

## Ectomycorrhizae of *Sarcodon imbricatus* on Norway spruce and their chlamydospores\*

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**Summary.** The ectomycorrhizae of *Sarcodon imbricatus* are comprehensively described and compared to other ectomycorrhizae of Thelephoraceae species. *Sarcodon imbricatus* ectomycorrhizae are distinguished from all previously described ectomycorrhizae by the unique shape of their chlamydospores.

**Key words:** Ectomycorrhizae – Characterization – Identification – Chlamydospores – *Sarcodon imbricatus*

### Introduction

The only ectomycorrhizae of the family Thelephoraceae which have been comprehensively described are those of *Thelephora terrestris* Pers.: Fr. (see Agerer and Weiss 1989; Schramm 1966). Shorter descriptions exist for a few other species, e.g. *Phellodon niger*, *Bankera violascens* and *B. fuligineo-alba* (see Discussion).

Methods for characterizing ectomycorrhizae have been previously explained by Agerer (1986, 1987–1990, 1991a), and a glossary of terms has already been published (Agerer 1987–1990).

### *Sarcodon imbricatus* (L.: Fr.) Karst

Reference specimen: Germany, Bavaria, Berchtesgaden, Ramsau, Wachterlsteig, under *Picea abies*, 10. 9. 1986, leg. R. Agerer, fruit bodies and ectomycorrhizae in Herb. RA10916 (in M).

### Morphological characters (Fig. 1a)

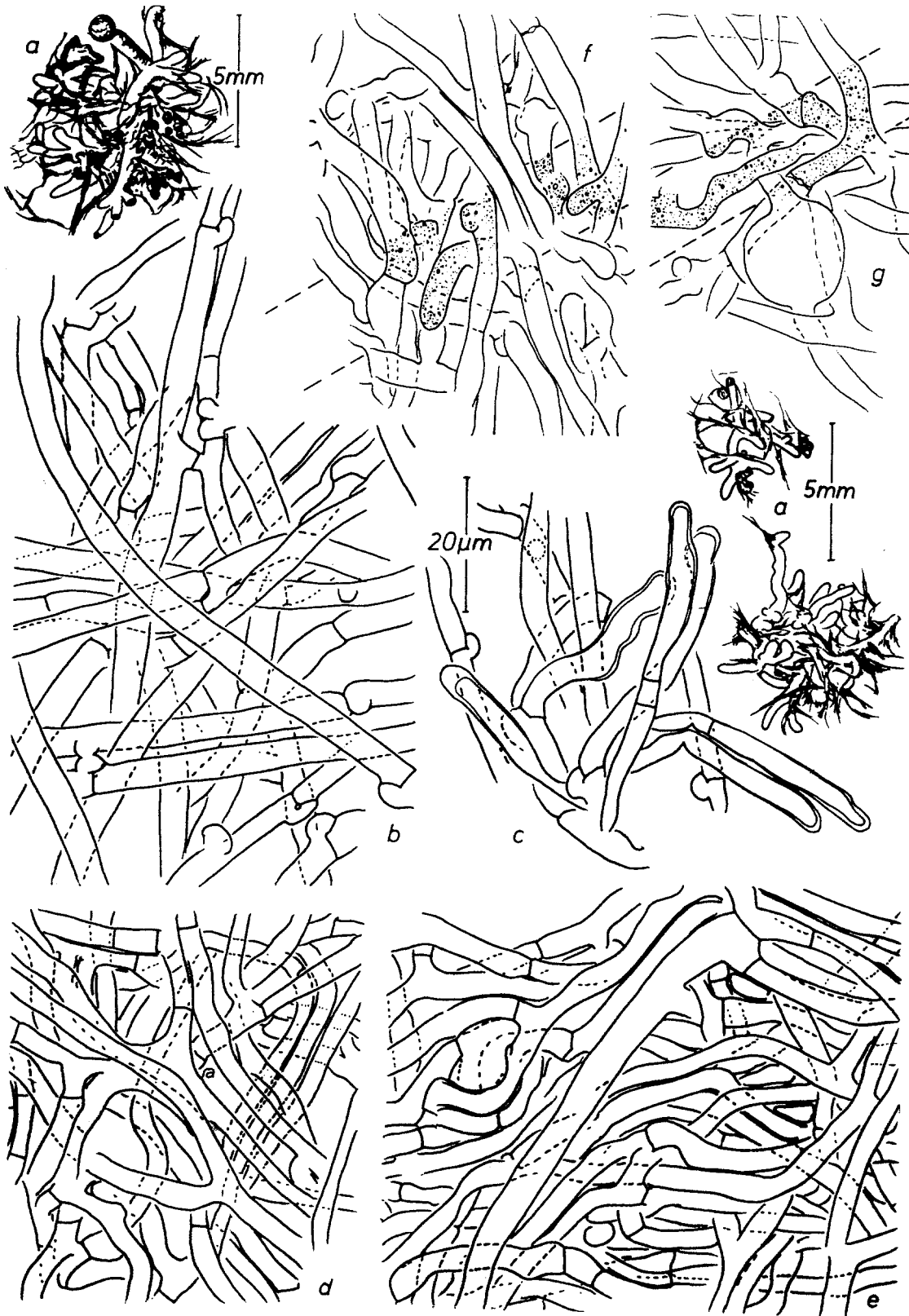
Ramification approximately monopodial, forming nest-like clusters beneath fruit bodies, ectomycorrhizae and rhizomorphs enclosing soil and humus particles, ectomycorrhizal nests 5–10 cm in diameter; unramified

ends straight to slightly tortuous, up to 2.3 mm long and 0.27–0.33 mm in diameter; axes 0.36–0.45 (0.75) mm in diameter; surface of unramified ends smooth or loosely stringy, with a silvery appearance due to air trapped between the mantle hyphae; rhizomorphs very abundant, in part fan-like and flat, in part roundish, repeatedly ramified or forming nets, mostly with abundant emanating hyphae, but thicker rhizomorphs often smooth, growing off from the ectomycorrhizae over longer distances, white, sometimes with slightly yellowish or light-brownish tint, rhizomorphs close to ectomycorrhizae up to 0.16 mm in diameter, and those more distant from the ectomycorrhizae flat and of larger diameter. Unramified ends and tips of ectomycorrhizae whitish-silvery caused by enclosed air, brownish after displacement of the air, older parts slightly darker due to the brown-coloured root.

### Anatomical characters of the surface (Figs. 1b–g, 2)

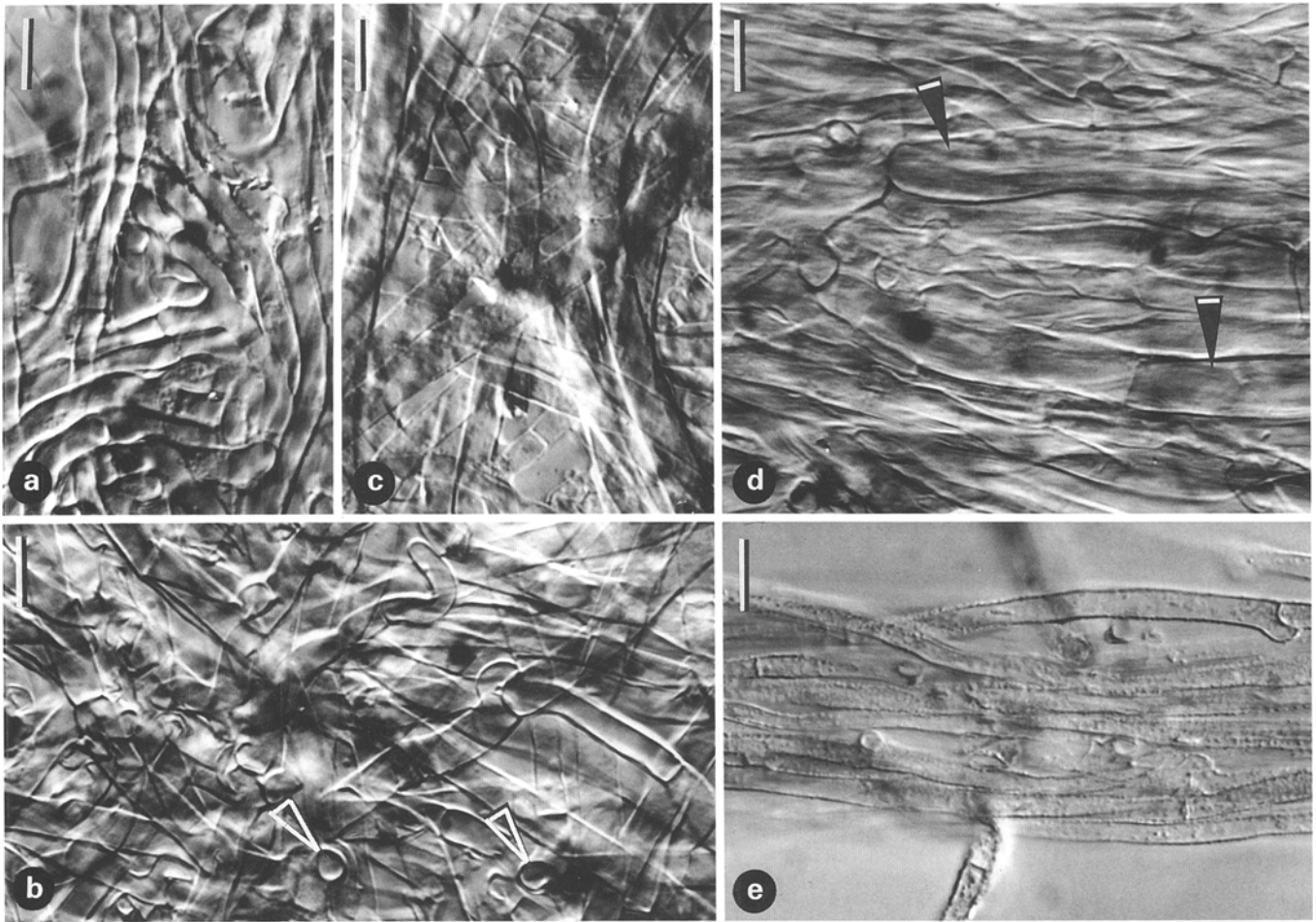
**Outer surface of mantle** (Figs. 1b, 2c, d) loosely plectenchymatous, weakly net-like (Agerer 1991a: type A/B), hyphae (3) 4–5 (5.5)  $\mu\text{m}$  in diameter, slightly thick-walled (thinner than 0.5  $\mu\text{m}$ ), hyphae in part slightly membranaceously brownish, surface of thicker hyphae finely rough, dissolving in formaldehyde acetic acid ethanol and then smooth. **Middle layers of mantle** (Fig. 1d) denser plectenchymatous, hyphae net-like in arrangement, (2) 2.5–4 (5)  $\mu\text{m}$  thick, smooth, slightly thick-walled, colourless. **Inner surface of mantle** (Figs. 1e, 2c) densely plectenchymatous, hyphae net-like in arrangement, 2.5–3.5 (5)  $\mu\text{m}$  in diameter, slightly thick-walled. **Surface of tip** (Fig. 1f, g) loosely plectenchymatous, hyphae 3–5  $\mu\text{m}$  in diameter, slightly tortuous, thin-walled, mostly densely filled with cytoplasm, very infrequently with thin-walled globose cells of up to 15  $\mu\text{m}$  in diameter. **Rhizomorphs** (Figs. 2d, e, 3, 4a) up to 160  $\mu\text{m}$  thick, roundish or rather flat, slightly differentiated (Agerer 1991a: type D), hyphae 8 (10)  $\mu\text{m}$  in diameter, irregularly distributed between hyphae of 3–5  $\mu\text{m}$  diameter, with walls up to 0.5  $\mu\text{m}$  thick, outer hy-

\* Considered as part XXXVI of the series “Studies on ectomycorrhizae”; part XXXV: Weiss (1991)



**Fig. 1.** a Habit, differently ramified systems. b Mantle in surface view, anastomoses with septum. c Mantle in surface view, short cystidia-like hyphal ends with thick-walled tips, in part cap-like. d Plan view of middle layers of mantle, hyphae net-like in arrangement, by dividing and anastomosing hyphal bundles. e Inner surface of mantle; thick hypha originating from a rhizomorph: note

repeated ramification of the basal part of hypha. f Plan view of the very tip of ectomycorrhiza, hyphae thin-walled and in part densely filled by cytoplasm (cytoplasm drawn only between the *dashed lines*). g Plan view of very tip of ectomycorrhiza, with one globular cell (cytoplasm drawn only between the *dashed lines*). a-g from RA10916



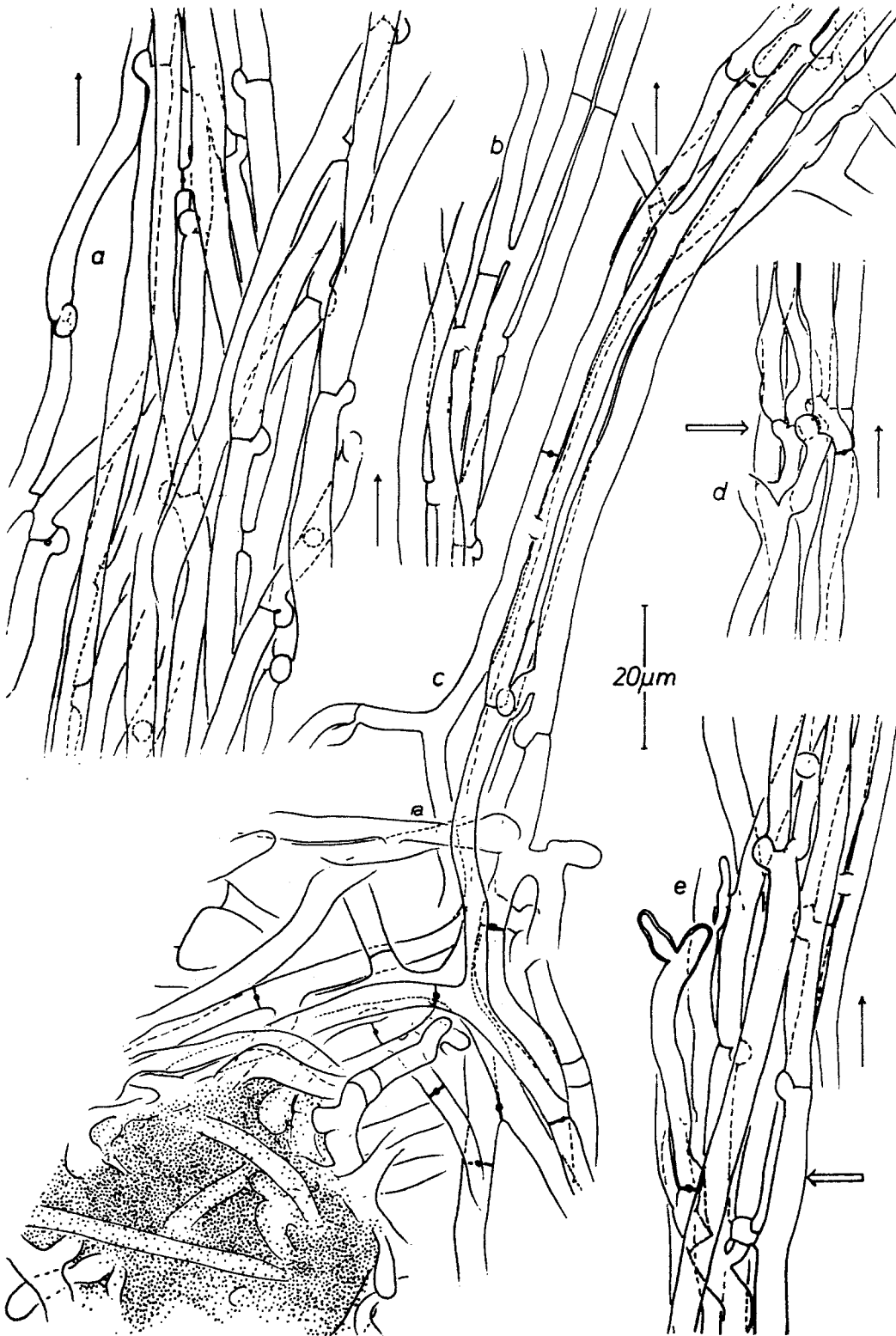
**Fig. 2.** **a** Mantle, inner surface, showing net-like arrangement of hyphal bundles. **b** Mantle, plan view of surface; note thick-walled anastomoses in optical cross-section (*arrows*), clamp and undifferentiated hyphal end. **c** Mantle, plan view of surface, rather thick hyphae possessing brownish contents. **d** Rhizomorph, optical sec-

tion, central part with thick ramified hypha. **e** Rhizomorph, optical section, central part, showing rough hyphae. **a-e** from RA10916, Normarski's interference contrast; **a-d** after fixation; **e** fresh material in water; *bar* = 10  $\mu\text{m}$

phae slightly rough, colourless or membranaceously and/or plasmatically slightly brownish, with simple septa as well as with clamps, with contact septa, contact clamps lacking, open anastomoses infrequent (then hyphae forming the anastomoses often with simple septa close to the anastomoses, Fig. 3b), walls of anastomoses often slightly thicker than remaining walls; central globular thickening of septa often very conspicuous, septal pores in part considerably enlarged; retrorsely ramifying hyphae present. *Emanating hyphae* (Fig. 4b-e) thin-walled, surface slightly rough, colourless or slightly membranaceously brownish, 3  $\mu\text{m}$  in diameter, with simple septa as well as with clamps, sometimes with coiled outgrowths (Figs. 4c, 5a-d), intrahyphal hyphae occurring (Fig. 4e). Hyphae near or within humus particles and some apical ends of those emanating hyphae which are in close contact to soil particles often rather thick-walled (up to 1 (1.5)  $\mu\text{m}$  thick, Fig. 4a-c). Short hyphae of mantle surface sometimes possessing apical cap-like thickenings of up to 3  $\mu\text{m}$ -thick walls (Fig. 1c), thus resembling cystidia.

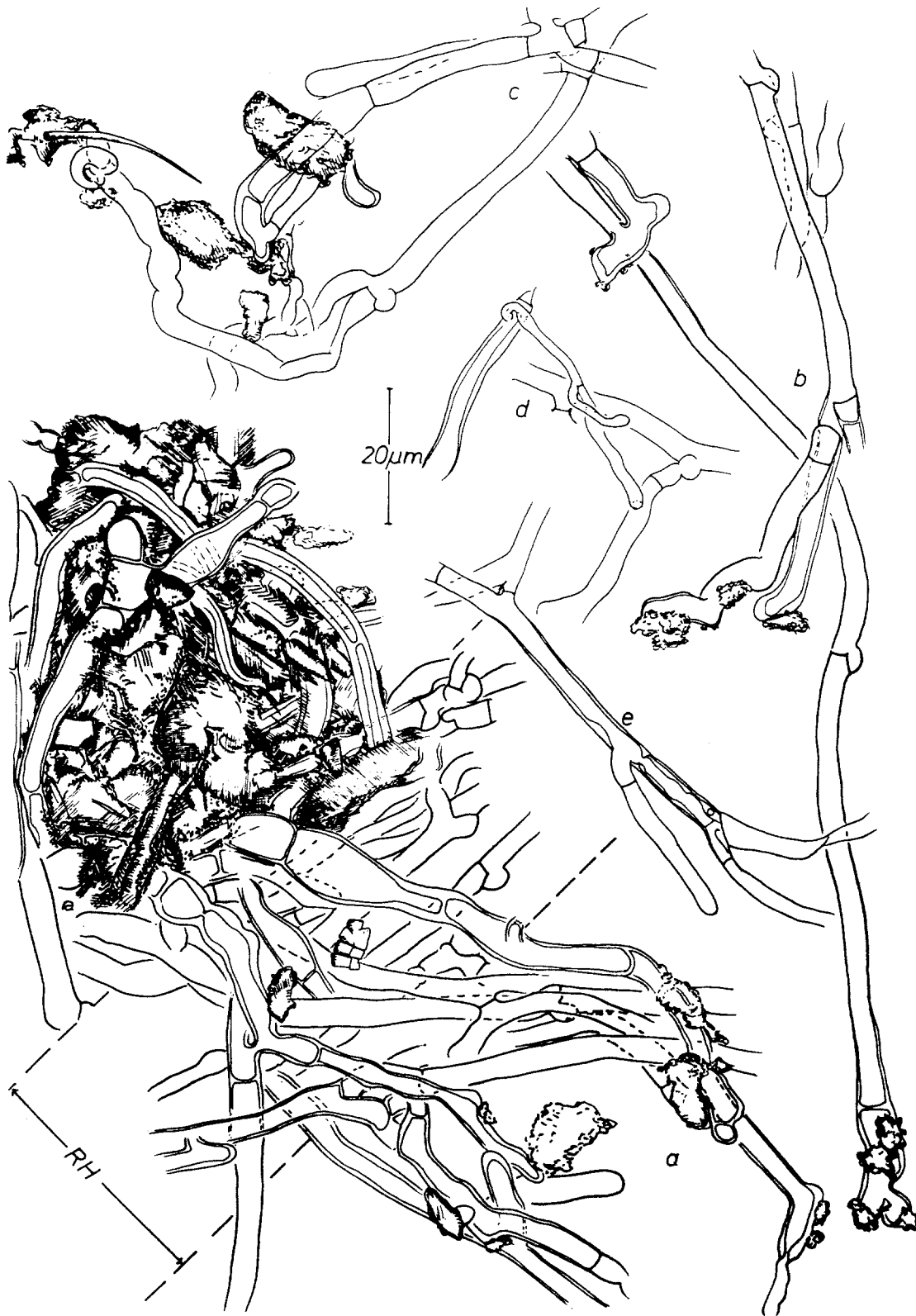
#### *Chlamydozoetes* (Figs. 6, 7a, b)

Star-like, with 10-20 cylindrical wart-like hollow outgrowths, 15-22  $\mu\text{m}$  in diameter measured with outgrowths, 9-13  $\mu\text{m}$  in diameter measured without outgrowths, outgrowths 3-5 (8)  $\mu\text{m}$  in length, ca. 3  $\mu\text{m}$  thick, walls 0.5-1  $\mu\text{m}$  thick; chlamydozoetes dark brown, with double walls, star-like shape originating from outer wall, inner wall also with hollow warts, walls also 0.5-1  $\mu\text{m}$  thick, but warts smaller and intruding into the outer warts; subtending hypha often with slightly thick walls but almost colourless; mostly intercalary, frequently with a short, thin-walled, easily collapsing hypha on the opposite side of the chlamydozoete from the subtending hypha, liberation probably by collapsing of the subtending hypha; mostly solitary, not infrequent.



**Fig. 3.** **a** Rhizomorph, surface view, hyphae repeatedly connected by anastomoses possessing a septum. **b** Rhizomorph, optical section, anastomoses with simple septa, some open anastomoses accompanied by simple septa within the adjacent hyphae. **c** Rhizomorph, basal part, transition zone to inner surface of mantle; note repeatedly ramifying hyphae of rhizomorph within mantle and frequent anastomoses of mantle hyphae with hyphae of rhizo-

morph, septa in part rather thick-walled and with a globular central thickening. **d, e** Different plan views of a single rhizomorph; **e** surface view; **d** beneath the surface; note backwards oriented ramification of hyphae. *Simple arrows* indicate growth direction of rhizomorphs; *open arrows* stand for the same position of the rhizomorph; *dotted parts* indicate surface of tannin cells. **a-e** from RA10916



**Fig. 4.** a Rhizomorph, thick-walled hyphae growing into roundish humus particle, hyphae in close contact to soil debris are remarkably thick-walled, normal hyphae of rhizomorph with rather thin walls. b Emanating hyphae, apically thick-walled with adhering

soil particles. c Like b but one hyphal end coiled. d Thin- and thin-walled hypha growing out of a thick hypha possessing thick walls. e Emanating hypha with an intrahyphal hypha. RH, Rhizomorph; dashed lines indicate borders. a-e from RA10916

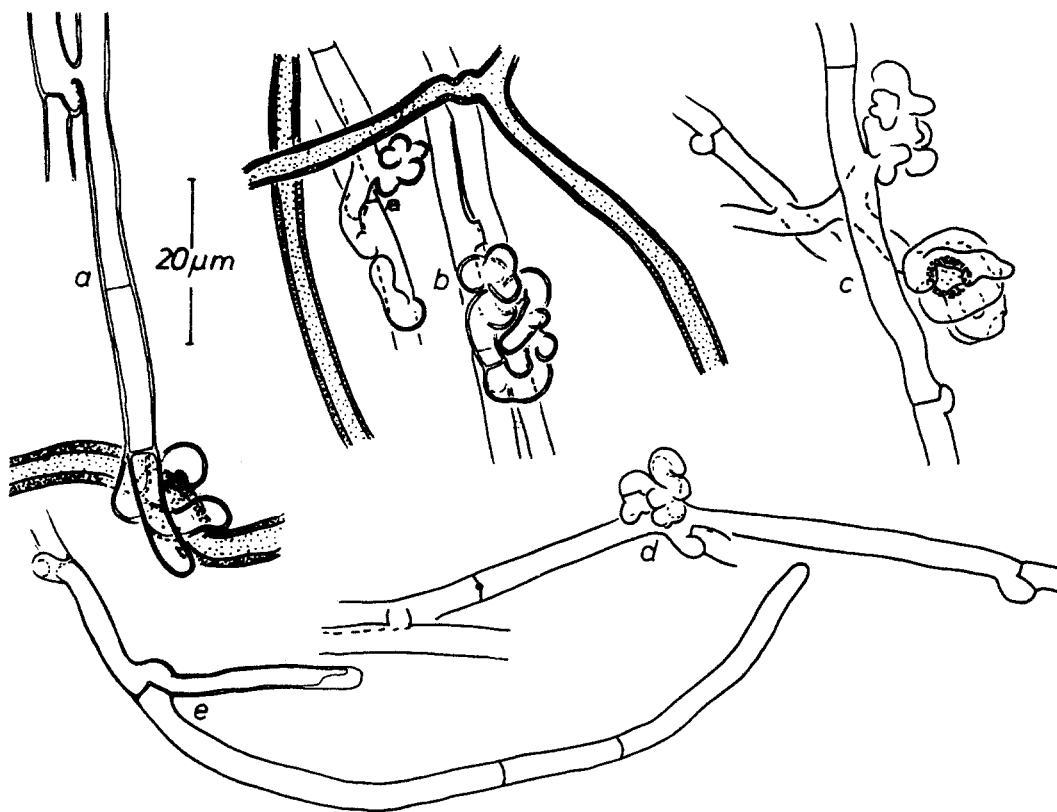


Fig. 5a-e. Emanating hyphae. a Coiled hyphae enveloping a brown foreign hypha. b Coiled outgrowths of emanating hyphae close to brown, foreign hyphae (natural position). c Coil hypha

enveloping a dark cell. d Young outgrowth. e Short side-branch possessing an apical cap-like thickening. a-e from RA10916

#### *Hyphae of stipe base*

Colourless, smooth, 3–4.5 µm thick, slightly thick-walled, with simple septa as well as with clamps, anastomoses with septa; if septum lacking then hyphae involved form simple septa close to anastomoses; sometimes forming chlamydospores with the same features as those of ectomycorrhizae.

#### *Anatomical characters, cross-section (Fig. 7d)*

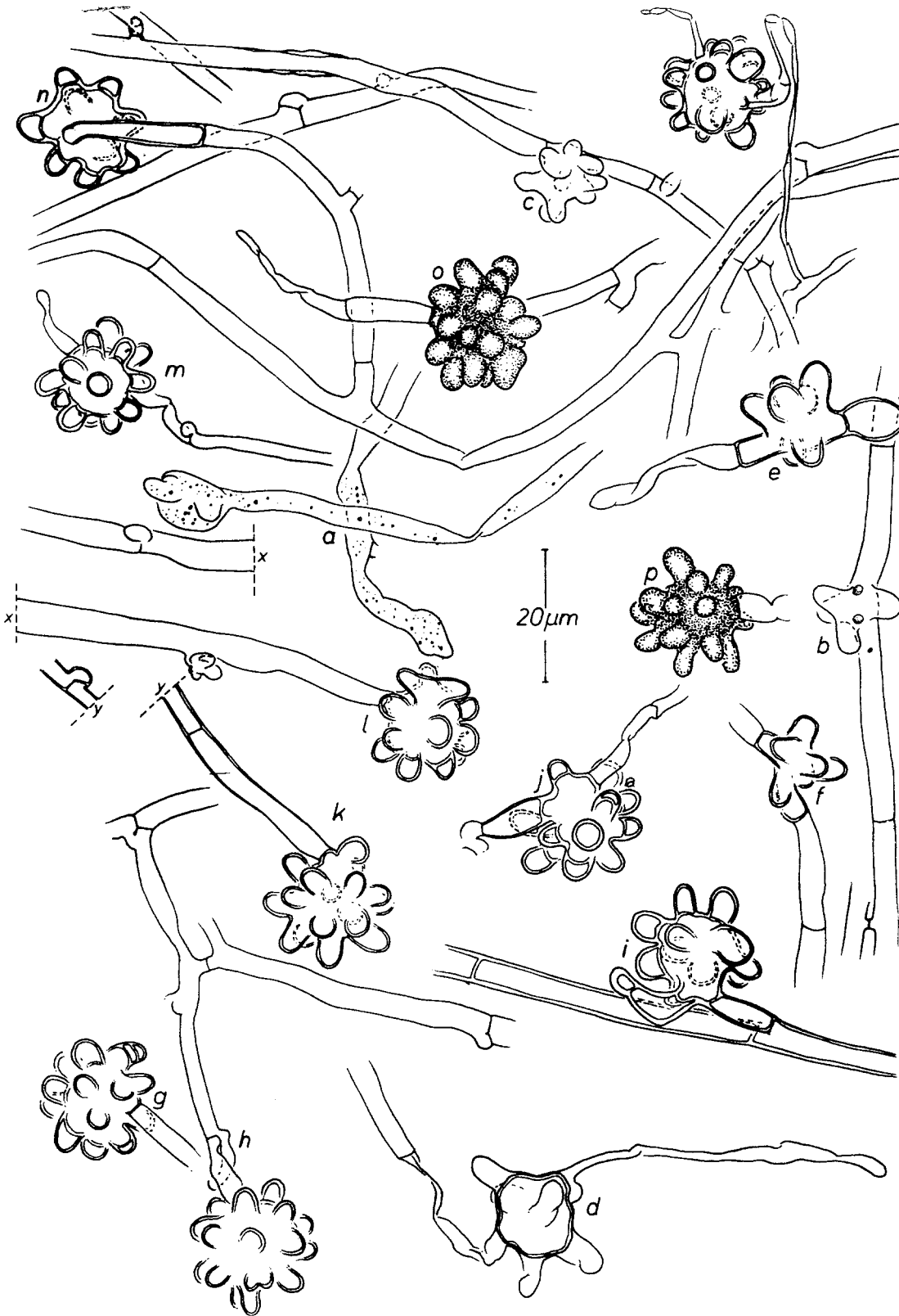
*Mantle* (Fig. 7d) loosely plectenchymatous throughout, lacking distinct layers, 15–25 (30) µm thick; residues of calyptra cells inconspicuous, mostly closely coherent to tannin cells; hyphae tangentially 3–30 (60) µm, radially (2.5) 3–4.5 (5) µm. *Tannin cells* (Fig. 7d) tangentially irregularly oval, 1–2 rows, tangentially 20–40 (54) µm, radially 6–15 (24) µm, TCt=31.4 µm, TCq=2.8; *Hartig net* (2) 3–4 µm thick, composed of one row of hyphal cells; hyphal cells in section roundish. *Cortical cells* (Fig. 7d) approximately round, tangentially (6) 15–30 (38) µm, radially (8) 15–32 (38) µm, CCt=23.7 µm, CCq=1.1; *Hartig net* 2 (3) cortical cell layers deep (tannin cells not included), mostly not reaching endodermis, a half or even one row of cortical cells free of *Hartig net*; *Hartig net* 2–2.5 (3) µm thick, composed of one row of hyphal cells; *Hartig net* cells short to long cylindrical, hyphal walls inconspicuous.

#### *Anatomical characters, longitudinal section (Fig. 7c, e, f)*

*Mantle* (Fig. 7e, f) corresponding to cross-section; mantle of mycorrhizal tip 10–15 µm in diameter, no distinct layers discernible, hyphae thin-walled, easily collapsing, slightly agglutinated, hyphae 2–3 µm thick. *Tannin cells* (Fig. 7e, f) irregularly cylindrical or slender elliptical, approximately parallel to root surface, tangentially (32) 95–145 (160) µm, radially (5) 8–17 (27) µm, TCt=110.6 µm, TCq=9. *Cortical cells* (Fig. 7e, f) cylindrical to oval, parallel or slightly oblique to root surface, tangentially (35) 55–125 (145) µm, radially (10) 15–30 (37) µm, CCt=85.7 µm, CCq=3.8. *Hartig net* (Fig. 7c) in surface view of palmetti type, weakly ramified, lobes (1.5) 2–3 µm broad.

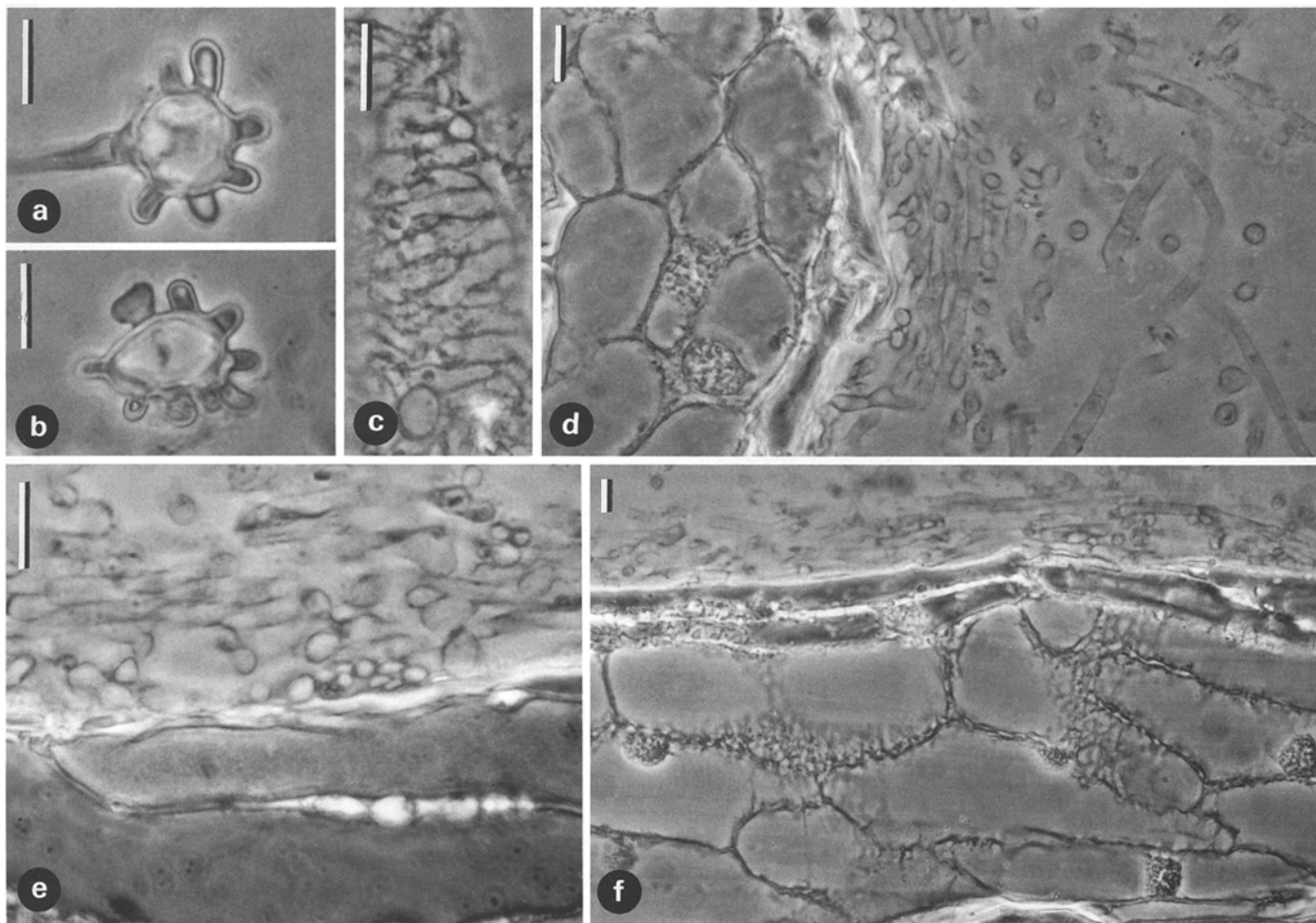
#### *Colour reactions with different reagents*

*Mantle preparations*: acetic-fuchsin: --; aniline: walls and cytoplasm pink; brilliant cresyl blue: walls slightly blue; cotton blue: walls slightly blue; ethanol 70%: --; guaiac: --; iron sulphate: walls and cytoplasm slightly greenish; KOH 15%: walls and cytoplasm more intensively brown than untreated; lactic acid: even after several weeks, inner mantle hyphae without indigo blue granula; Melzer's reagent: --; phenol: --; phenol-aniline: --; sulpho-vanillin: --. *Whole ectomycorrhizae*: iron-sulphate: ochre-brown; KOH 15%: ochre-brown, root bluish-green.



**Fig. 6a-p.** Chlamydospores with different shapes and different development. **a** Thin-walled hyphae with apical thickenings, one sample already showing short outgrowths. **b** Intercalary formation of a chlamydospore; four short, still thin-walled outgrowths, some storage droplets. **c** More developed chlamydospore, walls still thin; note anastomoses to hypha with a clamp. **d** Inner, thick-walled part of chlamydospore already formed, cylindrical out-

growths still thin-walled, with a short thin-walled hyphal end and a subtending hypha. **e, f** Small chlamydospores with rather few outgrowths. **g-n** Differently shaped chlamydospores, septa separating outgrowths from inner part of chlamydospore only drawn in some examples. **o, p** Chlamydospores in surface view, dark-brown walls indicated by dots. **a-p** from RA10916



**Fig. 7.** **a, b** Chlamydospore, longitudinal section, two consecutive sections of the same chlamydospore. **c** Longitudinal section, Hartig net of cortical cells in plan view. **d** Cross-section, from loosely woven emanating hyphae to endodermis. **e** Longitudinal (median)

section, from mantle to tannin cells. **f** Longitudinal section, from mantle to endodermis. **a-f** from RA10916, phase contrast; *bar* = 10  $\mu$ m

### Autofluorescence

*Whole ectomycorrhizae:* UV 254 nm: --; UV 366 nm: --. Mantle and rhizomorphs: UV-filter 340–380 nm: slightly bluish, brownish hyphae of rhizomorphs slightly yellowish-brown; blue filter 450–490 nm: slightly yellowish; green filter 530–560 nm: slightly reddish.

### Staining of nuclei

Aceto-carmine: normally two nuclei per hyphal cell, often closely together or at a distance of up to 20  $\mu$ m, roundish (1.5  $\mu$ m in diameter) or oval (2  $\times$  1.5  $\mu$ m); in hyphae connected by anastomoses often up to four additional nucleus-like structures (2.5  $\times$  0.5  $\mu$ m); central thickenings of septa stain similarly to nuclei; siderophilous granules in some hyphal parts rather dense, up to 0.5  $\mu$ m in diameter.

### Material studied and method of identification

Reference specimen: several rhizomorph connections between stipe base and ectomycorrhizae were found; hyphae of fruit-body stipe base and of mantle and rhizomorphs show the same features; hyphae of stipe base as well as rhizomorphs of the ectomycorrhizae producing the same type of chlamydospores. Reference for fruit body: Germany, Bavaria, Nationalpark Berchtesgaden, near Schapach under spruce, MTB 8443/2, leg. et det. H. Schmid-Heckel, 26. 8. 1987, No. 7307 (in M).

### Discussion

The above characterization is the first description of the ectomycorrhizae of *Sarcodon imbricatus*. The ectomycorrhizae of *S. scabrosus* (Fr.) Karst., however, have been briefly described by Ogawa (1981). These formed “witches’ broom”-shaped clusters, a thin hyphal mantle and an incomplete Hartig net. Masui (1927) described the ectomycorrhizae of *Hydnum affine* Lloyd, which ac-



ording to Maas Geesteranus (1971) is an unknown species of *Sarcodon*. These had a 7- to 29- $\mu\text{m}$ -thick mantle at first yellowish, later turning dark brown, and composed of rather loosely associated hyphae, 1.5–3.5  $\mu\text{m}$  in diameter, and a well-developed Hartig net. The ectomycorrhizae also formed nest-like clusters beneath the fruit bodies (Masui l.c.) similar to *S. imbricatus*. The hyphae were not characterized in more detail and there is no indication that chlamydospores were observed. The thinner hyphae of *Hydnum affine* would serve to distinguish the ectomycorrhizae of this species from those of *S. imbricatus*.

The best-known ectomycorrhizae of the Thelephoraceae are those of *Thelephora terrestris*. A comprehensive description and comparison of the existing literature is given by Agerer and Weiss (1989). There are several differences between the ectomycorrhizae of *S. imbricatus* and *T. terrestris*. *T. terrestris* lacks the highly characteristic chlamydospores of *S. imbricatus* but produces prominent cystidia with abruptly thickened walls above the basal clamp. Chlamydospore-like, globular, dark-brown cells with thick walls were infrequently found on the mantle of *T. terrestris*, but these deviate considerably from the chlamydospores of *S. imbricatus*. The mantle of *T. terrestris* ectomycorrhizae is not as loosely woven as that of *S. imbricatus*, which results in a smooth or, at the most, a spiny surface due to cystidia (type D: Agerer 1991a). *S. imbricatus* produces a rather stringy mantle caused by a net-like arrangement of hyphal bundles (type A: Agerer 1991a). The rhizomorphs of *S. imbricatus* are more frequent, usually repeatedly ramified and netted and not as smooth as those of *T. terrestris*. The rhizomorphs of *S. imbricatus* are more highly evolved (type D: Agerer 1991a), whereas those of *T. terrestris* are rather simple (type B/C: Agerer 1991a). Although the ontogeny of the rhizomorphs of both species seems to be very similar (Agerer 1988; Raidl and Agerer 1991), the anastomoses are different. In *T. terrestris* they remain open and in *S. imbricatus* they are usually interrupted by a simple septum.

The ectomycorrhizae of two species of *Hydnellum*, a neighbouring genus of *Sarcodon*, have been briefly described previously: *Hydnellum* (= *Calodon*) *suaveolens* (Scop.: Fr.) Karst. (Ogawa 1981), and *H. concrescens* (Pers.: Schw.) Banker (Otto 1989). After Ogawa (l.c.), the ectomycorrhizae of *H. suaveolens* are “witches’ broom” shaped, enveloped by a well-developed fungal sheath and form a “clear” Hartig net; the rhizomorphs have a differentiated inner tissue consisting of thick hyphae between thinner ones. *H. concrescens* on *Picea abies* is characterized by blackish-grey, straight or slightly bent, smooth ectomycorrhizae, but in part with distinct mycelium on the surface, and few rhizomorphs; thin, clampless hyphae (2  $\mu\text{m}$ ) occur on the colourless mantle but brownish hyphae (ca. 5  $\mu\text{m}$ ) and hyphae with clamps were also found (3  $\mu\text{m}$ ); the Hartig net is weakly developed (Otto 1989). The two *Hydnellum* species can apparently be distinguished from *S. imbricatus* either by the highly developed rhizomorphs or by the blackish-grey colour. Chlamydospores are not mentioned in either description.

*Boletopsis* and *Phellodon*, two other genera related to *Sarcodon*, are ectomycorrhizal. The ectomycorrhizae of *Boletopsis leucomelaena* (Pers.: Fr.) Fayod were briefly described by Masui (1927).

*Boletopsis* (= *Polyporus leucomelas*) *leucomelaena* ectomycorrhizae are clavate with long, thin “stalks” and numerous emanating hyphae; after the mycelium of the ectomycorrhizae has died out, a dark-coloured nodose root results (Masui 1927). Further features are not mentioned, but the clavate, thin-stalked ectomycorrhizae are distinctive enough to distinguish these ectomycorrhizae from those of *S. imbricatus*.

*Phellodon niger* (Fr.: Fr.) Karst. ectomycorrhizae were identified by Otto (1989) and characterized as follows: ectomycorrhizae straight or slightly bent, blackish-grey or even black, smooth but in part with distinct mycelium on the surface, with few rhizomorphs, mantle hyphae colourless, clampless, rather thin (2.5  $\mu\text{m}$ ), ca. 5  $\mu\text{m}$  thick on the mantle of black samples; Hartig net weakly or well developed (the latter case in black ectomycorrhizae). Chlamydospores are not mentioned. *P. niger* can be distinguished from *S. imbricatus* ectomycorrhizae by their blackish-grey colour and also by the lack of clamps.

Two species of the genus *Bankera* are known to form ectomycorrhizae: *B. fuligineo-alba* (Schmidt: Fr.) Pouzar (Danielson 1984) and *B. violascens* (Alb. & Schw.: Fr.) Pouzar (Otto 1989). Danielson (l.c.) synthesized ectomycorrhizae of *B. fuligineo-alba* on *Pinus banksiana*. The colour and the surface of the ectomycorrhizae are similar to those of *S. imbricatus* but those of *B. fuligineo-alba* can be easily distinguished by very thin (1.5–2  $\mu\text{m}$ ), clampless hyphae and by the formation of abundant globose terminal or intercalary pale-brown chlamydospores, 5–6  $\mu\text{m}$  in diameter with slightly thickened walls. Otto (l.c.) characterized the ectomycorrhizae of *B. violascens* as blackish-grey, straight or slightly bent, smooth or slightly granular, in part with distinct surface mycelium, with frequent rhizomorphs, hyphae slightly brownish, 3  $\mu\text{m}$  in diameter, clampless; Hartig net weakly developed. Chlamydospores are not mentioned. Thus, the ectomycorrhizae of both *Bankera* species can be distinguished from those of *S. imbricatus* by the formation of another type of chlamydospore and/or by clampless hyphae.

*Tomentella* ectomycorrhizae were described by Danielson and co-workers (Danielson et al. 1984; Danielson and Pruden 1989). One *Tomentella* species (*Tomentella* spec.) is characterized, like the ectomycorrhizae of *Thelephora terrestris*, by seta-like cystidia and an epidermoid mantle surface, turning green in KOH (Danielson et al. 1984; Danielson and Pruden 1989). The ectomycorrhizae of another *Tomentella*, also without a specific epithet, is described as dark-brown to almost black, a mantle with angular to epidermoid (“jigsaw”) cells in surface view, lacking cystidia (Danielson and Pruden 1989). In both species, the ectomycorrhizae can easily be distinguished from those of *S. imbricatus* by their cystidia and/or their mantle. Chlamydospores are not known in either case.

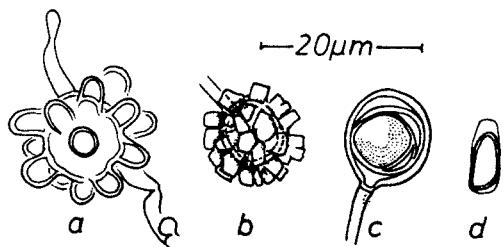


Fig. 8a-d. Chlamydospores from ectomycorrhizae of different Thelephoraceae. **a** *Sarcodon imbricatus*. **b** *Hydnellum peckii*. **c** *Phellodon niger*. **d** *Boletopsis leucomelaena*. **a** from RA10916; **b** from RA11530; **c** from RA11270; **d** from RA10950

The absence of conidia is said to be typical of ectomycorrhizal fungi and it is argued that "conidial anamorphs may have been selected against in ectomycorrhizal fungi in favour of basidiospores for dissemination and infection" (Hutchison 1989). Structures of *Elaphomyces muricatus* described by Miller and Miller (1984) as chlamydospores were re-interpreted as bulbil initials (Hutchison l.c.). However, Berg (1989) found chlamydospores in cultures of *Cenococcum* obtained from sclerotia, although synthesis experiments so far failed.

The only chlamydospores found and published to date are those formed by *Bankera fuligineo-alba* (Danielson 1984) and of *Gomphidius roseus* (Fr.) Karst (Gomphidiaceae) in ectomycorrhizae of *Suillus bovinus* (L.) Kuntze (Agerer 1990, 1991b). Other species of Thelephoraceae are able to form chlamydospores. *Hydnellum peckii*, *Phellodon niger* and *Boletopsis leucomelaena* all form characteristic chlamydospores different to those of *Sarcodon imbricatus* and from these other species; all are formed intrahyphally (Fig. 8, R. Agerer, in preparation).

Although the ectomycorrhizae of only a very limited number of species of Thelephoraceae have been comprehensively studied, it is tempting to argue that the formation of chlamydospores is a common phenomenon of this group, and that different species - if not genera - produce their own types of chlamydospore. Ecologically, the production of chlamydospores could be advantageous. As surviving diaspores, they could serve to establish new ectomycorrhizae either at the place where they were formed or - if they are disseminated, e.g. by invertebrates - they could act as effective propagules for the fungi given the opportunity to germinate adjacent to roots.

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