

Contribution to the morphology, anatomy, and biology of *Lyophyllum palustre* and its relationships to *L. rancidum* and *Typhula phacorrhiza*

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The morphology and anatomy of the different parts of *Lyophyllum palustre*, *L. rancidum* and *Typhula phacorrhiza* were studied by light microscopy. Full details of the hyphal composition of hymenium and subhymenium, the morphology of the hyphae of the trama and cortical layers of the stipe and the pileus are described and illustrated with line drawings and microphotographs. The formation of the sclerotia of *Lyophyllum palustre* in pure culture and *Typhula phacorrhiza* has been analyzed. The combination of the following characteristics – primitive built hymenium and subhymenium without any cystidia, surface hyphae with non-structured hyphal outgrowths (“caulo- and dermatocystidia”), necrotrophic invasion in plants and the formation of sclerotia – has a systematic significance. Using these characteristics one can more easily define a natural relationship. The systematical value of siderophilic granulation is also discussed in detail. It is probable that a closer relationship than previously considered exists between *Lyophyllum* spp. and other white-spored Homobasidiomycetes, such as *Collybia pro parte* and *Typhula pro parte*.

In swamps the common, sphagnicolous *Lyophyllum palustre* fruits between the beginning of June and August. In comparison with other sphagnicolous fungi, *Lyophyllum palustre* has a wide ecological tolerance. It follows several species of the genus *Sphagnum* to quite different habitats, for example, moist forests (always with *Sphagnum*), overgrown ditches draining a moor and mesotrophic swamps. This species does not inhabit ombrotrophic swamps with hummocks; rather it prefers to grow together with *Sphagnum fallax* KLINGGR. (JAHN, 1964; EINHELLINGER, 1976; HAAS & KOST, 1985; KOST, 1988b; KOST & HAAS, 1989).

Mycologists have long since noticed that *Sphagnum* plants bleach out and are damaged in the presence of *Lyophyllum palustre* (FAVRE, 1939, 1948; LANGE, 1948; SMITH, 1949; EINHELLINGER, 1976; HAAS & KOST, 1985; SIMON, 1987; KOST & HAAS, 1989).

REDHEAD (1981) infected in vitro-cultivated *Sphagnum* plants with a culture of *Lyophyllum palustre*. After a short time the *Sphagnum* plants were dead. UNTIEDT & MÜLLER (1985) discovered a formation of secondary cell walls in infected *Sphagnum* cells. They inter-

puted this as a reaction of a living cell against the invasion of the parasite. Whereas all *Sphagnum* plants die after in vitro infection, in the natural habitat bleaching of *Sphagnum* plants occurs only locally (KOST, 1988a).

Examination of the morphology and anatomy of the fruiting body of *Lyophyllum palustre*, together with parallel studies of *Lyophyllum rancidum* (type species of Sect. *Tephrocycbe*) and *Typhula phacorrhiza* (type species of the genus *Typhula*), revealed certain common characteristics which point to a possible natural relationship between the three species, and which may help to find the correct systematic position of *Lyophyllum palustre*.

Material and methods

Fresh, as well as dried, material was studied by light microscopy as described by KOST (1978, 1981). The dried material was soaked in 10% KOH and stained with phloxine B, brilliant cresyl blue or cotton blue to intensify the contrast of the hyphal structure. For the analysis of some hyphae the sections were squashed to provide a thin layer of hyphae. The siderophilic granulation was confirmed by staining with acetocarmine in concentrated acetic acid.

Results and discussion

The morphological and anatomical studies of fruiting bodies have revealed characteristics, which can be used for a better systematic evaluation of the relationship between the studied *Lyophyllum* species within their genus and with some other genera.

The following characteristics seem to be important:

a) Structure of the hymenium and lamellae

- Only in the centre of the lamellae is the arrangement of the thin-walled hyphae typically regular. At the base between two lamellae the hyphae are interwoven (Figs. 3, 4, 11).
- A thin subhymenium of non-inflated, short cells, and not a typical thickening hymenium; subhymenial hyphae are weakly developed, intercalary or subseptally branching from the tramal hyphae forming basidia within a short distance (Figs. 3b, 4a, 8a, 14b).
- Basidia, unspecific type, clavate, sometimes pleurobasidial, forming four or more rarely two basidiospores. Basidiospore oval, colourless, smooth, thin-walled (Figs. 5c, 8d, 14b).

- No pleuro- or cheilocystidia, only some outwardly directed undifferentiated tramal hyphae, which are similar to those of the sterile parts of the fruiting body (Fig. 3b, 4a, 8a-c, 14b). Their apex shows occasional diverticulae or coral-like outgrowths (Fig. 4c).

The patterns of intercalarly branching hyphae in weakly developing subhymenia are not widespread within the agarics as far it is known. CORNER (1967) described very similar hyphal patterns in the hymenium of *Typhula phacorrhiza*, and included excellent line drawings. Apparently some *Typhula* species develop a thin subhymenium only; the basidia are borne immediately after branching from the tramal hyphae. Some basidia are pleurobasidial and aberrant ones cover the fertile edge of the lamellae. *Lyophyllum rancidum* forms a typical subhymenium on the side of the lamellae, but the simple type of subhymenium can be observed at the lamella-edge (Figs. 8a-c).

The region at the base of the lamellae is very sensitive to stretching: it is easy to peel off the lamellae, hence the name "lyo-phyllum". At the lamella-base of *Lyophyllum rancidum* a special layer marks the transition from pileal trama - which derives directly from the stipe trama - to the tramal hyphae of the lamellae. The direction of hyphal growth is changed in that area by spherically inflated elements. From these elements new hyphae branch off positive-geotropically, forming the trama of the lamellae.

In *Calocybe gambosa* (FR.) DONK and *Lyophyllum connatum* (SCHUM.: FR.) SING., on the other hand, a layer of densely packed, parallel and non-inflated hyphae exists in that area (KOST, unpublished data). The hyphal construction of *Calocybe gambosa* is very similar to that known for *Tricholoma* species (KOST, 1981).

b) Structure of the cortex hyphae

- All cortex hyphae have a similar morphology. The cylindrical, repent hyphae of the cutis are weakly inflated, have slightly thickened cell walls and form numerous anastomoses (Fig. 5a). They build a somewhat separate layer above the pileal trama (Figs. 5a, 9b-d).
- The surface hyphae have lateral, short finger- or coral-like outgrowths and branch off in the same intercalarly manner (Figs. 3a, 9a-d, 10b-c, 13a-d, 14a). In *Lyophyllum rancidum* some scattered hyphae arise from the cutis; only these terminal cells have thickened and intensely brown-pigmented cell walls (Fig. 9d).

- As the development of the fruiting body is gymnocarpic, all surface hyphae can be interpreted to be homologous.

In *Collybia* Sect. *Cirrhatae* SING., which is related to *Typhula* (OBERWINKLER, 1979), the cortical structure corresponds very well to this cortical type. The sterile cortex hyphae described above are also well known from some species of several genera, such as *Delicatula* FAYOD, *Hemimycena* SING., *Marasmiellus* MURR., *Mycena* (PERS.) ROUSSEL etc. In connexion with other characteristics the morphology of sterile surface hyphae should be considered more in defining systematical relationships.

c) Structure of the stipe trama

- In the trama of the small, slender fruiting bodies of *Typhula phacorrhiza* the hyphae are longitudinally arranged, not interwoven and strongly inflated (Fig. 13c). Locally some coiled and interlaced hyphae are pressed between them (Fig. 13d). The space between the hyphae is filled with water; there is no air space. A thin layer of firmly agglutinated hyphae with thicker walls covers the inner trama completely. The inner pressure caused by inflation of the hyphae stabilizes the slender fruiting body, functioning like a hydro-skeleton.

The same hyphal construction can be found in *Lyophyllum rancidum*:

- The trama of the stipe is built of two types of parallel, inflated hyphae: (i) strongly inflated, long (>100 μm) hyphae, (ii) thin or irregularly inflated hyphae varying in diameter (Figs. 10, 12). Scattered between the hyphae are small crystals. The small and slightly thickened hyphae of the cortical layer of the stipe are separated from the trama by thick-walled, agglutinated hyphal cells (Fig. 9a).

- The construction of the stipe of *Lyophyllum palustre* is similar but with simpler structure and that may be the reason for its fragility (Fig. 3a).

d) Sclerotia formation

Many phytopathogenic and crop-damaging fungal parasites (*Botrytis* spp., *Sclerotinia* spp., *Typhula* spp.) persist through unfavourable environmental conditions in the form of sclerotia. The definition of sclerotia is often used in the broad sense (LOHWAG, 1941), with which it was introduced by DE BARY (1887). When one considers the differences in function and the divergences between the species during their ontogeny, the classification of these organs (sclerotia, pseudosclerotia, transition sclerotia, bulbillae) seems to be artificial

(KENDRICK & WATLING, 1979). The systematical value of sclerotial formation is significant although sclerotia are analogously formed within very different taxa (BUTLER, 1966). The genus *Typhula* contains species, which strongly deviate in many characteristics, such as the morphology and anatomy of basidia, spore, cystidia, trama, and sclerotia. It seems obvious, therefore, that this genus is not a natural taxon.

The morphology of sclerotia of some *Typhula* species (BERTHIER, 1976) is very similar to that of *Lyophyllum palustre*. In two-week-old cultures, the hyphae grow and twist into conglomerations. The figures 6 a – c show the successive development of such coiled hyphal structures. These conglomerations are an early stages of sclerotia-like structure which consistently appear in the surface of the agar medium. The outer layer of the sclerotia is covered by large, inflated, isodiametric hyphal cells with thickened and brownish walls (Fig. 6d).

The inner hyphae are more elongated and filled with spherical vesicles (Fig. 6e). They are very similar to those observed at the base of the stipe (Fig. 4b). The in vitro formed sclerotia could be homologous to the swollen base of the stipe, because vesicle-containing hyphae exist in no other part of the fruiting body.

Using the developmental classification of sclerotia the *Lyophyllum*-sclerotium can be designated as a "loose type" (TOWNSEND & WILLETTS, 1954; WILLETTS, 1972). In *Lyophyllum*, the formation of sclerotia is in the early stages very similar to that observed in *Coprinus* PERS. by BREFELD (1877). It can be assumed that the same sclerotial structures of *Lyophyllum palustre* as those found in cultures are formed in nature under certain environmental conditions.

Sclerotia would be a useful adaptation to help *Lyophyllum palustre* survive the environmental conditions in a swamp with changing water supply. During drier periods this species would survive more easily with thick-walled sclerotia than with thin-walled simple hyphae (See WILLETTS, 1971; COLEY-SMITH & COOKE, 1971; CHET & HENIS, 1975). About sclerotia formation in *Lyophyllum rancidum* nothing is known.

e) Biology of *Lyophyllum*

The hyphae of *Lyophyllum palustre* (Fig. 7) penetrate living *Sphagnum* cells parasitically (UNTIEDT & MÜLLER, 1985; KOST, 1988a, 1988b). Aside from this primary lesion a secondary destructive effect is remarkable. While actual invasion of plant cells by hyphae can be observed at the basal living parts of the *Sphagnum* plants, which are embedded deeply in the boggy, moist peat, the upper parts of *Sphagnum* bleach out and die without actual penetration by hyphae. This kind of parasitism can be called necrotrophic (KOST, 1988b). Infection

studies in the natural habitat (KOST, 1988a) proved that the infection rate depends on high water level in the moor and proper moisture-content in the moss carpet.

It is possible that, like other fungi and bacteria, *Lyophyllum palustre* plays a part in the saprotrophic decomposition of dead *Sphagnum*. Only under special physiological conditions (i.e. increased consumption of substrate during the fruiting body formation) would the normally saprotrophic *Lyophyllum palustre* switch to parasitic existence.

The principles of this mode of life – necrotrophic parasitism – described here with regard to *Lyophyllum palustre* can be found in some *Typhula* spp., *Nyctalis* spp. and in the closely related *Collybia* spp. In combination with morphological characteristics it is an additional indicator for the taxonomic relationship of genera.

One would expect related species of *Lyophyllum palustre* to have a similar mode of life, most species of the genus seem to live only saprotrophically. *Lyophyllum rancidum* is considered to be a saprotrophic (lignicolous?) species on rich and chalky soil. Some species of the genus *Lyophyllum* have been thought to form ectomycorrhiza (MASUI, 1927; NORKRANS, 1950; VASILIKOV, 1955; SINGER, 1986), but these data need confirmation.

f) Systematic aspects

Until now the systematic position of *Lyophyllum palustre*, which appears in earlier lists as *Collybia leucomyosotis* LGE., is uncertain. This species has been placed in many different genera (SINGER, 1939; METROD, 1959; HORAK, 1968): *Collybia*, *Mycena*, *Prunulus*, *Tephrocycbe*, *Tephrophana* since the original description by PECK (*Agaricus paluster* PECK, 1872).

KÜHNER (1938) described a dark granulation [carminophilic or siderophilic granulation after CLÉMENÇON (1968)] in the basidia of some agarics after staining with a solution of acetocarmine in concentrated acetic acid. Because many species of the genus *Lyophyllum* KARSTEN possess this dark granulation, KÜHNER used it to redefine this genus and created a new tribe (Lyophylleae) within the Tricholomataceae (KÜHNER, 1938).

DONK (1962) replaced the genus *Tephrophana* EARLE, which had contained species with siderophilic granulation, with the new genus *Tephrocycbe*, because the selected type species of *Tephrophana*, *Collybia fimicola* EARLE, was found to be identical (SINGER, 1943) with *Marasmius albogriseus* (PECK) SING. a member of the *Marasmius* Section *Globulares* KÜHN. In the systems of agarics by KÜHNER (1980) and SINGER (1986) all species of *Tephrocycbe* are classified in the genus *Lyophyllum*.

JÜLICH (1981) without giving new information or detailed explanation changed the tribe Lyophylleae into two new taxa Lyophyllaceae JÜLICH (with the two genera *Lyophyllum* and *Calocybe*) and the monogeneric Nyctalidaceae JÜLICH.

These taxonomic changes were based on the hypothesis that the presence of siderophilic granulation could indicate natural relations within the agarics. CLÉMENÇON (1978, 1984) had already found siderophilic granulation not only in the cited genera, but also in *Agrocybe* FAYOD, *Calocybe* KÜHN. ex DONK, *Entoloma* (FR.) KUMM., *Hypsizygos* SINGER, *Lactarius* S.F. GRAY, *Lindtneria* PIL., *Lyophyllum* KARSTEN, *Melanoleuca* PAT., *Rhodocybe* MAIRE, *Russula* S.F. GRAY, *Termitomyces* HEIM, *Tylopilus* KARSTEN.

Such granules also recently have been found in basidia of *Mycenella magaritospora* LANGE (BAUER, pers. comm.). In order to preserve the taxonomic value of siderophilic granulation, CLÉMENÇON (1966, 1972, 1978) introduced a typology of that characteristic.

Because siderophilic granulation is scattered across quite different taxa of Basidiomycetes, it is absolutely necessary to define once again its systematic importance and taxonomic value if it has any at all. Information about the function and the chemical composition of the granules in the basidia is scant. The granules appear in very late stages of basidial development, especially in post-meiotic basidia.

While *Lyophyllum rancidum* has clearly visible granules, *L. palustre* produces only indistinct ones (CLÉMENÇON, 1968); on occasion, the granules seem to be altogether absent or difficult to detect (GRUND & MAAR, 1965). KÜHNER (1980) noted that the formation of siderophilic granulation coincides with a certain stainability of spore walls with carminic acetic acid. As the granules appear in the late phases of basidial development just before spore formation, there may be a correlation here. The stainable materials synthesized in granules could be chemical precursors of the spore wall material.

The morphological and anatomical characteristics between the species studied should be interpreted as significant indicators of a group of naturally related species. As the genera *Lyophyllum* and *Typhula* are composed of unrelated species, it seems apparent that the criteria for defining these genera (SINGER, 1986; BERTHIER, 1976) are misleading. However, this analysis and interpretation can only include the studied species of both genera.

SINGER (1986) and KÜHNER (1980) attempted to justify the genus *Lyophyllum* by stating that the heterogeneity of the genus shows the same nebulous systematical situation found in the genera *Cortinarius* S.F. GRAY and *Entoloma* (FR.) KUMM. This analogy is questionable, for it seems unreasonable to try to explain the hetero-

geneous composition of *Lyophyllum* using examples of such genera as in *Entoloma* and *Cortinarius*, which are themselves problematical.

Are there any characteristics – aside from the questionable siderophilic granulation – which hold the genus *Lyophyllum* together? It is beyond doubt that there are some naturally related groups of species which are now classed under the one genus *Lyophyllum*. Only an intensive monographic study of *Lyophyllum* can clarify these groups and their relationships. New data of morphology, anatomy and hyphal construction of fruiting bodies have been given as first steps toward a better systematic arrangement and classification within the present genus *Lyophyllum*. Moreover it is reasonable to recognize natural relations between certain species of the genera *Lyophyllum*, *Typhula* and *Collybia*.

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Fig. 1. *Lyophyllum palustre*. – a: section across the outer region of the stipe apex; in the short transitional zone (200–300 μm) between the sterile surface of stipe and the insertion of the fertile lamellae some solitary, aberrant basidia can be detected (bar = 20 μm). – b: habit of the fruiting bodies, $\frac{2}{3}$ of natural size.



Fig. 2. *Lyophyllum palustre*. – Section across the outer trama of the upper parts of the stipe, surface hyphae with some non-septate, shorter and coral-like outgrowths; hyphae of the inner trama strongly inflated, numerous anastomoses (bar = 20 μ m).

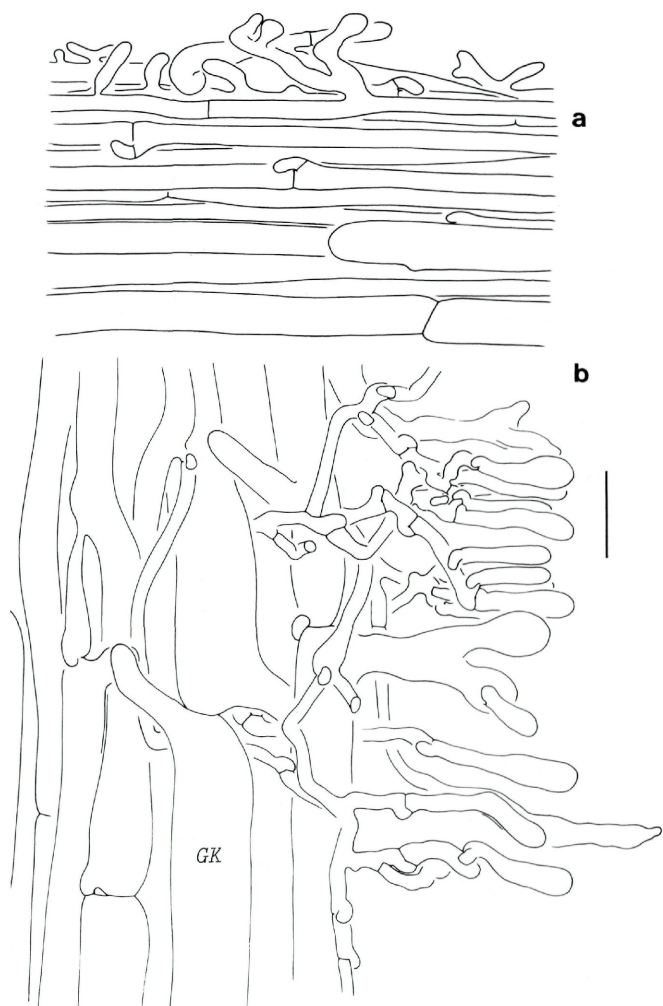


Fig. 3. *Lyophyllum palustre*. – a: surface of stipe near the base; long hair-like outgrowths. – b: section of hymenium and subhymenium; some sterile hyphae of the trama of lamellae intruding into the hymenium and ending as cystidia-like structures; trama of lamellae of parallel and inflated hyphae (bar = 20 μ m).

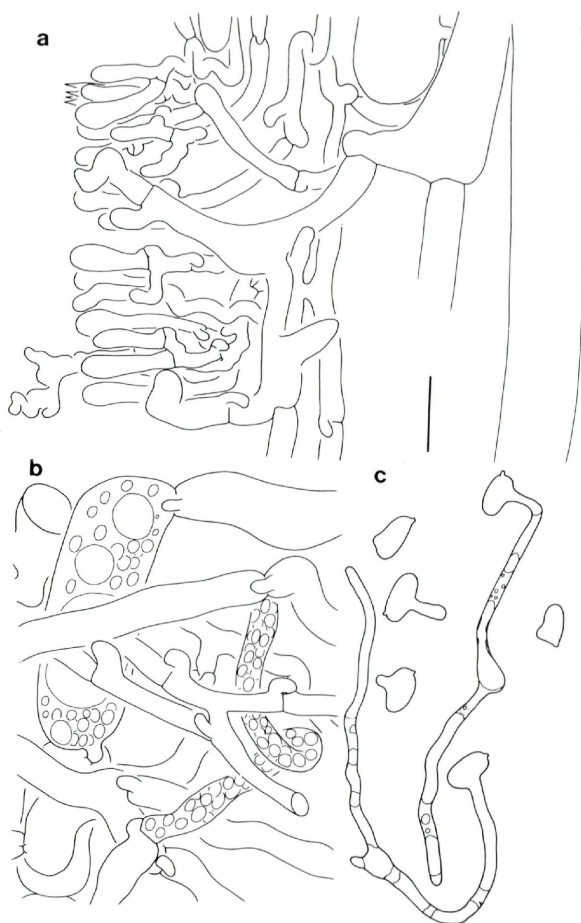


Fig. 4. *Lyophyllum palustre*. – a: section of the hymenium, subhymenium and trama of lamellae; some sterile hyphae intruding into the hymenium and end as cystidia-like structures, their apex shows occasional naps or coral-like outgrowths; trama of lamellae of parallel and strongly inflated hyphae. – b: base of stipe, two hyphal types: small, plasmatic hyphae interwoven by intensive vacuolate and inflated hyphae. – c: different stages of the germination of the spores. The germ tube can emerge anywhere on the spore, but it prefers the adaxial surface of the spore (bar = 20 μ m).

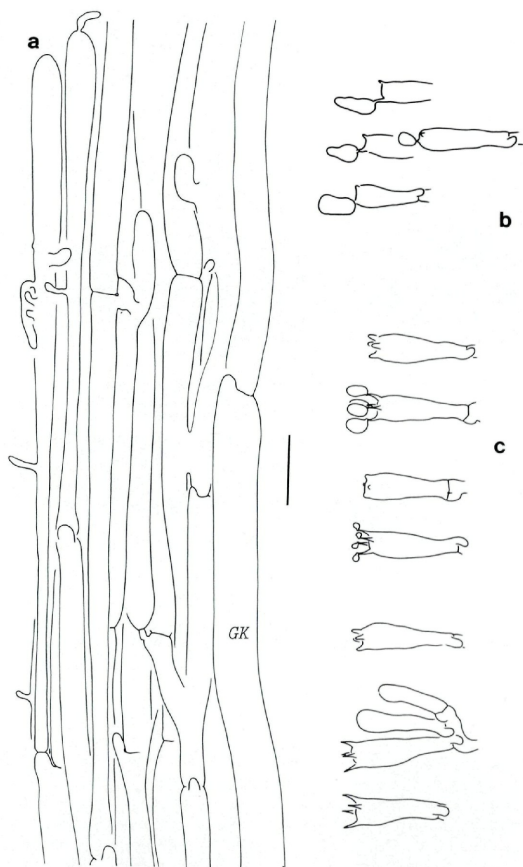


Fig. 5. *Lyophyllum palustre*. – a: repent hyphae of the cutis of the cap, surface hyphae with some irregularly shaped knobs and short outgrowths. – b: aberrant basidia ("gasteroid") after treatment with low temperature. At the apex of these basidia only one or two spores can be found. The morphology of the sterigmata on such basidia is atypical. Sometimes these atypical basidiospores are symmetrically attached at the sterigmata, like gasteroid spores. In some of the remaining basidia the spore formation is completely suppressed and a simple hypha grows out of the apex of the basidia. – c: different stages of development of the basidia. During maturation the small, clavate basidia apically enlarge slightly and form four or more rarely two basidiospores (bar = 20 μ m).

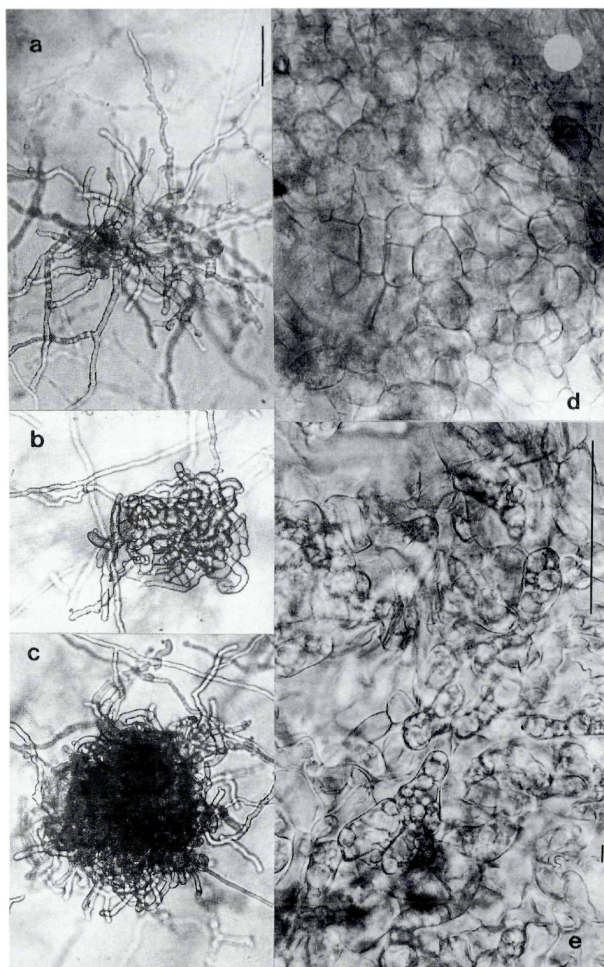


Fig. 6. *Lyophyllum palustre*. – a – c: development of the sclerotia starts with conglomerations of coiled, dikaryotic hyphae with clamp-connexions on solid agar medium. – d: the cortical layer of the sclerotia is covered by large, inflated, isodiametric hyphal cells with thickened and brownish walls. – e: the inner, more elongated hyphae of the sclerotium are filled with many spherical vesicles (bar = 20 μ m).

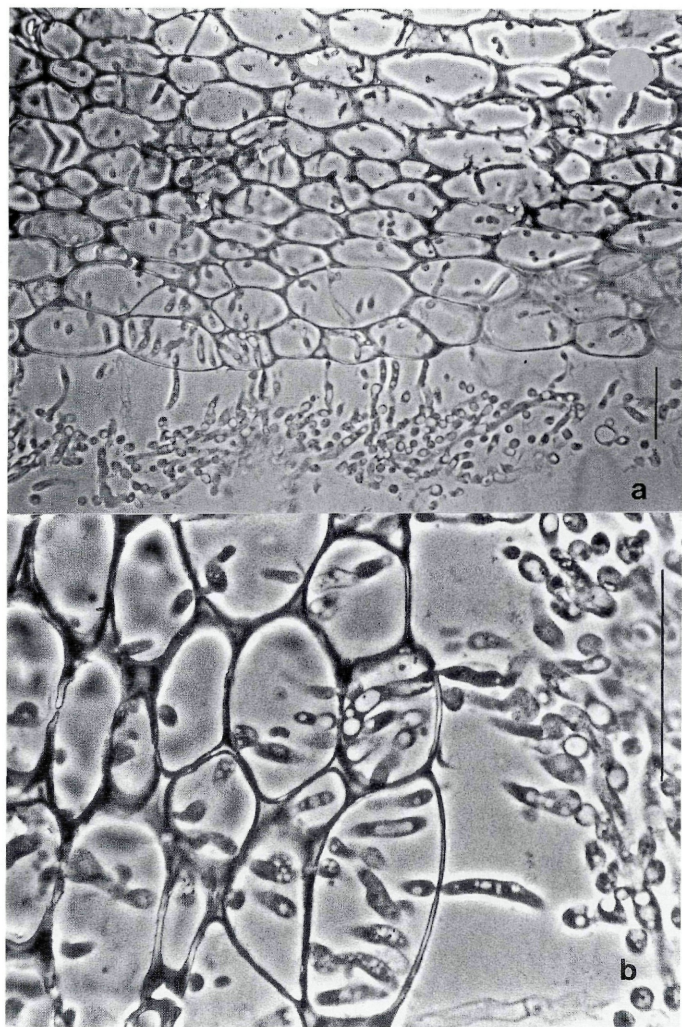


Fig. 7. *Lyophyllum palustre*. – a, b: penetration of the hyphal cells into the basal parts of the stem of the *Sphagnum* (bar = 20 μ m).

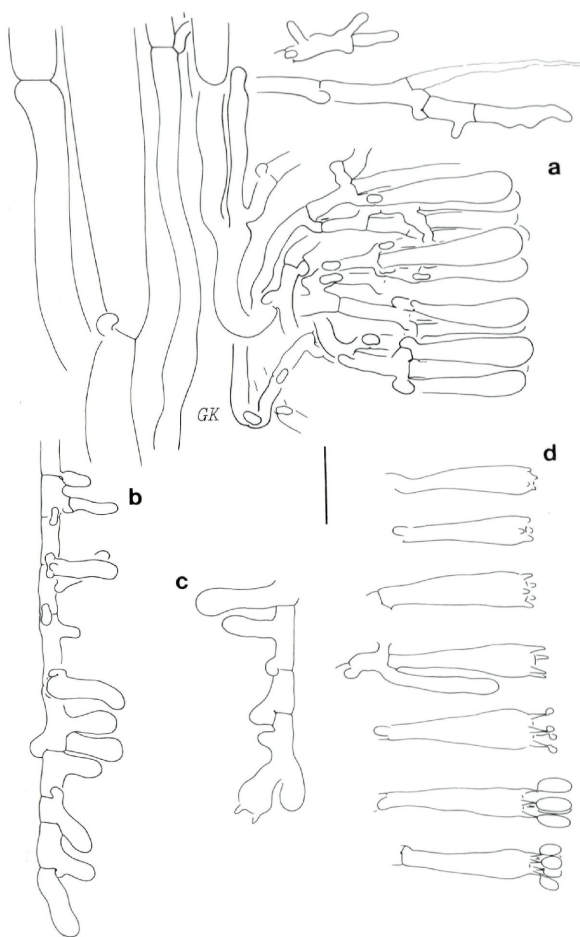


Fig. 8. *Lyophyllum rancidum*. – a: section of the hymenium, subhymenium, and some sterile hyphae of the trama of lamellae intruding into the hymenium; trama of lamellae of parallel and inflated hyphae. Often the subhymenial hyphae are bent back in the direction of the lamella base, because the trama hyphae of the lamellae elongate after the subhymenial hyphae branch off. – b: + c: aberrant basidia at the edge of the lamellae. – d: different stages of basidial development. The basidia are most four-spored, seldom two up to five-spored (bar = 20 μ m).

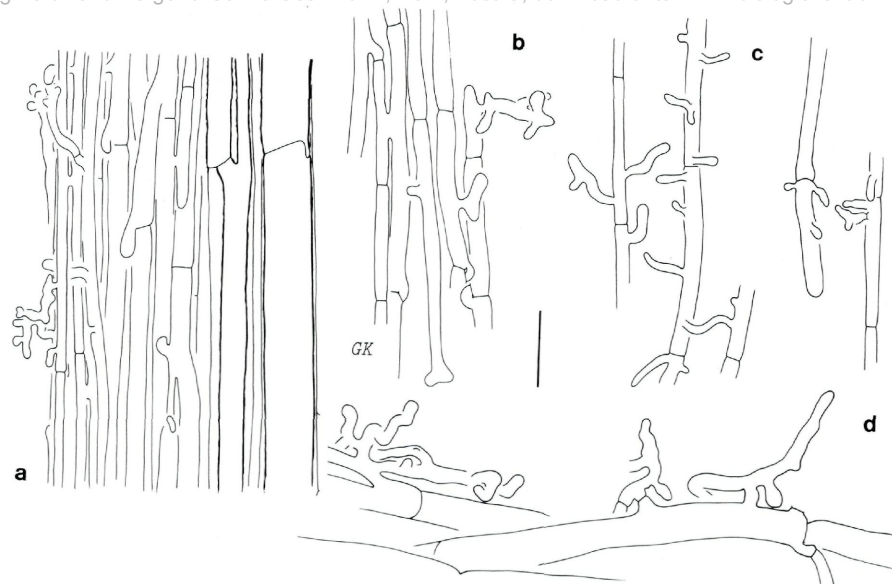


Fig. 9. *Lyophyllum rancidum*. – a: outer parts of the stipe with knob-like outgrowth, to the centre a layer of agglutinated hyphae with thickened walls. – b: outgrowths of repent hyphae of the cortical layer of the stipe near the insertion of the lamellae. – c: hyphae with hyphal outgrowths at surface of the cutis. – d: section across the cutis with short branching hyphae. Some scattered hyphae erect from the cutis (bar = 20 μ m).

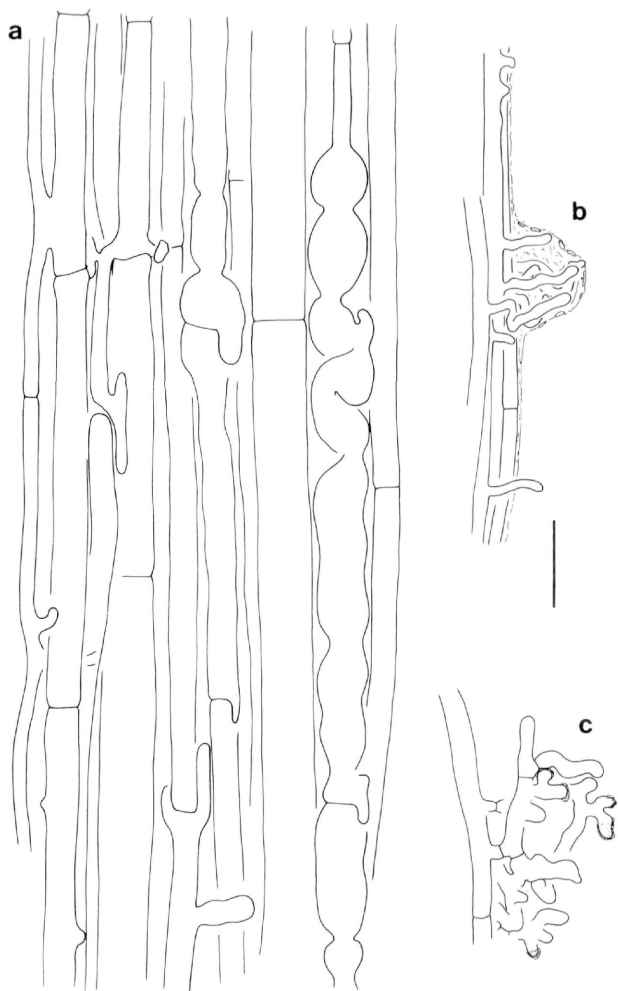


Fig. 10. *Lyophyllum rancidum*. – a: hyphae of the trama within the pseudorhiza; in the pseudorhiza the arrangement of hyphae generally correspond to the stipe trama. – b – c: surface of the stipe; clusters of terminating hyphae and hyphal outgrowths with exudate (bar = 20 μ m).



Fig. 11. *Lyophyllum rancidum*. – Lamellae trama, inflated and narrow hyphae (bar = 20 μ m).



Fig. 12. *Lyophyllum rancidum*. – Trama of the central parts of the stipe: two types of parallel, inflated hyphae: a) strongly inflated, long ($>100\ \mu\text{m}$) hyphae, b) thin or irregularly inflated hyphae varying in diameter (bar = $20\ \mu\text{m}$).

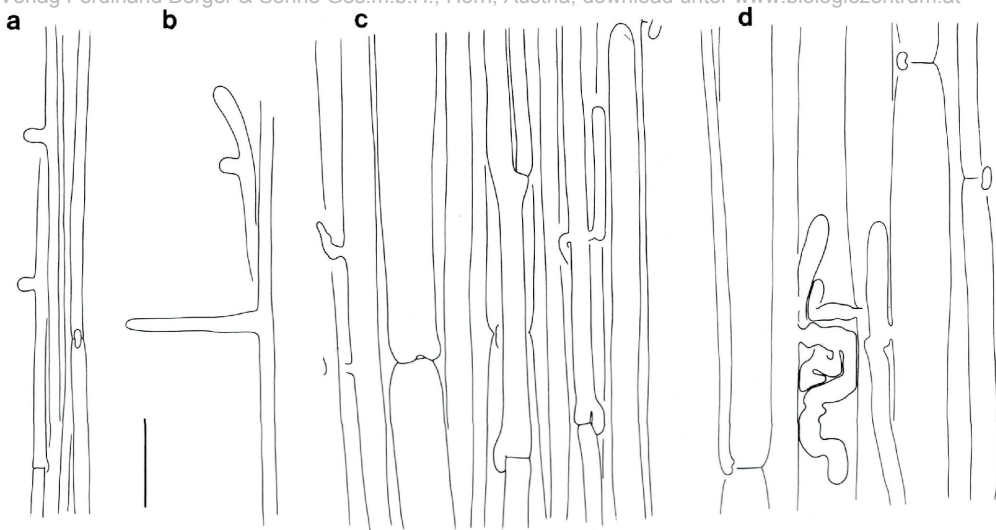


Fig. 13. *Typhula phacorrhiza*. – a: small knob-like outgrowth near the apex of the fruiting body. – b: cystidia-like outgrowths, intercalarily branched off hyphae above the hymenium. – c: outer layer of the stipe; longitudinally arranged, not interwoven or strongly inflated trama hyphae. – d: inner trama hyphae of the stipe, inflated and parallel arranged hyphae. Locally some coiled and interlaced hyphae are pressed between them (bar = 20 μ m).

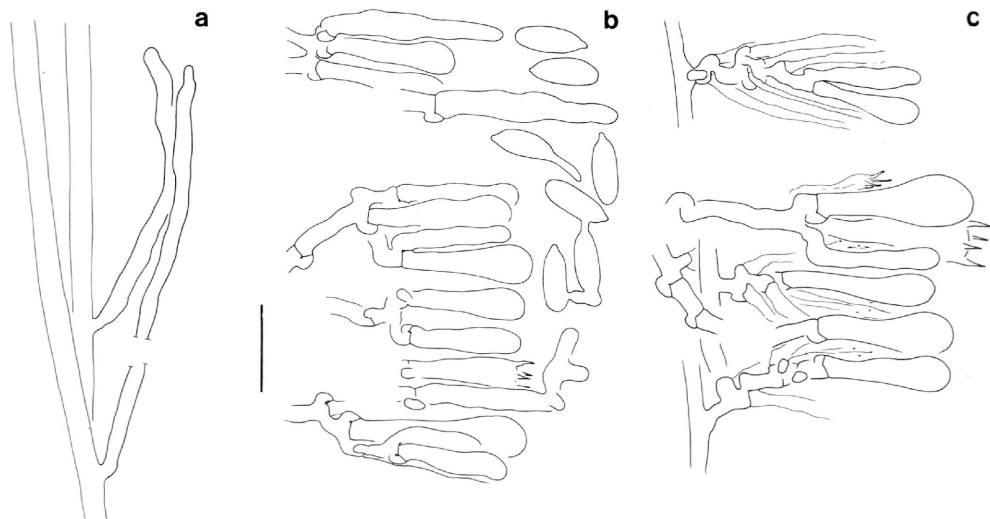


Fig. 14. *Typhula phacorrhiza*. – a: long hair-like caulocystidia intercalarily branched off the outer hyphae at the stipe base below the hymenium. – b: candelaber of basidia, with sterile elongated ending hyphae. – c: fully developed candelabrum of basidia; in fully developed hymenia the old, collapsed basidia can still be found throughout the thickened hymenium (bar = 20 µm).

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