — 22. Detail of the the preceding section showing the veil-meristemoid and the rows of spherocysts formed by it × 320.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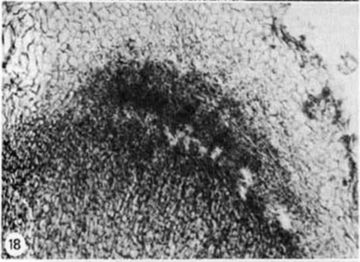
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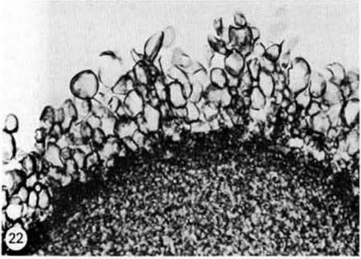
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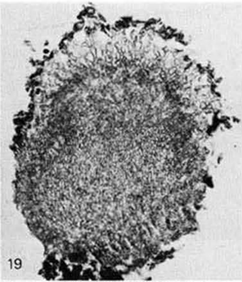
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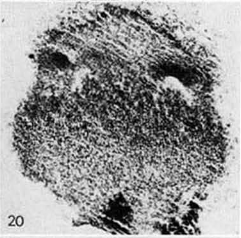
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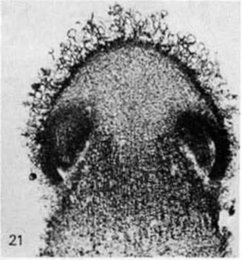
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expected that their development will not differ a great deal, the most striking difference being the fact that the veil in older stages is not completely concrete with the pileus, but that a rather inconspicuous dermium is formed instead. Furthermore, the veil seems to be specialised in this species.

(1) Three successive young stages reveal the same disposition of the tissues as in the preceding species. At first, there is a central core of longitudinal hyphae, but somewhat beneath the upper end of the primordium there is a region where the hyphae are somewhat more intricated and consist of short cells (Fig. 19). The universal veil is present in the youngest stages and is made up of chains of rounded cells, radiating outward and widening. Soon the palisade-hyphae of the hymenophore, growing downward, appear, and the three fundamental parts of the carpophore are present (Fig. 20 at the level of the hymenophore 265 μm). At this point, no more important changes of this disposition occur, as is shown in Fig. 21 (diameter 536 μm).

(2) For a considerable time during development, the pileus-trama and the veil pass into each other without perceptible demarcation. At the base of the veil there is a kind of meristemoid where cell division is frequent. The rows of spherocysts or oblong cells are here more individualised than in the preceding species, and the cells themselves are also more specialised, their walls being rather thick and often brown in colour (Fig. 22, diameter 536 μm). Finally, in a still more advanced stage, the veil is separated from the pileus-trama by a single layer of isodiametric cells, and the outer layer of the pileus-trama becomes pseudoparenchymatic, so the chains of spherocysts are pinched off and become loose flocks on the pileus-surface (Fig. 23).

(3) The development of the hymenophore is of the rupthymenial type. There is evidence that the arches of the palisade-hyphae are isolated from the beginning. Through the activity of the downward-growing hyphae of the gill-trama folds, there are soon salients developing in a radial direction, but there remain some original protenchymatic hyphae passing from the lipsanenchyma into these folds (Fig. 24 and Fig. 25). These hyphae are nearly always divided into short cells. It is quite probable that in this species hyphae from the gill trama also grow afterwards into the lipsanenchyma. So the connections between gills and lipsanenchyma last for some time (Fig. 26).

COPRINUS FLOCCULOSUS

(1) The youngest primordium of *Coprinus flocculosis* (Fig. 27, diameter of the widest part 410 μm) consists of a centre of longitudinal hyphae surrounded by large cells of the universal veil (diameter up to 13 μm). On the left-hand side, the veil has been torn off. The veil is particularly

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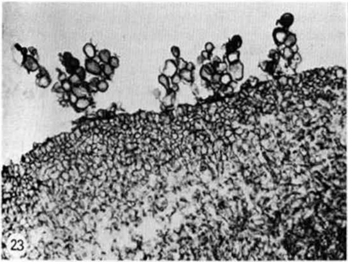
Figs. 23–26. *Coprinus poliomallus.* — 23. Rests of the veil and epithelium with individualized outer layer at a more advanced stage × 160. — 24. Young gill with open edge and hymemial palisades in a rather young primordium × 320. — 25. Detail of the preceding section showing the nature of the connection of the gill-trama and the lipsanenchyma, the latter being composed of short cells × 800. — 26. The open gill-edge of the primary lamellae and the edge of the secundary lamellae surrounded by hymenial elements, the lipsanenchyma over the stem surface at a more advanced stage × 320.

Figs. 27–28. *Coprinus flocculosus.* — 27. Youngest stage with longitudinal rather uninflated hyphae in the centre, and a meristemoid in the upper portion surrounded by the veil × 125. — 28. Detail of the preceding section, showing the nature of the veil × 320.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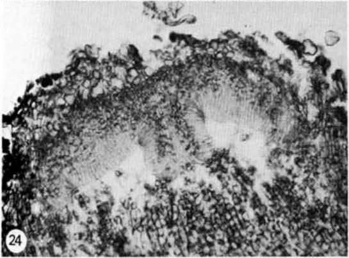
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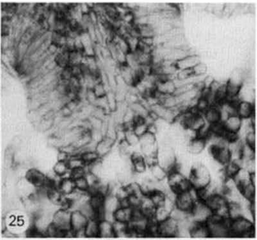
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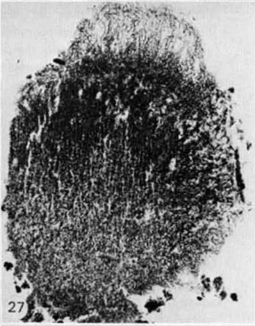
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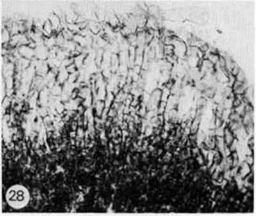
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well-developed at the tip (width *c.* 130 μm). Here we find gradually widening hyphae, divided into short cells (but no spherocysts) with a diameter up to *c.* 13 μm (Fig. 28, detail of the same section under higher magnification). Between the stem part and the ascending hyphae of the veil, a zone of narrow protenchymatic hyphae made up of isodiametric small cells is to be found. One can observe a longitudinal direction in these hyphae too, but the mass of small cells rather represents a meristemoid which gives rise to the pileus-trama and the undermost layer of the veil, which consists of short cells. Beneath the parallel hyphae of the stem is a basal plectenchyma with already inflated cells (diameter up to 6.5 μm).

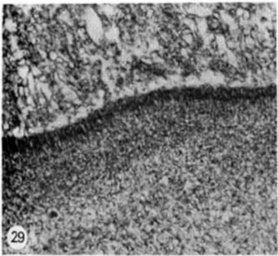
(2) The next stages are not described in detail here as they show a normal coprinoid development. Soon after the initial structure observable in stage 1, the palisade-hyphae of the hymenophore manifest themselves, giving rise to an isocarpous primordium, in which all parts develop proportionally. The extension of the veil is notable in older stages: width over the tip of the cap is 479 μm in a primordium with a diameter of 3.5 mm; width over the stem is only 126 μm. Though immediately over the pileus-surface the hyphae are still radiating, they are more interwoven toward the periphery (diameter of the largest cells about 16 μm).

We will describe here only the development of the pileipellis, which in this case is a true palisadodermium. When the primordium has reached a diameter of about 0.9–1 mm, we see between the narrow lower end of the hyphae which pass into the veil, peg-like cells—at first only a few but thereafter rapidly increasing in number. In a young carpophore of 3.5 mm width, the palisade-layer is well-established (Fig. 29), with transversal cross-walls in the cells which give rise to the hymenium-like dermium. As these cells multiply and enlarge (length up to 20 μm, diameter *c.* 3 μm), the hyphae of the universal veil are pinched off, and the veil is separated from the pileustrama and can be found on mature specimens as loose flocks.

(3) The development of the hymenophore is decidedly rupthymenuous, as Fig. 30 shows. The primordium to which the tangential section of this photomicrograph belongs has a diameter (at the level of the hymenophore) of 718 μm. The radiating rows of palisade-hyphae, cut transversally, alternating with sterile bands with hyphae passing into the lipsanenchyma which descends from the pileus-trama, are conspicuous. This structure is present from the beginning throughout the entire layer of palisade-hyphae. Nevertheless, there may be a peripheral portion where the bands of protenchymatic hyphae are less striking; this is the youngest part of the palisade-layer, at the exterior of which new elements are deposited during the primordial growth (Fig. 31, diameter 441 μm). As in most other species of *Coprinus*, the edge of the lamellae is open in older primordia, and there is no indication of the lamellae pressing against the stem, and some hyphae run across interspaces.

Figs. 29–31. *Coprinus flocculosus.* — 29. The palisadodermium at an intermediate stage × 225. — 30. Rupthymenial orgin of the hymenophore × 200. — 31. Peripheral palisade-hyphae in a somewhat later stage × 415.

Figs. 32–34. *Coprinus macrorhizus* — 32. Youngest stage. As in *C. flocculosus* × 160. — 33. A somewhat older stage. The initially at most pileostipiticarpous development has changed into an isocarpous one × 200. — 34. Intermediate stage with profusely developed veil and meristemoid under it × 100.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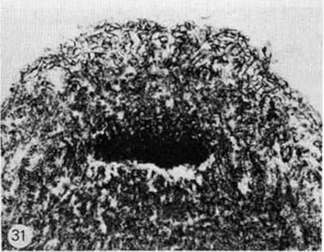
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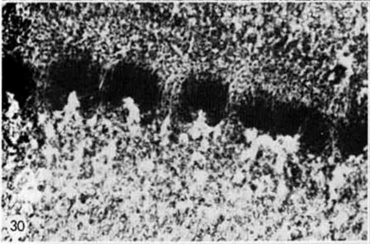
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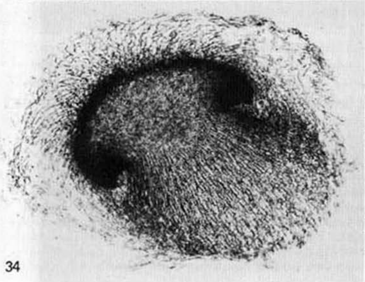
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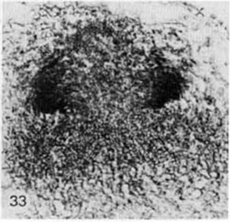
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COPRINUS MACRORHIZUS AND COPRINUS MACROCEPHALUS

It is appropriate to treat the closely related *Coprinus macrorhizus (Pers. ex Fr.)* Rea and *C. macrocephalus* Berk.—of which the latter is far less well known—together. The differences between our specimens, collected in hothouses at Kortenhoef, corresponded to those mentioned by Orton in his key (*1957*: 270), with the exception of the fact that the spores of our *C. macrocephalus* were narrower, the longest ones having a somewhat cylindrical shape and therefore probably belonged to another race. The other characteristics of the two species were in agreement with those described and depicted by J. Lange (*1939*: 110). Measurements of our spores were as follows: *C. macrorhizus* 9.5–11.2(–12.8) × 6.5–7(–8) μm. Orton's were 10–11.5 × 6–7 μm. For *C. macrocephalus*, we found: (9.5–)11–14.5 × 6.5–7.5 μm. Orton's were 11–14 (–17) × 7–9 μm.

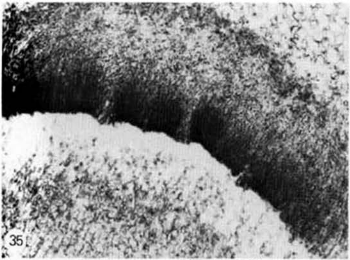
There is a high degree of conformity between the ontogenetic structures of the two species. A similar form has been described earlier, which we called *C. fimetarius* (Reijnders, *1952*: 73, cited in my book under the erroneous name *C. radiatus*).

(1) The youngest stages of these species have the same construction (length of *C. macrorhizus* 504 μm, width 288 μm; length of *C. macrocephalus* 182 μm, width, including veil, 315 μm; Figs. 32, 36). The center consists of longitudinal, somewhat inflated hyphae (diameter up to 5 μm), and over it is a zone of dark staining hyphae which are divided into short cells, the longitudinal direction of which is less evident. Towards the tip, longitudinal hyphae can again be observed, widening gradually into inflated cells (up to a diameter of about 10 μm), with a reduced protoplasmic content. These are the hyphae of the universal veil, which is concrete with the inner portion of the primordium. The veil also covers the sides of the primordium where it is narrower and consists of ascending hyphae with large cells which are formed at an early stage. The radiating hyphae of the veil at the upper part of the primordium are particularly conspicuous in *C. macrocephalus*. In both cases, beneath the dark staining centre, there is a well-developed basal plectenchyma with inflated cells (up to about 8 μm).

(2) Soon after this stage, the inner aspect of the primordium is changed considerably by the appearance of an annular bundle of chromatic hyphae in the upper part, growing outward and downward. This represents the origin of the pileus margin and the hymenophore. No annular gill-cavity precedes this formation. Beneath it, we find the hyphae of the lipsanenchyma in sections of *C. macrorhizus* (Fig. 33). In *C. macrocephalus* the hyphae of this annular bundle project through the longitudinal hyphae of the lower part of the primordium and a lipsanenchyma is still lacking. The sections in *C. macrorhizus* have a height and a diameter of 315 μm; the height is 454 μm and the diameter 441 μm in *C. macrocephalus*. In the sections of the latter species, the hyphae of this bundle are convergent in the beginning (see, e.g. Reijnders, *1971*: 306, pl. 1 fig. 2b). With the

Fig. 35. *Coprinus macrorhizus*. Tendency towards a rupthymenial origin of the hymenophore. The layer of palisade-hyphae is locally interrupted × 320.

Figs. 36–39. *Coprinus macrocephalus*. — 36. Youngest stage with remarkable development of the universal veil × 200. — 37. Section, showing a lateral portion of the cap grown together with the veil meristemoid × 200. — 38. The universal veil forming a coif over the pileus in a more advanced stage × 80. — 39. Tangential section of a rather young stage demonstrating the tendency of the palisade hyphae to become arranged in groups × 200.



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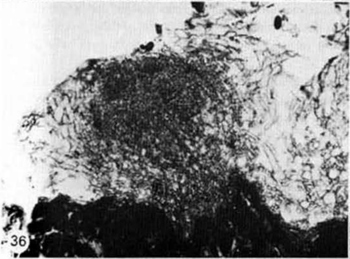

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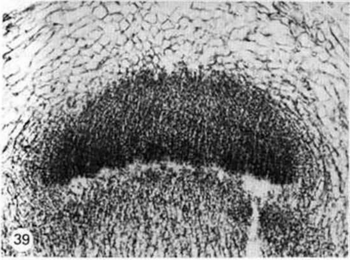

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appearance of this structure, the primordium shows three clear rudiments: that of the stem, that of the pileus (the tissue of the pileus-trama is still very dense but the hyphae are more or less interwoven) and that of the hymenophore. The stem is still low, its longitudinal hyphae are somewhat inflated, and the demarcation between stem and pileus-trama is abrupt.

(3) In the course of development, a few more small changes take place in the proportions of these parts. The veil increases, principally over the cap, where the radiating hyphae are abundant. Their oblong cells remain coherent and widen towards the periphery. The veil is always concrete with the cap. Between the trama of the cap and the differentiated cells of the veil is a zone with a strong cell-division—a tissue we called meristemoid (Reijnders, *1977*). Only one older stage of *C. macrorhizus* was depicted (Fig. 34, diameter 756 μm), which shows the disposition of the growing tissues clearly. The lipsanenchyma is scanty and consists merely of hyphae which are directed obliquely upward: these are the outermost hyphae of the young primordium which are not incorporated into the stem.

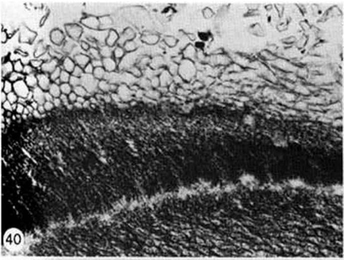
The veil over the cap is extremely well-developed in *C. macrocephalus;* there it forms a coif (Fig. 37). It also extends over the stipe; at the outside of the pileus margin are longitudinal hyphae, a remnant of the original longitudinal hyphae. The lateral trama of the cap consists of parallel protenchymatic hyphae, and the veil and its meristemoid between them have been somewhat more highly magnified in Fig. 38.

(4) We can study the continuity or interruption of the layer of the palisade-hyphae, which always precedes the formation of the hymenophore in tangential sections. Figure 35 represents this layer in *C. macrorhizus* (diameter of the section at the level of the hymenophore: 441 μm). In this section, the layer is interrupted here and there, but not regularly. A similar section, but somewhat further from the axis, shows an almost continuous layer of palisade-hyphae (diameter of the section 504 μm). It is therefore impossible to speak of a rupthymenial origin of the hymenophore in this species. With *C. macrocephalus* on the other hand, we find a more pronounced rupthymenial origin. Figure 39 represents this layer in a section, which has a diameter of 567 μm; Fig. 40 shows a somewhat older stage (diameter 756 μm). One observes clearly the arched arrangement of the palisade-hyphae.

Another interesting point in the development of the hymenophore is the fact that the edge of the gill salients in the primordia are mainly open toward the stem. This is also the case in these two species. Much has been written about this subject (the literature has been compiled in Reijnders, *1948*: 266–277; *1963:* 248). Ascending hyphae, running from the stem or lipsanenchyma into the gill-trama are generally present (Fig. 41). These hyphae, divided into short cells, are wider than the hyphae of the trama but sometimes merge into each other. In the beginning, the palisade-hyphae push their way through the longitudinal hyphae of the primordium. Also in cases where the layer of palisade-hyphae is continuous, some hyphae of the orginal protenchyma remain between them. When an annular gill-cavity has formed, these hyphae initially traverse the

Figs. 40–41. *Coprinus macrocephalus.* — 40. Tangential section of a similar stage as in Fig. 39 showing the same phenomenon × 200. — 41. Tangential section of a more advanced stage showing the open gill-edges and the ascending hyphae which continue into the trama of the lamellae where they narrow down × 400.

Fig. 42–44. *Coprinus curtus.* — 42. Very young stage showing an isocarpous origin and the first spherocysts of the veil × 400. — 43. Somewhat later stage showing the structure of the veil × 250. — 44. Intermediate stage × 125.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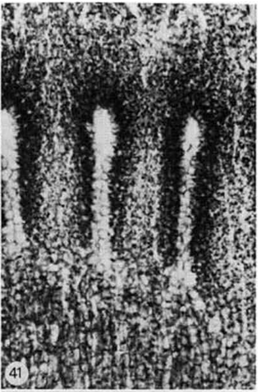
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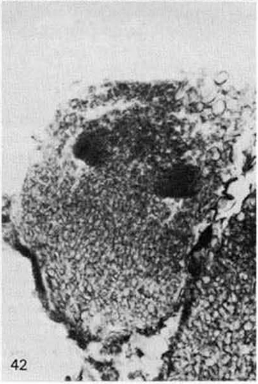
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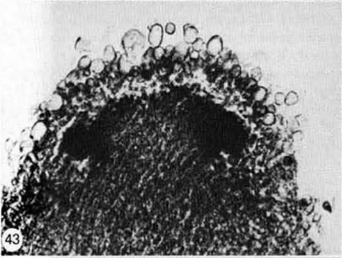
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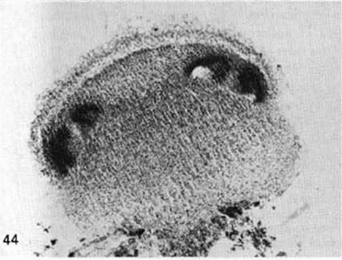
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cavity; later, they are torn apart (see, e.g. Reijnders, *1952*, pl. 7 fig. 5). Here there is no cavity; the hyphae of the lipsanenchyma are wider than those of the gill-trama, but it is quite possible that these cells of one hypha differ under the influence of local factors. With these two species no hyphae growing from the gill-trama into the lipsanenchyma could be observed to reinforce this—a phenomenon which is to be found in *Coprinus* as well. (This will be dealt with later.) The open edge of the lamellae has been imputed to a pressure excerted by the young gills against the stem (Atkinson, *1916*), but this cannot be the case. In all the series of sections which are being and have been analysed by the author, no indication of pressure in this region has been found (e.g. compressed hyphae). On the contrary, we stated that the tension arising during the development produces a stretching in this part of the primordia.

COPRINUS CURTUS

This species has already been subjected to thorough investigation by Buller (*1931*). The anatomy of the mature carpophores is, therefore, well-known. However, our results concerning the ripening of the spores are not in complete agreement with Buller's findings. This question will be treated following the description of the development.

(1) The youngest stage, a microtome-section of which has been presented in Fig. 42 (length 160 μm, diameter 114 μm), already shows the rudiments, however small, of all important parts: the veil, the stem, the pileus-trama and the palisade-hyphae of the hymenophore. Comparison with other species of *Coprinus* leads to the conclusion that this isocarpous construction has been preceded by the presence of the longitudinal hyphae only, giving rise in the lower portion to the stem and in the upper part under the veil to the pileus-trama. But in a very early developmental stage, the palisade-hyphae appear and spherocysts become apparent in the veil.

(2) Three photomicrographs of median sections have been included here. The primordia are respectively: very young (Fig. 43, diameter 256 μm), somewhat more developed (Fig. 44, diameter 460 μm), and representing a young toadstool (Fig. 45, height 820 μm, width of the cap 180 μm). As the development is quite normal, no further description is necessary. Before stretching of the stem, the primordium remains low for a long time (Fig. 44). It appears that the veil is made up of two layers: an inner portion consisting of interwoven hyphae and an outer envelope of spherocysts, which are also present at the sides of the stem. No chains of spherocysts exist, however. These cells appear at the boundary between these two layers, and some cells in the hyphae enlarge considerably to become spherocysts. The hairs typical of this species are still lacking in the stage shown in Fig. 44. It may be that this section shows the very beginning of the

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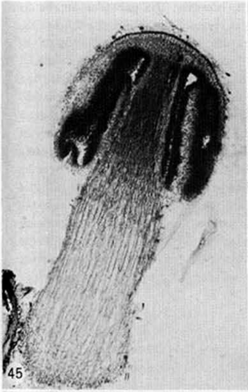
Figs. 45–47. *Coprinus curtus*. — 45. Median section of an advanced stage, with a conspicuous palisadodermium over the centre of the cap, spherocysts of the veil, and hairs on the cap and, more scattered, along the stem × 100. — 46. Detail of the upper portion of the cap; showing the palisadodermium with dark staining protoplasm in the upper end of the cells, spherocysts of the veil, and club-shaped dark staining hairs × 250. — 47. Tangential section of a young stage showing isolated arches of palisadehypae × 400.

Figs. 48–49. *Coprinus hexagonosporus*. — 48. Youngest stage, with centre of subparallel hyphae, upper part of very small isodiametric cells, and universal veil reduced the some vesiculose elements × 250. — 49. Somewhat later isocarpous stage. The universal veil is not coherent and consists for the greater part of vesiculose elements with a long narrow neck; the lipsanenchyma is evident × 160.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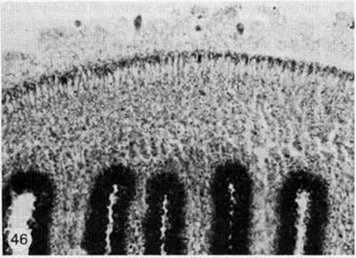
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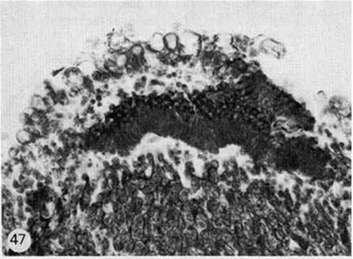
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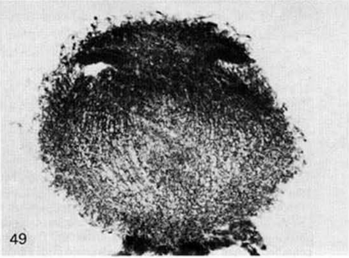
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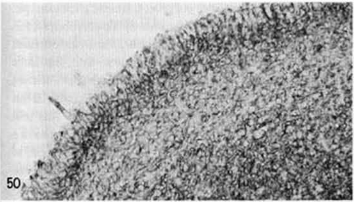
palisadodermium over the centre of the cap surface; however, the palisades are barely distinguishable. The construction of the outer layers has changed notably in the third of the median sections (Fig. 45), and we note the important development of the palisade of the pileipellis (cf., also Fig. 46, pileipellis and veil of a still more advanced young toadstool, height 2.8 mm, width of the cap 907 μm). These palisade-cells have a dark-coloured tip, which is caused by a protoplasmic concentration. The inner layer of the veil has disappeared completely, all the cells of which probably having changed into spherocysts. Some of these cells at the outside have a thicker, brown-coloured cell-wall, but these modified veil-cells (used in systematics for the distinction of the species) are not always present. The hairs characteristic of the species, deeply stained by protoplasmic contents, clavate and *c*. 5–8 μm at the ends (at this stage) appear over the entire cap, but also at the side of the stem. The late appearance of these hairs and the fact that young, dark-staining elements are present between the palisade-cells of the dermium, lead to the assumption that they belong to the pileipellis, rather than to the veil. Nevertheless, their presence at the side of the stem, where they arise from the cortex, seems to contradict this. We still note that the development of this palisadodermium, which becomes afterwards a hymenidermium (the cells become cubical), begins at the centre of the pileus and progresses toward the exterior (Fig. 45).

(3) The development of the hymenophore is rupthymenial (Fig. 47, diameter of the primordium 235 μm). The layer of palisade-hyphae growing downward and representing the first differentiation of hymenophore development, is not continuous, and, as can be seen in this tangential section, there are sterile bands between the arches of the palisades.

(4) In very young specimens, sporulation begins. We measured the spores which were present in microtome-sections of very young carpophores. The first spores formed in *Coprinus curtus* appear to be different from spores produced in more mature carpophores. They are less pigmented, have a rather thin wall, and the germ-pore is less evident or lacking. Sometimes they are somewhat deformed and do not have the regular eliptical shape which is usually apparent; at any rate, they are smaller. Spores from exsiccata of specimens growing on the same dung which yielded our primordia measured 11–13.5 × (6.5–)7–8 μm; the first spores in question 6.7–9 × 5.5–6.5 μm (in a longitudinal section of a glandiform, unexpanded cap with a height of 457 μm and a width of 208 μm) or 8–9.5 × 6.5–7 μm (when the cap was 956 μm high and 819 μm wide). Nevertheless, it is highly unlikely that we are dealing here with young, unripe spores, as spores were measured which were generally well-pigmented and had been released from the basidia which had already aged and thrown off their spores. Unpigmented, unripe spores were as much as ever present in the preparations (perhaps only a few of these were measured). So we must conclude that the spores which are formed first are smaller, and that their sizes increased gradually until spores of normal dimensions were released. This is in agreement with the observations of Clémençon (*1979*).

Figs. 50–52. *Coprinus hexagonosporus*. — 50. Palisadodermium and pilocystidium of an advanced stage. Note the cellular structure of the cap-trama × 200. — 51. Hymenidermium with young hairs in an advanced primordium × 250. — 52. Rupthymenial hymenophore in a young stage × 200.

Figs. 53–55. *Coprinus angulatus*. — 53. Young stage showing a somewhat isocarpous texture × 200. — 54. Somewhat older stage with remnants of the veil (lipsanenchyma) under the pileus-margin and with a palisadodermium × 100. — 55. More advanced primordium with hymenidermium and pilocystidia × 160.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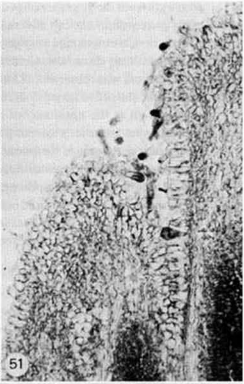
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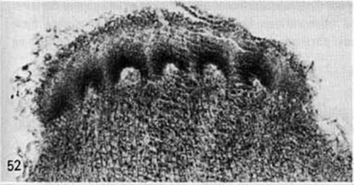
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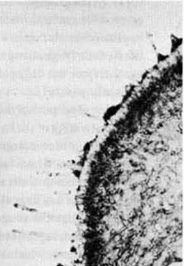
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Another feature which may be significant is the simultaneous ripening of the spores over the whole gill from the youngest stages. We observed this peculiarity in several sections, for example, of the primordium, the cap of which had a height of only 457 μm (see above). To corroborate this observation, we examined very young specimens of the related *Coprinus hepthemerus*, obtained from a culture from the Centraalbureau voor Schimmelcultures, Baarn, and the same phenomenon was observed. That the spores formed in early stages are smaller—mature specimens: (11–)12–15.5 × 6.5–8(–8.8); very young (8–)9.5–12 × 6.5–7(–8)—was also clear in this case, as well as the simultaneous ripening of the spores over the whole young gill. This is in contradiction to Buller's assertion that in *Coprinus curtus* the ripening of the spores begins in a zone near the margin of the pileus and progresses centripetally, as in so many other species of *Coprinus*. Neither in *Coprinus curtus* nor in *C. hepthemerus* can this be true. We must also call into question the deliquescence of these small membraneous species of the genus. Non-deliquescence has been reported only for *Coprinus disseminatus*, but the relationships of the latter have been disputed. Very detailed observations have still to be made concerning these generalized phenomena in this genus, particularly concerning the direction of spore-ripening along the gills.

COPRINUS HEXAGONOSPORUS

This species is also related to *C. curtus*.

(1) In the youngest stage (Fig. 48, largest dimension 315 μm, width 208 μm), we can see that some differentiation has already taken place. A basal plectenchyma with somewhat inflated hyphae (diameter up to 8 μm) occupies the lowest part and the centre. From a point at about one-third of the height from the bottom, hyphae extend toward the tip and toward the left side (they are therefore not only parallel to the axis), and they are somewhat interwoven, although they are generally parallel.

In the upper part of the section, the hyphae are again divided into small isodiametric cells, and the intertwining of the hyphae is here somewhat more striking. There is no well-defined universal veil, although some larger, round cells at the periphery (diameter up to 7 μm) certainly belong to this structure, which appears to be much reduced in this species. It is somewhat more conspicuous in the next stage (Fig. 49, height 334 μm, width at the level of the hymenophore 277 μm). It comprises several elements: the rounded or club-shaped cells mentioned above, which are also present at the stem-surface; some undefined extremities of protenchymatic hyphae; and bottle-shaped, lageniform hairs (length 25–37 μm, diameter of inflated portion 6.5 μm, diameter at neck 3–4 μm), which are in no way incorporated into the tissue of the cap, but rather lie on it. There is as yet no rudiment of the pileipellis. At the left side we see a scanty lipsanenchyma, and at the right the gill-chamber is filled with this tissue or with the hyphae passing between the arches (rupthymenial hymenophore). The narrow zone of parallel stem-hyphae is evident; below it is the basal plectenchyma.

(2) When the buds have reached a diameter (at the level of the hymenophore) of about 400 μm, the palisade-cells of the pileipellis appear and push forward between the inflated lower ends of

the velar hairs (diameter *c.* 13 μm, length 60 μm). Most of these inflated elements are the lower ends of hairs with or without a visible neck (often the neck will be cut off) and not, properly speaking, spherocysts. They are empty at this point and have thin walls, and they are almost colourless. But between the palisade-cells of the pileipellis, new hairs appear, initially as deeply-staining club-shaped elements. Most of these hairs remain blunt, somewhat clavate (length *c.* 60 μm, diameter at tip up to 10 μm; Fig. 51, height of cap 1.5 mm), but the neck of some is narrow, tapering somewhat (Fig. 50, diameter of the cap 1.15 mm). In these stages the hymenidermium is made up of wide, almost cubical cells.

(3) It is beyond question that the rupthymenial mode of hymenophore construction is to be found here. Arches of palisade hyphae, interrupted by bands where they were lacking, were always observed (Fig. 52). As with other species of *Coprinus*, the edges of the gills are widely opened, there is no indication that they press against the stem. Hyphae passing from the gill-trama into the scanty lipsanenchyma are frequently present.

COPRINUS ANGULATUS (= *C. boudieri*)

(1) The youngest stage represented (Fig. 53, height 265 μm, width 202 μm) already demonstrates some differentiation. The material used in the investigation of this species deteriorated to some degree (there were traces of putrefaction, not of drying). So for cytological research, it was of little use, but it did permit some observations on the histological texture of the primordium. Though a coherent universal veil seems to be lacking, there are, particularly at the side of the stem, masses of short cells, originating partly from longitudinal hyphae, with many cross-walls, and partly from short, club-shaped branches, directed outward and also divided into short cells. This peripheral tissue also reaches over the point where the palisade-hyphae of the hymenophore will arise more internally. There are already long hairs, which are in this stage mainly restricted to the pileus (length up to 80 μm, diameter at the lower end 9 μm, at the neck about 6 μm, rounded at the tip). The areas of pileus-trama, stem and hymenophore are well-demarcated.

(2) From a stage with a diameter of 472 μm and a length of 548 μm, the palisadodermium becomes evident (Fig. 54). Over the cap, there are only the long hairs which have arisen partly between the palisade-cells. Some of these hairs may also occur at the side of the stem, but we find here chiefly the club-shaped, outward-directed elements. In a still older stage (Fig. 55, diameter of the cap 2.1 mm), there are large hairs over the cap (about 60–100 μm long, lower end 10 μm wide, neck about 5 μm), but now they are present over the stem as well (e.g. 102 μm long, 20 μm wide, neck 6 μm). As is the case with the preceding species, it remains problematic whether these hairs belong to the universal veil or to the pileipellis. Their presence along the stem (in older stages) and their early appearance (before the palisododermium) would appear to suggest the first supposition, but when the hymenidermium (the cells of which become more or less cubical) is well-established, they continue to appear.

(3) We observed the rupthymenial mode of gill-formation, but because of the poor condition of the material, this conclusion is somewhat questionable.

DISCUSSION

THE SEQUENCE OF DEVELOPMENT

The sequence of the development of the parts is one of the most remarkable features of carpophore development in Agaricales. On the basis of an analysis of several hundreds of species, in 1963 we made up a scheme of various sequences in the earliest phases of development. Nevertheless, the number of species investigated appeared to be insufficient to determine exactly the systematic value of these phenomena. At first, we thought that differences in sequence were significant only for larger groups, as we found concentrated forms with reversed sequences of development only in well-defined, highly evolved sections of the system. But exceptions were encountered, as Singer (*1975*: 28–29) states in his 'Agaricales in Modern Taxonomy'. Since then, we have considered the subject several times (Reijnders, *1974a*: 363; *1975*: 308, 309; *1979a*: 345–346), and it is especially in the context of this investigation into many species of *Coprinus* that we can focus on this problem with greater precision.

It is obvious that all species of this genus have a concentrated development: in general, and under normal conditions, the primordia remain short and wide for a long time. Nevertheless, external factors seem to have a great influence upon the shape of the young primordium. A lack of light causes the primordia to become extended (etiolated), yet it may be admitted that such environmental factors affect the sequence of development far less, as we have stated, for example, in *C. stercorarius* (Reijnders, *1948*).

Examining the very young primordia of *Coprinus* (the dimensions of which amounted to only some tenths of a mm.), we frequently encountered somewhat confusing structures, which might have resulted in some erroneous interpretations. In this initial phase, the hyphae most often run in a longitudinal direction, so the primordia must be considered stipitocarpous, and this mode does not occur in concentrated types. In reality, the longitudinal hyphae in the earliest stages of *Coprinus* indicate something quite different from what they do in the primordia of the unquestionable stipitocarpous types: in the latter slender primordia, they curve outward at the tip to form the pileus which is continuous with the stipe. When we carefully observe the longitudinal hyphae in the initial phases of *Coprinus*, we always find in the upper portion more or less interwoven hyphae—or, when this is not the case, a meristemoid, i.e. a zone where the longitudinal hyphae are divided into isodiametric cells which increase rapidly.

Furthermore, the time factor interferes with these processes. We are obliged to draw our conclusions from series of fixed images, so it is difficult to estimate the speed of these processes. The primordia of *Clitocybe*, *Tricholoma*, *Hygrophorus*, etc., being composed of a slender stalk, remain stipitocarpous for a long time; in those of *Coprinus*, the phase with longitudinal hyphae is soon succeeded by the isocarpous state, which seems to be the real starting point for the development of the parts. So the longitudinal hyphae in the first stages of *Coprinus* (and this will probably also be the case in some other genera of Agaricales) are merely uninflated protenchymatic hyphae which are not interwoven, and here they cannot be considered indicative of beginning stem development. We have, therefore, classed these species with the pileostipitocarpous ones; when we do not have the youngest stages at our disposal for study, we arrive at the somewhat questionable conclusion that these species are isocarpous.

We found only one exception: the pileocarpy of *Coprinus brassicae*. In the description of the species and in the phylogenetic considerations we paid some attention to this phenomenon which up to now seems isolated. We should also take into consideration the possibility that pileocarpy can be close to isocarpy, while in other cases pileocarpy means a quite different sequence of development. Here the time factor is again significant; it is the appearance of stem-, cap-, and hymenophore-rudiments which tips the scale (cf., Singer *1975*: 29, on *Psathyrella pyrotricha*).

DEVELOPMENT OF THE HYMENOPHORE

According to the investigations of Atkinson and his school, the origin of the hymenophore seems to be a rather consistent process in Agaricales. Atkinson (*1914b*) recognizes only one exception: the gill formation in *Amanita*, which we called the schizohymenial mode. However, since Levine (*1914*) described another deviation in *Coprinus micaceus* and afterwards (*1922*) in *Agaricus* and some other Coprini, this question has become a controversial one and has been strongly contested by Atkinson (*1916*). Kühner (*1928*), who at first adopted Levine's view, described a somewhat intermediate mode in *Coprinus disseminatus*; Chow (*1934*) agreed with Atkinson for quite a number of species, although in our opinion his observations cannot be exact in all cases, and his descriptions and representations are not convincing. We dealt with the history of these opinions already in an previous article (Reijnders, *1948*: 266–277). It is not necessary to recapitulate the implications of this question (cf., Reijnders, *1963*: 247–248), but, after many comparisons, we think we better understand the complicated nature of these elusive structures now.

The existence of a conspicuous mode is undeniable. It can be demonstrated in series of tangential sections from the axis toward the periphery, where, in all these sections, the palisade hyphae (the first hymenial elements) show up as groups, alternating with lighter staining bands of sterile tissue. In reality, these are horizontal, radiating stripes, alternating with sterile tissue. We met this most typical form of rupthymenial development earlier in *Coprinus ephemerus* (Reijnders, *1948*: pl. 12 fig. 64) and in *C. stellatus* (at that time erroneously called *C. miser*; Reijnders, *1948*: pl. 13 fig. 69, 71). The groups of palisade hyphae soon become arched (cf., Fig. 30, *Coprinus flocculosus*; Fig. 52, *C. hexagonosporus*). A less obvious expression of this mode exists when the sterile interspaces are narrow and we see somewhat arched groups of palisade hyphae which almost touch each other (Fig. 39, 40, *C. macrocephalus*).

Another modification which seems to occur rather frequently is caused by the very early action of the gill-trama. For a short time, there is a continuous layer of palisade hyphae, but almost simultaneously, growth in the trama of the arising gill folds begins, pushing the palisade hyphae sideways. This development begins near the centre and is directed outwards (Fig. 6, *C. phaeosporus*). Kühner (*1928*) described this process in *C. disseminatus*; it is evident that in this case, a peripheral continuous layer of palisade hyphae will often be found, while the sections nearer the centre show the rupthymenial structure.

Finally, cases can be found where the layer of the palisade hyphae is interrupted only here and there, in an irregular manner (Fig. 35, *C. macrorhizus*). These unexpected interruptions seem not to be very rare; we met with such structures earlier, e.g. in *C. radians* (Reijnders, *1952*: pl. 22 fig. 4). All these modifications occur, and we are not well informed as to the variation of these phenomena in a single species: these facts may at least partly explain the controversial opinions on this question.

Apart from the fact that the first palisades develop between the protenchymatic hyphae which are continuous with the tissue underneath (the gill cavity is therefore often traversed by such fringed elements (e.g. Reijnders, *1952*: pl. 7 fig. 5, *Tricholoma focale*), connecting elements in the spaces between the rupthymenial hymenophore are quite obvious. So we find from the beginning some hyphae which run from the lipsanenchyma over and into the young gill-trama. As we stated before, the hyphae in the initial phases of *Coprinus* often run in a longitudinal direction, such hyphae can be found which pass into the gill-trama (Fig. 41, *C. macrocephalus*). In most species of *Coprinus*, if not in all, the edge of the gills (primary lamellae) remains open for a long time during development. Some authors (Atkinson, *1916*: 123, 124) believe that this opening of the gill edge is due to pressure exerted against the stem. This cannot be the case, however. We analyzed hundreds of sections with such structures, and only in a few exceptions could we find a disposition that could be explained by pressure (Fig. 13 *C. brassicae*). Usually, the tissues of the gill trama and the lipsanenchyma seem to be stretched out locally by the tension caused by the growth processes of the primordium (Fig. 7, *C. phaeosporus*; Fig. 24, *C. poliomallus*; Fig. 41, *C. macrocephalus*). We encountered the same facts in other species with a rupthymenial development (Reijnders, *1952*: pl. 16 fig. 3–5, *Bolbitius vitellinus*). We believe that the wide, open gill edge in *Coprinus* represents an efficient adaptation: it may explain the parallel faces of the lamellae in *Coprinus*. However, the secondary gills or lamellulae have an edge surrounded by hymenial elements and, in primordia, they are wedge-shaped, as in other Agaricales. Moreover, the open gill edge is necessary for the further joining of stipe and lamellae.

Atkinson (*1916*), as well as Kühner (*1928*) and Chow (*1934*), observed the fact that soon after their origin, the lamellae become attached to the stipe. This involves a situation in which hyphae grow out from the gill-trama into the lipsanenchyma. An extension of the gill-trama with no bordering elements of the hymenium was encountered in several cases (Reijnders, *1963*: pl. 17 fig. 6, *Tricholomopsis rutilans; 1971*: pl. 2 fig. 6a–c, *Agrocybe aegerita*); it appears to be quite common in *Coprinus*.

As a rule, the lipsanenchyma itself does not increase significantly (e.g. by intercalary growth) in this genus. This might explain why these species, discounting a few exceptions, have no ring. But the sometimes scanty lipsanenchyma is a bit reinforced by hyphae coming from the gill-trama. This process serves to fix the lamellae to the stem. When this has happened and the primordium is surrounded by a universal veil, it is sufficiently protected, for example against drought (evaporation). We mentioned the extension of the lipsanenchyma and the connections between lamellae and stipe for each species separately in Table I. We photographed such connections in Fig. 7 (*C. phaeosporus*), Fig. 13 (*C. brassicae*), and Fig. 26 (*C. poliomallus*). The passing hyphae have been photographed once more under higher magnification in a younger stage of the latter species (Figs. 24, 25). This photomicrograph might demonstrate a striking case of cells of the same hyphae, which have differentiated into other forms where they have been influenced by various developmental factors: the cells of the lipsanenchyma are larger and nearly isodiametric (cf. Reijnders, *1963*: 277–278).

VEIL AND PILEIPELLIS

The great variation in the veils in *Coprinus* gives us an excellent opportunity to deal once more with the 'cortical layers' in general, particularly in view of the difference between universal veil and pileipellis. Recent descriptions of pelles have demonstrated clearly that this important distinction has not been observed everywhere, probably because a determination of the universal veil is somewhat hazardous in mature specimens. So we will first treat the modifications of the veils in *Coprinus*, and consider afterwards the differences between veil and pileipellis and questions of terminology.

Many *Coprinus* species have a well-developed universal veil, while in others this veil is lacking. A lipsanenchyma is present, except in *Coprinus plicatilis*, which has no veil at all. As a consequence, most *Coprinus* species are bivelangiocarpous; if one does not take into consideration the same peculiar hairs which are present on the cap as well as on the stipe, the *Setulosi* are paravelangiocarpous, and *Coprinus plicatilis* is gymnangiocarpous. As we stated before, the lipsanenchyma is in most cases not very voluminous, but the gills are attached to it. Our comparisons of hundreds of species has led us to the conclusion that the protenchymatic veil, consisting of generative hyphae, is the most primitive and the extending lipsanenchyma often remains for a longer time in this condition (Reijnders *1963*: 224–232, 351–352). We found the most undifferentiated veil in this genus in *C. brassicae*. We shall comment only on some questions concerning the modifications of the universal veil which are useful for the survey: the details for each species are dealt with separately in Table I.

First, one encounters the problem of the protenchymatic tissue, which partly constitutes the universal veil, but in the beginning, it is not separated from the pileus-trama. A wide zone of protenchymatic tissue between the developing cap and the veil has been described in many species. After the downward growth of the hyphae of the cap-trama has become evident, there is a clear demarcation between these tissues in the lateral portion of the pileus, but in the centre they remain continuous for a long time. Nevertheless, a distal zone of this protenchyma belongs to the veil and takes part in its further differentiation; as it also envelops the pileus-margin or the point where the hymenophore will appear, it must be considered a universal veil. It also happens that such a zone does not exist; in very early stages, the pileus surface is present immediately under radiating hyphae and at the contour of the pileus a meristemoid develops.

The universal veil is subject to some characteristic transformations in *Coprinus*, including the formation of chains of long, wide cells, a dichophysoid structure, spherocysts, and isolated hairs. The spherocysts arise scattered throughout the protenchymatic layer of the veil, but they can also be arranged into chains, formed by a meristemoid. We notice that only in the *stercorarius* group and some other species spherocysts are lacking over the stem: this is one case of a peculiar differentiation of the veil over the pileus (see below).

We are inclined to consider isolated hairs, which are present over the cap as well as along the stipe, to be a transformation of the veil as well. Sometimes, these are visible in the veil itself without being connected to the underlying tissue (Reijnders, *1952*: Pl. 19 fig. 5, Pl. 20 fig. 2, *Psathyrella multipedata*; Fig. 49, *C. hexagonosporus*, etc.). In most cases, they arise between the cells of the pileipellis, and then it becomes interesting to determine whether or not these hairs of later origin have quite the same shape as those of the universal veil. Indeed, such hairs, with their specialized appearance, cannot represent the first stages of universal veil development. We met with such features when the young primordium was encircled by a few protenchymatic threads, having an innate veil (e.g. Reijnders, *1948*: Pl. 8 fig. 35–37, *Alnicola melinoides;* Reijnders, *1963*: Pl. 34 fig. 3–6, *Hypholoma elongatipes* Peck, as *Nematoloma polytrichi*) and when it was surrounded by outward-growing generative hyphae, we encountered an emanated veil (Reijnders, *1948*: Pl. 18 fig. 101, 102, *Gomphideus roseus*; Pl. 22 fig. 129–133, *Strobilomyces floccopus*). These are examples of very primitive veils, as the evolution of the veil has not started with the formation of isolated, particular hairs. Nevertheless, an interpretation of their nature becomes somewhat confusing when we find the same hairs arising abundantly afterwards amid the palisades of the pileipellis. Many authors have called them pilocystidia.

Above, we mentioned the fact that spherocysts are sometimes present only in the veil over the cap: this is one of the instances in which influences from the developing pileus interfere with structures in the veil. As this phenomenon seems to be rather rare in Agaricales, it is easily passed over. It may, however, once more corraborate the conclusion that the development of structures in agaric fruit bodies is locally determined (Reijnders *1963:* 277–278; Reijnders *1975*: 309, *Chamaemyces fracidus;* Reijnders, *1979b*, *Limacella glioderma*). However, even if some structures exist which seem to make the distinction between the universal veil and pileipellis somewhat indefinite (our schemes are seldom adequate to account for all modifications in nature), we should always be careful not to confuse these notions: the veil and the pileipellis are essentially different structures. We analyzed these questions in our book in 1963: the universal veil shows up in the youngest stages and is characteristic for the primordium as a whole; the pileipellis originates later on and is restricted to the pileus. The first mentioned organ sometimes increases considerably, serving the purpose of protecting the developing carpophore, the pileipellis forms a roof only over the mature cap, and its function is in accordance with this fact. Nevertheless, in mature carpophores, the remnants of the universal veil cannot be easily distinguished from the pileipellis. This fact might be of paramount importance.

Two recent publications (Bresinsky & Schwarzer, *1969;* Watling & Largent, *1976*), Singer's (*1975:* 60–69) detailed account, and the problems of nomenclature which are urgent here lead us to make some observations. Although the authors of these publications emphasize the importance of this distinction, only in the second are misinterpretations absent. The opinion of Bresinsky & Schwarzer that the veil has to be considered 'funktionell und ontogenetisch als Schicht des Hutes' is erroneous (see Reijnders, *1963*: 13, 14, 224). The universal veil has been treated as equivalent to pileipellis structures, e.g. in fig. 5 (*Cortinarius*), fig. 6 (*Rozites*), figs. 7, 8 (*Hypholoma*), fig. 22 (*Naucoria*), fig. 23 (*Phaeolepiota*), figs. 24, 29 (*Lepiota*), etc. The covering of *Amanita* and *Phaeolepiota* is not an epithelium but a universal veil (Singer, *1975*: 62). The dichophysoid structure in the *Coprinus* sect. *Alachuani*, is relative to the universal veil, not to the pileipellis, etc.

As we stated above, it is not always easy to determine whether we are dealing with the universal veil or with the pileipellis in mature carpophores. But we suppose that some authors could strive for greater accuracy here. When scattered, repent, narrow hyphae are encountered over the cap, one should be very careful about their interpretation, and the same applies to all kinds of spherocysts, loose or coherent (for the cells of the hymenidermium are mostly cubic). Finally, a great number of genera has been examined ontogenetically, exact descriptions of these developments have been published since Atkinson's times, and monographers studying genera or anatomists examining pileipellis structures should use these data. Furthermore, one can profit by including very young specimens (not necessarily primordia) in the examination; the nature of the universal veil may often be determined by freehand sections of the outer portion of the pileus margin, also in fresh material.

The diverse modifications and the corresponding terminology of pileipellis formation have been thoroughly analyzed in Watling and Largent's paper, and we agree with their conclusions in every respect. As the homology of the pileipellis layers can as yet be established only in genera with closely related species, it is reasonable to distinguish structural and topographical modifications and to create two series of names for them. As for the terms which denote morphological differences, we adopted Lohwag's terminology in our book in 1963, as many authors have done (e.g. Singer). As it may be superfluous to repeat all the definitions, the names in question are: 'trichodermium', 'palisadodermium' ('hymenodermium'), 'epithelium', 'cutis' and 'cortex'. We note that only the difference between palisadodermium and hymenodermium is somewhat arbitrary: we called that layer with greatly inflated cells which become cubic in the end the hymenodermium. We use the term 'epithelium' in the same sense as Singer: a pluristratous complex of isodiametric cells (definitely excluding the spherocysts of the veil). We prefer the term 'cortex' to Singer's 'dense layer'; a cortex is merely a condensation of the unaltered underlying hyphae. The cortex represents the transition to the complete absence of the pileipellis, so we must often refer to the periclinal hyphae of the outer zone of the pileus-trama (under the veil) as a cortex. There may be no differentiation and we find such hyphae often at the periphery of the stem as well. As the terms 'dermium' and 'cutis' have been used to designate morphological differences, we agree with Watling and Largent that it is highly confusing to use them in compound words in order to describe topographical layers. It is far better to apply to the latter category the terms proposed by Bas (*1969*).

PHYLOGENETIC CONSIDERATIONS

Although phylogenetic hypotheses are seldom satisfactory in mycology, one can scarcely avoid, when examining a series of morphological structures, attempting to imagine how one could have developed out of another. When doing this, however, one has to be well aware of the fact that present forms can seldom be derived from other, still extant, ones; it is better to consider which of the attributes can be considered primitive and which specialised, and then to try to find a modern species that shows many of the primitive characteristics. In this manner, one can more or less imagine the course of evolution.

As far as the structures which we have dealt with are concerned, in the interest of attempting to decide which are primitive and which have developed further, we make the following assumptions.—

(1) We consider the generative hyphae, which combine to form the protenchyma, more original than all the cells which developed therefrom. Inflated cells can in any case be considered characteristic of evolution, and this is especially true of certain types, such as palisades, spherocysts, pseudo-paraphyses, etc. There are certain groups of carpophores (e.g., *Mycena*,

TABLE I

Developmental anatomy of *Coprinus*

species	succession	origin of the hymenophore	universal veil, lipsanenchyma	pileipellis
Coprinus phaeosporus Karst.	the youngest stage available ($567 \times 529\ \mu m$) is isocarpous; young prim. wide and short	somewhat rupthymenial (by the activity of the young lam. tr. the groups of palisade-hyphae are pushed apart); gill-edge open; connections gill-tr. and lipsanenchyma evident	u. v. consisting of a wide protenchymatic zone and a layer of radiating threads becoming dichophysoid at the periphery. Lips. rather abundant, somewhat reinforced by h. coming from lam. tr.	none; the h. of the pileus-tr. merge into the prot. zone of the u. v.
Coprinus brassicae Peck	pileocarpous; young prim. wide and short	levhymenial; gill-edge open from the outset; connections evident	u. v. a wide zone of protenchyma, only slightly altered at the periphery in older stages; lips. rather abundant, reinforced by h. from lam. tr.	none; as in the preceding species
Coprinus niveus (Pers. ex Fr.) Fr. R., *1948*	pileo-stipitocarpous, soon isocarpous; young prim. slender	levhymenial; gill-edge also in older stages for the greater part surrounded by cells of the hymenium	a large zone of protenchyma remains outside the cap; in this tissue spherocysts arise by inflation of cells; short rows are present only in older stages; lips. rather abundant	none; also in older stages the tissue of the pil. tr. merges into the outer prot. zone; spherocysts over the cap only
Coprinus stercorarius Bull. ex St-Amans) Fr. Brefeld, *1877*; Levine, *1922*; R., *1948*	pileo-stipitocarpous, soon isocarpous	levhymenial; gill-edge open in later stages, at first surrounded by hymenial cells	protenchymatic zone over the cap less extensive, with radiating threads, but in young stages spherocysts not in rows; lips. rather abundant	in older stages the upper surface of the cap is delimited by short cells, a sort of epithelium, but outward they pass into the isodiametric elements of the veil; spherocysts over the cap only

Coprinus narcoticus (Batsch ex Fr.) Fr. R., *1963*	unknown	unknown	a wide zone of protenchyma over the cap, at the outside radiating threads with short rows of spherocysts	in the etiolated specimen which has been examined the tissue of the pil. tr. is continuous with the protenchyma of the u.v.; spherocysts over the cap only
Coprinus patouillardii Quél.	pileo-stipitocarpous	at first the layer of palisade hyphae is continuous but soon afterwards there are arches, probably by the activity of the young lam. tr. — a tendency towards a rupthymenial mode	over a narrow protenchymatic zone surrounding the cap there is a close layer of isodiametric cells; the veil along the stem (also short cells) is somewhat different; lips. scanty	finally the whole veil is divided into cells which inwardly are not well delimited from the peripheral layers of the pil. tr. which forms an epithelium; spherocysts over the cap only
Coprinus bulbillosus Pat. Chow, *1934* (as *C. hendersonii*)	stipitocarpous or pileo-stipitocarpous, probably soon isocarpous	levhymenial; in a later stage: 'les arêtes des feuillets se soudent au pied'	the description of Chow is not clear; probably there are isodiametric elements at the outside of the u. v. and a prot. layer within, the latter grown together with the pil. tr.; lips. abundant	'Le chapeau ne présente pas un revêtement différencié à sa surface'
Coprinus cortinatus Lange R., *1952* (as *C. roris*)	not well known	levhymenial; edge of gills also in later stages not open and surrounded by cells of the hymenium	a wide zone of prot. around the cap and an outer layer with spherocysts or oblong cells, which are absent along the stipe; lips. rather abundant	an epithelium, at last not well demarcated from the veil
Coprinus cubensis Berk. & Curt. Johnson, *1941*	'Stipe, pilear, and hymenial primordia have almost simultaneous origin.'	levhymenial; (structures as described by Levine occur in abnormal buttons?); gill-edge afterwards open: 'loosely attached to the stipe'	the layer of prot. over the cap appears to be thin or absent according to the photographs; lips. not mentioned	'a single layer of highly differentiated cells is formed just below the upper blematogen'

TABLE I (cont.)

species	succession	origin of the hymenophore	universal veil, lipsanenchyma	pileipellis
Coprinus poliomallus Romagn.	pileo-stipitocarpous, soon isocarpous	a tendency to the rupthymenial mode; by the activity of the young lam. tr. the palisades which arise at the same time are pushed apart (arches); gill-edges open; connections from the beginning	there is practically no layer of prot. underneath the radiating h. forming the spherocysts, also occurring along the stipe; lips. consisting of longitudinal h.	in later stages there is an epithelium, the upper layer well differentiated and made up of cubic cells (somewhat hymeniform)
Coprinus flocculosis DC. ex Fr.	pileo-stipitocarpous, soon isocarpous; a portion with small isodiametric cells over the longitudinal h. of the stem rudiment	rupthymenial; palisade-h. in isolated groups from the beginning; edge of lam. open from the beginning	there is a wide zone of protenchymatic h. over the cap and an outer portion of radiating h., which widen gradually (without spherocysts), the prot. later divided into short cells and less evident along the stipe; lips. scanty	a palisadodermium also in later stages (width 3.5 mm). the palisades arise already when the prim. has a width of *c.* 900 μm
Coprinus radians Desm. R., *1952*	pileo-stipitocarpous, soon isocarpous	rupthymenial	prot. zone over the cap narrow, disappearing in more advanced stages; the outer part of the veil consisting of radiating rows of spherocysts, also present along the stem; lips. scanty	a palisadodermium (also in 3 mm wide prim.) developing centrifugally at the pileus margin and centripetally over the centre
Coprinus micaceus (Bull. ex Fr.) Fr. Levine, *1914*; Atkinson, *1916*	pileo-stipitocarpous, soon isocarpous	rupthymenial (denied by Chow, *1934*); gill-edge open; connections in later stages admitted by Atkinson	u. v. and lips. as in the preceding species	a palisadodermium already present in young stages (width ±400 μm

	centre longitudinal; the upper portion is a meristemoid	of ordinary prot.; tendency towards the rupthymenial mode; gill-edge open; connections present	spicuous over the cap-centre); somewhat later a veil-meristemoid is formed at the surface of the cap; lips. made up of ascending h.	ards the adjacent cells of the veil
Coprinus macrocephalus Berk.	pileo-stipitocarpous, soon isocarpous	somewhat rupthymenial; isolated arches of palisades really present; edge of gills open; hyphae of the lips. merge into the lam. tr.	as in the preceding species; u. v. in later stages luxuriant over the cap, reduced along the stem; lips. consisting of ascending h. of small cells	none
Coprinus lagopus (Fr.) Fr. Chow, *1934*	'Le prim. du chapeau commence à se différencier tardivement par rapport au développement du pied.'	levhymenial; gills in a later stage connected with the stipe	u. v. presumably as in the preceding species	none
Coprinus comatus (Müller ex Fr.) S. F. Gray Atk., *1916*	probably pileo-stipito-carpous, soon isocarpous	levhymenial; after having grown across a wide gill-cavity the edges of the gills press against the stem (?), open and some elements interweave with the lips.	'An outer zone of radiating threads ('blematogen') remains 'concrete' with the pileus; lips. present	none
Coprinus atramentarius (Bull. ex Fr.) Fr. Atk., *1916*	youngest stages not studied 'Fundament of pileus present in the earliest stages'	with slight tendency towards rupthymenial structures; later on the gills become attached to the plectenchyma surroundig the stem	an outer zone of radiating h. remains concrete with the pileus; lips. as in the preceding species, probably abundant	none
Coprinus auricomus Pat. R., *1974*	the palisade hyphae of the hymenophore develop somewhat lately; by this phenomenon the species seems to be pileocarpous, but it is almost isocarpous	levhymenial; gill-edges soon open towards the stem; gill-trama connected with the lips.	the u. v. of repent h. has its greatest extension outside the cap margin; it consistst of long and thin yellow hairs, mainly along the stipe	a serried palisadodermium develops from a stage of about 300 μm wide (at the cap margin), it contains large yellow hairs with the walls thicker than those of the hairs in the veil

TABLE I (cont.)

species	succession	origin of the hymenophore	universal veil, lipsanenchyma	pileipellis
Coprinus curtus Kalch. s.s. J. Lange	the youngest stage available (height 160 μm, width 112 μm) is isocarpous	rupthymenial; only the most peripheral part of the layer of palisade hyphae can be continuous; gill edge wide open in later stages; as to the ripening of the spores see Descriptive Part	with an inner initially rather thick, protenchymatic layer and short rows of spherocysts at the outside; soon the radial arrangement of these rows is lost; lips. scanty	a palisadodermium already present in young prim.; the protoplasmic content is to be found in the upper part of the palisades, which afterwards become about cubical; most hairs arise between the cells of the dermium, a few also along the stem
Coprinus disseminatus (Pers. ex Fr.) S. F. Gray Kühner, *1929*	pileostipitocarpous, soon isocarpous	according to Kühner, in the initial stage levhymenial, but by the activity of the lam. tr. the palisades are pushed sidewards and form isolated arches; the gill trama becomes attached to the lips. and is open at later stages	as in the preceding species; protenchymatic part perhaps less wide; lips. scanty	a palisadodermium which becomes a hymenidermium, with large hairs arising between its cells
Coprinus hexagonosporus Joss.	in the youngest stage available the upper part of the prim. is occupied by a meristemoid; this may be a pileostipitocarpous structure, but soon the prim. is isocarpous	rupthymenial (from the beginning — a classical case)	the u. v. is not coherent even not in young prim.; with some scattered h., a few spherocysts, and vesiculose elements usually showing a long neck; these presumably empty elements are less frequent along the stem; lips. scanty	since a young stage a palisadodermium which becomes afterwards a hymenidermium; with characteristic dark staining clavate hairs arising between the cells of the dermium; the vesiculose cells of the veil mostly on the outside
Coprinus angulatus Peck (= *C. boudieri* Quél.)	pileostipitocarpous soon isocarpous (youngest stage	probably rupthymenial	the u. v. is not coherent and consists of scattered h.	a palisadodermium arising in a young stage (diam. 440

			which are present in the youngest stages; lips. present	much inflated later on (hymenidermium); many hairs present between the cells of the dermium
Coprinus ephemerus (Bull. ex Fr.) Fr. R., *1948*	at least isocarpous	rupthymenial; gill-edge in later stages wide open; some slight connections	the young u. v. does not cover the whole prim.; it consists of longitudinal h. which run along the stipe and the pileus margin, and of long vesiculose hairs with a tapering neck all around the prim.; lips. consisting of ascending h.	a palisadodermium with long hairs, similar to those of the veil, between the cells
Coprinus bisporus J. Lange Kühner, *1926*	unknown	rupthymenial	not described in detail	a palisadodermium present when young, with hairs between its cells
? *Coprinus stellatus* Bull. R., *1948*, *1963* erroneously called *C. miser*, because of the absence of pilocystidia in sections of many advanced primordia; cf. R., *1948*: 293–295)	the youngest stage available is isocarpous	rupthymenial; gill-edge open from the beginning	as in *C. ephemerus*; lips. rather scanty	a palisadodermium present from the youngest stages, with the cells soon inflated (hymenodermium), with numerous acuminate small hairs (length 30–40 μm) in young prim., almost disappearing with age
Coprinus plicatilis (Curt. ex Fr.) Fr. R., *1952*	at least isocarpous, possibly hymenocarpous (youngest stage 350 μm wide)	rupthymenial; gill-edge open from the beginning but no connections because lips. is absent	u. v. and lips. absent; gymnangiocarpous	a palisadodermium present from the youngest stages; the palisade-cells becoming large and strongly inflated

ABBREVIATIONS USED. –
Atk. = G. F. Atkinson
h. = hyphae
lam. tr. = trama of the gills
lips. = lipsanenchyma
pil. tr. = pileus trama
prim. = primordium
prot. = protenchyma
R. = A. F. M. Reijnders
u. v. = universal veil

Conocybe, Coprinus), in which the primordia are already distinguished by a dominant pseudoparenchymatic texture, and this may be considered an indication of specialisation.

(2) A universal veil with spherocysts is even more specialised than a veil consisting of long series of inflated cells.

(3) When the same kind of hairs is found over the cap and along the stem, this is considered a reduced and altered universal veil, and a characteristic of specialisation.

(4) A universal veil which no longer has a plectenchyma, but which is formed by a meristemoid, is more specialised.

(5) The simplest enclosure of the adjacent tissue of a carpophore is a condensation of this tissue, as can often be seen at the surface of the stem. This is called a cortex. A single cortex is also often found on the upper side of the cap in advanced primordia, despite the fact that in mature carpophores, it may have altered.

An epithelium, which consists of a few layers of somewhat isodiametric cells, is more evolved than a cortex, although the difference is not always easily seen in the case of a dense cortex in sections. There is also an epithelium with a clearly distinguishable outer layer, as in *Coprinus poliomallus*.

A palisadodermium is without question an even more specialised enclosure of the cap, the difference between a palisadodermium and a hymenidermium being minimal: we could consider the latter to be a palisadodermium with strongly inflated cells.

(6) As far as the sequence of the emergence of the first structures is concerned, it is not quite clear whether the pileocarpous structure is more evolved than the isocarpous one; the latter is certainly more highly developed than the pileo-stipitocarpous mode. For an exact definition of these terms, see the section on succession.

(7) Compared to the greater part of the Agaricales, the rupthymenial development of the hymenophore is a peculiarity which is seen only once in a while with very highly concentrated primordia. Usually, a continuous layer of palisade-hyphae is formed (levhymenial mode). There are, however, all kinds of transitional forms between these structures, and they are often present with *Coprinus* (see 'Origin of the hymenophore').

We will now try to apply these points of view to the facts of development of *Coprinus* species which are presently known and which have been presented in the table. We can start from the assumption that a species in *Corpinus* is primitive when it has a veil that remains protenchymatic, that is pileo-stipitocarpous (but soon to be isocarpous), levhymenial, and that does not have a differentiated pileipellis. Of those studied in this article, we will find no species that correspond exactly. Those species, however, which, according to Romagnesi, belong to the *Impexi*, and, according to Singer, to the *Alachuani*, come closest.

One could object that the wide veil which consists mainly of unchanged generative tissue, has a special texture in *C. phaeosporus* because of the radiating dichophysoid hyphae, and, further, that this species is more or less rupthymenial, whereas *C. brassicae* is the only species studied till now which shows a clear pileocarpous primordium. These facts cannot be denied, and they do detract somewhat from the plausibility of the hypothesis that the *Impexi* should be the most primitive Coprini. We have to realise, however, that the pileocarpous and isocarpous types appear to be close together (in some cases the former might even be more primitive than the latter) and that the rupthymenial development of *C. phaeosporus* is not the most explicit form of this structure.

In this connection, it is regrettable that the development of so few species of this group is known, but it is not always easy to find material. According to the descriptions in the 'Flore analytique', the veil can vary a great deal in this group.

Other groups that might come close to a primitive form are those of *Coprinus niveus* and *C. stercorarius* of the section Singer called *Cycloidei* Fr., and Kühner & Romagnesi termed *Vestiti* J. Lange. *Coprinus narcoticus* is probably linked to these species. These species are characterised by a thick layer of spherocysts over the cap, the function of which is not very well known, but which appears in different non-related genera (*Cystolepiota, Phaeolepiota, Phaeomarasmius,* etc.) among the Agaricales.

It is peculiar that these spherocysts in the species mentioned, form only over the cap and not along the stem, although they originate in the universal veil (see 'Veil and pileipellis'). If we consider a universal veil to be a tissue which surrounds part of the primordium or the complete primordium, but which, in any case, stretches along the pileus-margin, then this consists here of a wide band of protenchyma, in which the spherocysts develop in a rather irregular way. These spherocysts are pushed outside, but no chains develop.

Coprinus niveus and *C. stercorarius* do not have a differentiated pileipellis; the original protenchyma of the pileus-trama is confluent with the inner layer of the veil. These species are levhymenial.

In *C. patouillardii*, we find in the universal veil a thinner layer of protenchyma over the cap and, outside that, short chains of spherocysts, that, however, do not appear along the stem. In later stages, the upper part of the pileus consists of an epithelium, which is difficult to distinguish from the short cells belonging to the veil which has almost completely split into cells (Fig. 16, 17). This species shows rupthymenial structures, but we also found peripheral tangential sections with continuous layers of palisades (see 'Origin of the hymenophore'). *Coprinus cortinatus* is linked to *C. patouillardii*. In this case as well, no spherocysts form along the stem, and a thinner layer of protenchyma in the veil and, finally, an epithelium over the pileus appear. However, the species is probably levhymenial, which could be connected to the fact that we also found a closed edge of the lamellae in later stages (an exception!).

What appeared only in later stages in the last two species—i.e., that between pileus and veil a zone of cells appears that belongs partly to both tissues, we find with *C. poliomallus* from the beginning. Almost no plectenchyma appears in the veil here, the first spherocysts being formed in a very early stage (to a lesser extent also along the stem) and a meristemoid develops in which the cell divisions occur mainly in a radial direction, so that the spherocysts often range in chains. In later stages, there is an epithelium over the cap with an outer layer of one-cell thickness, and this layer can be distinguished from the other cells. This species also shows a more or less rupthymenial hymenophore (see Table I).

The species from the section, *Micacei* Fr., can be compared with *C. poliomallus*. *Coprinus radians* already has almost no plectenchyma over what will later become the demarcation line between pileus and veil. This zone is very narrow, and it forms radiating hyphae which divide into short cells out of which series of spherocysts originate. This tissue is possibly less a meristemoid than is the case with *C. poliomallus*. According to Atkinson's description (*1916*),

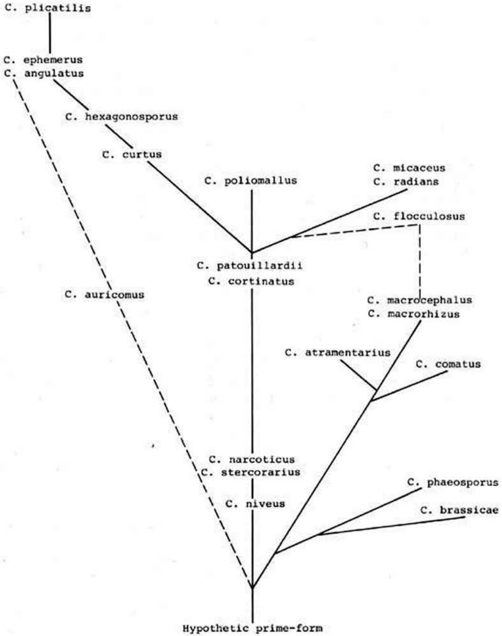

TABLE II

Possible interrelationships of *Coprinus*-species there is no plectenchyma present in the veil of *Coprinus micaceus*. Singer divided the *Micacei* into *Domestici* Sing., with filaments between spherocysts, and *Exannulati* Lange, where this is not the case. Both types have clearly rupthymenial structures, and the pileipellis is made up of a palisadodermium, which distinguishes the *Micacei* from the *Vestiti*. In the *Lanatuli* Fr. that have been studied up to the present, a meristemoid also plays a large part in creating the veil. In this way, these species can be compared with *C. poliomallus* as well. Virtually the entire trama of the very young pileus has been divided into cells in *C. macrorhizus* and *C. macrocephalus*. From the centre of this trama, radiating hyphae arise, which have already also divided into short cells. Later, the pileus-trama and the universal veil will separate because of the formation of a meristemoid at the juncture. This continues to form externally radiating filaments, the cells of which increase in breadth toward the surface. Very thin protenchymatic hyphae, growing downward, appear over the rim of the cap. No pileipellis is present. The strongly developed velum probably takes over the function of the pileipellis. The universal veil is highly specialised in these species, as far as its growth and development are concerned. There is a clear tendency toward the formation of a rupthymenial hymenophore in these species, although this structure is not present in its most conspicuous form. It has been claimed that *C. flocculosus* is an intermediate form of *Lanatuli* and *Micacei*. This is due to the structure of the veil, which will eventually consist of round and long elements (Kühner & Romagnesi, *1953*: 383). In earlier stages, there is quite a lot of protenchyma present in the veil as an inner layer; however, this soon divides into small isodiamatric cells. The veil is notably less radiating than in *Lanatuli*—at least in later stages. There are no real spherocysts present, although thin-walled, round elements do occur in the veil. The species has a well-developed palisadodermium and is clearly rupthymenial. It shows little similarity with *Lanatuli*, although it could be grouped with *Micacei* if one assumes that the spherocysts in this group have developed later. But if one assumes that in the course of evolution, spherocysts occurred even before the development of a palisadodermium (*C. poliomallus*), then the position of *C. flocculosus* remains somewhat enigmatic.

Singer (*1975*) divides the *Hemerobii* into three subsections: *Setulosi* Lange, *Auricomi* Sing., and *Glabri* Lange. Kühner & Romagnesi (1953) mention only *Setulosi* Lange and *Hemerobii* Fr. The first are divided into three groups, of which two, apart from peculiar hairs on the cap, have spherocysts as well.

There are three species of these *Setulosi* with spherocysts of which the development is known. *Coprinus curtus* has a universal veil from the beginning, with a protenchymatic inner layer and short series of spherocysts. Soon, however, the hyphae of this layer divide into round cells which become spherocysts, which are also present along the stipe. The number of spherocysts is much smaller than in, for example, the *Micacei*.

With these partly thick-walled and specialised spherocysts, the peculiar hairs which grow only more numerous in later stages, the strongly inflated palisadodermium, and a strongly pseudoparenchymatic texture, *C. curtis* is certainly a highly evolved form.

Probably *C. disseminatus* does not deviate from this very much. Judging by Kühner's figures (*1928*: pl. 1 fig. 1-8), protenchyma is present in the veil here as well, and on the outside of the veil and along the stipe, spherocysts occur. So these species, except for the dermium and the hairs, can very well be linked with certain *Vestiti*, although *C. patouillardii* has no spherocysts along the stipe.

The veil of *C. hexagonosporus* is different from the beginning. Besides some few spherocysts, we also find inflated elements with long, tapering necks here. The pilocystidia that occur later are different from these veil hairs. Because of the special nature of the veil, we can endorse the conclusion of M. Lange (*1952*: 110) in which he states: 'This species is probably the best link between the *Nudi* and *Farinosi*.'

We found these three species to be rupthymenial, although Kühner also draws a section with a continuous layer beside an interrupted one. Apart from that, *C. disseminatus* is of the type that becomes rupthymenial very quickly through the activity of the gill-trama.

The layer of spherocysts in the veil in these species is probably in a state of reduction, since *C. hexagonosporus* points to that conclusion. In this way, we could derive the *Nudi* among the *Setulosi* from this group with spherocysts. From a number of distinguishing characteristics, we can conclude that the *Setulosi* without spherocysts are a very specialised form.

We consider specialised hairs (pilocystidia, caulocystidia) that occur over the cap and along the stem as an altered universal veil and not as an initial phase (see 'Veil and pileipellis'). These species have all been provided with a palisado (hymeno)-dermium, and in this group one finds the typical rupthymenial formation of hymenophore with groups of palisade-hyphae occurring even before there is any growth in the trama of the lamellae. Here the remarkable thing is that deliquescence is often less strong or does not occur at all (*C. disseminatus*). According to M. Lange (*1952*: 108–130), deliquescence occurs in different degrees and is dependent on environmental factors. We are inclined to take the decreased deliquescence as a reduction: these small species with an often expanding cap do not need deliquescence. Although *C. heptemerus* deliquesces according to Lange, we had a culture of this species from Baarn, the well-developing fruit bodies of which did not deliquesce.

A somewhat amazing experience was discovering, in young primordia of *C. curtis*, that the initial ripening of spores occurred over the complete lamella. We have already mentioned the particulars in the description of this species. We could establish the same fact with very young specimens of *C. heptemerus* (cultivated). For these species, this disposes of the significant distinguishing peculiarity of inequihymeniferous fruit bodies, which is considered a characteristic of the genus. We also found that the initially formed spores were smaller than the ones which developed later (Clémençon, *1979*). Closer scrutiny of these smaller species could demonstrate that certain opinions concerning the genus *Coprinus* are generalizations.

Coprinus auricomus (Reijnders, *1974b*) occupies a very special position, which is not easily defined. Here the universal veil contains protenchyma, beside the known yellow-brown hairs which cover the greater part of the young primordia. It is notable that the bristle hairs which develop later in the pileipellis are larger and have a thicker wall than the original hairs in the veil. The species has a welldeveloped palisadodermium, but is levhymenial, and, in that respect, primitive.

It could be supposed that further reduction of the veil could have resulted in the origination of the *Nudi* (*Setulosi*) form types like *C. auricomus*. But we would rather derive this group from *Setulosi* with spherocysts via, for example, a type like *C. hexagonosporus*. It is quite possible that the numerically rich group of *Setulosi* without spherocysts is polyphyletic. Only a very exact knowledge of the development of a great number of species of this group could solve this problem.

The *Glabri* Lange or *Hemerobii* Fr. (sensu Fl. anal.) should also be considered. *Coprinus plicatilis* is the best-known representative of this small group. If we take the reduction hypothesis further, then this species (which has no veil at all) would stand for the final stage. There is neither universal veil nor lipsanenchyma. We called such forms gymnangiocarpous if the hymenophore has an endogenous origin. The palisadodermium occurs in an early stage and assumes huge proportions. The mature carpophore consists mainly of isodiametrical cells. The hymenophore is rupthymenial, although perhaps not in its most significant form. We unfortunately did not have a section of a primordium which was young enough to determine this exactly.

In Table II we have assembled the more or less probable relationships existing between sections and species of *Coprinus* discussed above; we are, however, very well aware of the fact that this table can only be approximate and incomplete because of the insufficient number of species studied, especially in the *Impexi* and in the *Setulosi*, and because of the difficulty in proving phylogenetic relationships.

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Résumé

Ce travail vise à approfondir notre connaissance des relations mutuelles d'espèces du genre *Coprinus* à l'aide de recherches ontogénétiques. La comparaison d'environ 27 espèces a mis à même l'auteur de préciser quelques critères du développement surtout en ce qui concerne la succession des structures initiales des parties principales du champignon, et l'origine rupthyméniale de l'hyménophore. La thèse que tous les Coprins sont du type inéquihyménifère est une généralisation inadmissible. Les variations dans les voiles et du piléipellis, si importantes pour la classification des espèces dans ce genre, ont été considérées intégralement; la terminologie générale des structures corticales, qui paraît être très confuse de nos jours, a été discutée en détail. Pour finir, l'auteur a essayé de dresser un schème des relations phylogénétiques dans le genre mais il faudrait la connaissance du développement d'un plus grand nombre d'espèces pour acquérir des résultats plus exacts dans ce domaine.

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P. D. Orton & R. Watling, *Coprinaceae Part 1: Coprinus*. *In* D. M. Henderson, P. D. Orton & R. Watling (editors) — British fungus flora—agarics and boleti **2** (H.M.S.O., Edinburgh, 1979) Pp. 149. Price: £ 12.

This long expected second part of the British fungus flora covers the genus *Coprinus*. Each of the 90 species is described and illustrated. Information about cultures and genetics is added. Taxa, only differing in the number of spores formed on a basidium, are treated as separate species. A key is provided for the determination of sections, stirps, and species.