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THE GENUS SQUAMANITA

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(With 42 Text-figures)

By transferring *Cystoderma paradoxum* Smith & Sing. and *Vaginata umbonata* Sumst. to the genus *Squamanita* and the description of the new species, *S. pearsonii*, the number of species of that genus is raised from two to five. In addition two more species of *Squamanita* are provisionally described. An emended description of the genus and a key to the species is given. The production of abundant chlamydospores on special conidiophores is described in three species. The relationships of the genus are discussed.

In 1918 Miss Catharina Cool, at that time curator of the herbarium of the Netherlands Mycological Society, described the species *Lepiota odorata* Cool from material collected in The Netherlands. The simultaneous discovery of such a remarkable fungus (a small violet-grey *Tricholoma*-like fungus with a scaly cap and base of the stem, a sclerotial bulb and a strong aromatic smell) from several places in this country caused some sensation among the Dutch mycologists, especially after it appeared that it was unknown to such famous mycologists as Patouillard and Ricken.

After that time *Lepiota odorata* was found in The Netherlands several times again, but after very irregular intervals. In 1943 Huijsman published observations on a number of species of *Lepiota* and on that occasion erected the genus *Coolia* to accommodate *Lepiota odorata*, unfortunately without furnishing a Latin diagnosis.

In about 1935 another striking fungus turned up in Switzerland and was described and depicted by Schreier (1938: 97, pl. 2) as "*Tricholoma* X". Probably it was due to the beautiful coloured plate that this publication immediately aroused much interest. The tricholomatoid habit, the scales on the cap and at the base of the stem and the sclerotial bulb of Schreier's species are reminiscent of *Lepiota odorata*, but the brownish yellow colour and the much larger size point to a distinct species.

Schreier's publication caused three independent reactions. First, Imbach (1942: 152) proposed the creation of the genus *Squamamanita* [!] for *Tricholoma* X and to name that species *S. schreieri*, but Latin descriptions were lacking. Some years later, Imbach (1946: 18) validly published the generic name *Squamanita* and the specific name *S. schreieri*.

Secondly, Huijsman (1943: 60), in his paper on *Coolia*, proposed the epithet 'schreieri' for *Tricholoma* X and the tentative combination *Coolia schreieri* Huijsman, an abortive name for several reasons.

Thirdly, Maire & Konrad, who studied a part of Schreier's material, published the name *Tricholoma schreieri* in a paper by Maire (1945: 27) the publication of which was delayed because of the war: it escaped notice for the same reason. Although Maire & Konrad's name is the first validly puplished one for the Swiss fungus it can not be transferred to *Squamanita* because the resulting recombination would be a later homonym of *Squamanita schreieri* Imbach, reason why Imbach's later name has to be used.

The combination *Squamanita odorata* (Cool) is usually attributed to Imbach. But he (1946: 83) did not definitely accept this name and so the combination has still to be validly published.

The author's attention was drawn to the genus *Squamanita* rather accidentally. Among material of Malayan species of *Amanita* collected by Mr. E. J. H. Corner, one species (*Amanita* 6) showed some features unknown in the genus *Amanita*. For one thing, in the button-stage the gills did not touch the stem thus having free edges during their development, and for another, the basal bulb was apparently able to produce more than one fruit-body. Moreover the gills were narrow, rather irregular and slightly decurrent and the margin of the cap was not striate, while the spores were non-amyloid. The sclerotial bulb particularly reminded one of the genus *Squamanita*. A comparison of the descriptions of Corner's *Amanita* 6 and *S. schreieri* showed that those species resemble each other closely.

While screening the American literature for descriptions of species of *Amanita*, the author came across *Vaginata umbonata* Sumstine. The conical cap and the rings of pointed scales at the base of the stem and the top of the bulb reminded him again of *S. schreieri* Imbach and a study of the type of *V. umbonata* revealed that this species differs from the Swiss one mainly by the occurrence of large hymenial cystidia. It was a piece of luck that *S. umbonata* was collected during the meeting of the Mycological Society of America at Amherst in August 1963, so that the author had the opportunity of studying this species in fresh condition.

Talking over the genus *Squamanita* with Dr. A. H. Smith, Ann Arbor, this great expert on North American Agaricales and Gasteromycetes drew the author's attention to a remarkable fungus, collected by him in the western U.S.A. and described by Smith and Singer (1948: 454) as *Cystoderma paradoxum*, a species later recorded from Europe by Herink (1954: 60) and by Horak (1962: 16). Although this species has a loosening universal veil mainly made up of chains of spherocysts, the pigmentation and the fact that a number of fruit-bodies were found to grow on a sclerotial body are reminiscent of *Squamanita odorata*, which species is undoubtedly more closely related to it than the other species of *Cystoderma*.

Having come to this, it seemed of interest to bring together all the available information on *Squamanita*.

Pearson (1952: 99) reported *Tricholoma odoratum* (Cool) Konr. & Maubl. from Scotland. However, this material turned out to represent a new species. A collection of another new species from the same area was preserved at Edinburgh under the same name.

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SQUAMANITA Imbach

Squamanita Imbach *in* Mitt. naturf. Ges. Luzern **15**: 81. 1946. — Protonym: *Squamamanita* [!] Imbach *in* Schweiz. Z. Pilzk. **20**: 152. 1942 (nom. nud.; no Latin descr.). — Type: *Squamanita schreieri* Imbach.

Coolia Huijsman *in* Meded. Nederl. mycol. Ver. **28**: 59. 1943 (no Latin descr.). — *Tricholoma* sect. *Coolia* (Huijsman) Konr. & Maubl., Agaricales **1**: 345. 1948 (no Latin descr.). — Type: *Lepiota odorata* Cool.

Cystoderma subgenus *Dissoderma* A. H. Sm. & Sing. *in* Mycologia **40**: 454. 1948. — Type: *Cystoderma paradoxum* Smith & Sing.

Fruit-bodies tricholomatoid, terrestrial, gregarious to subcaespitose, sometimes solitary, arising from simple to compound sclerotial bodies. Cap fleshy, dry, radially fibrillose to scaly, sometimes slightly squarrose, violaceous grey, yellow-brown or buff, young margin straight or very slightly involute. Gills crowded to distant, very narrow to broad, always more or less adnate (narrowly adnate, sinuate, emarginate, broadly adnate or subdecurrent), often uncinate, often with irregular edge, whitish or concolorous with cap, often intervenose. Stem solid, mostly equal, relatively short, fibrillose, concolorous with cap, often on lower half or at base with fibrillose, pointed, erect to appressed scales similar to those on cap, or if these scales are absent, base surrounded by a volval limb; sometimes with a fibrillose annular zone. Flesh without or, more often, with a strong smell. Sclerotial bodies either simple, subcylindrical, fusiform, napiform, or subglobose, or compound with a varying number of subglobose, ellipsoid or cylindrical bodies on a common basal one, solid, sometimes becoming hollow, firm, whitish to ochraceous, in 3 of the present 7 species with abundant thick-walled chlamydospores on surface or just under cortical layer.

Spores medium to small, thin- to rather thick-walled, colourless (or very slightly coloured ?; see p. 351), ellipsoid, subreniform or globose, smooth, without germ-pore, binucleate in at least 1 species, non-amyloid or amyloid or pseudo-amyloid, sometimes distinctly metachromatic in Cresyl Blue. Basidia mainly 4-spored, but often partly 1-, 2-, and 3-spored, without carminophilous granules. Edge of gills homomorphous; large, fusiform, colourless hymenial cystidia present in one species. Trama of gills regular, becoming very slightly irregular by inflation of cells of central hyphae. Subhymenium very narrow, densely ramose. Cuticle, scales on cap, and if present scales on base of stem consisting of parallel, rather broad, coloured hyphae. Trama of stem confluent with that of cap. Pigments intercellular-encrusting or membranal, distinctly intracellular in oleiferous type of hyphae. Clamps abundant.

Development of *S. odorata* studied by Reijnders (1952: 23); monovelangiocarpous + gymnangiocarpous according to Reijnders's, hemiangiocarpous according to Singer's, terminology. Probably bivelangiocarpous in some species.

ECOLOGY.—Terrestrial, probably always near trees (deciduous or coniferous) in temperate and tropical regions.

DISTRIBUTION.—Europe, North America, south-eastern Asia.

In the above generic description the terms universal veil and partial veil have been avoided as the velar relations in *Squamanita* are far from being clear (see p. 352).

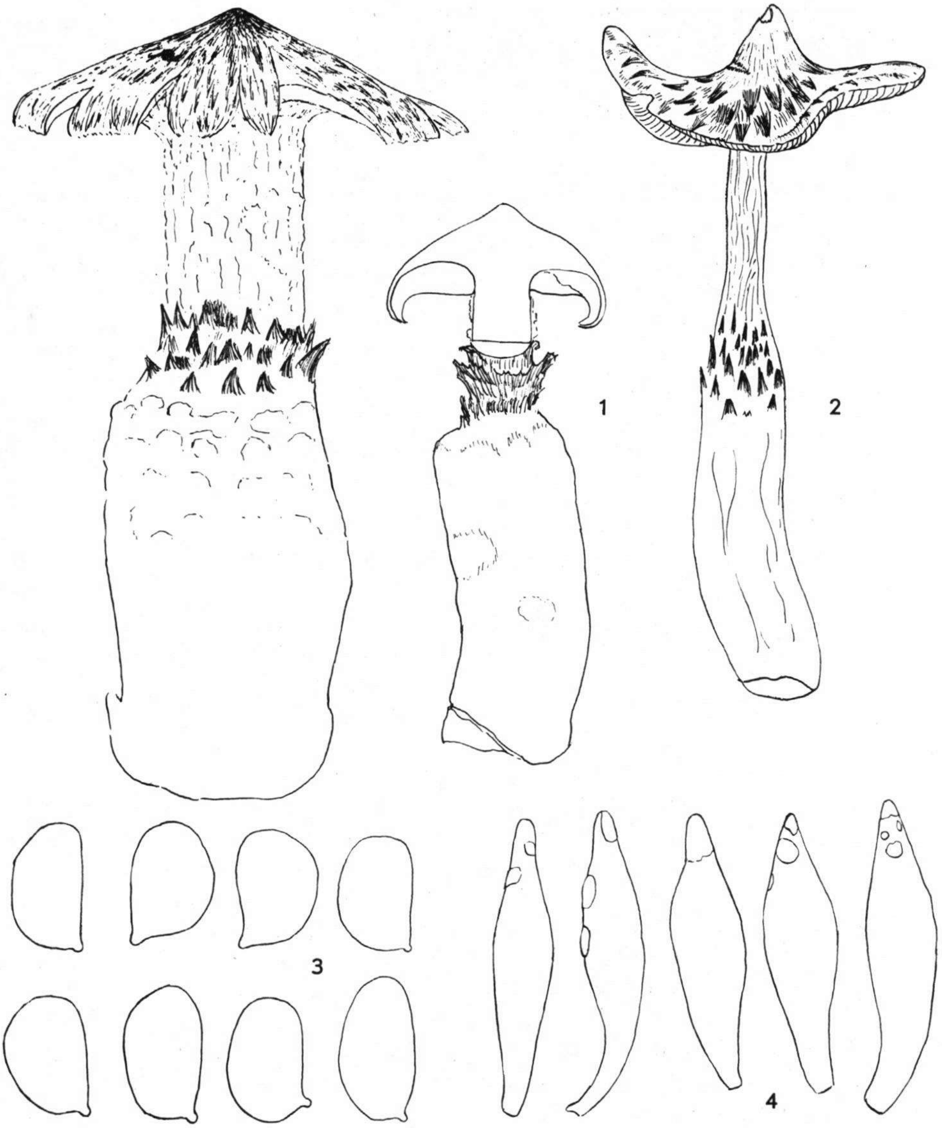
KEY TO THE SPECIES OF SQUAMANITA

- 1. Cortical layer of sclerotial bulb, if present, without spherocysts and disappearing from buds in a very early stage.
  - 2. Cap whitish, yellowish, ochraceous, tawny or reddish brown.
    - 3. Large hymenial cystidia present . . . . *S. umbonata*, p. 334
    - 3. Hymenial cystidia absent.
      - 4. Base of stem and top of bulb set with pointed fibrillose scales; smell indistinct *S. schreieri*, p. 337
      - 4. Base of stem surrounded by a thick rim or low volva; smell distinct.
        - 5. Base of stem surrounded by a 10–15 mm high, sheathing, distant volva; smell rather strong, fruity . . . . *S. tropica*, *p.* 338
        - 5. Base of stem surrounded by an appressed thick rim; smell farinaceous *S.* species?, p. 340
  - 2. Cap greyish lilac, greyish violet, purplish grey or brownish grey.
    - 6. Spores globose, amyloid . . . . *S. scotica*, p. 341
    - 6. Spores ellipsoid, non-amyloid or pseudo-amyloid.
      - 7. Spores non-amyloid, thin-walled . . . . *S. odorata*, p. 342
      - 7. Spores pseudo-amyloid, rather thick-walled . . . . *S. pearsonii*, p. 345
- 1. Cortical layer of sclerotial bulb with chains of spherocysts, covering young fruit-bodies like a volva; cap violaceous grey . . . . *S. paradoxa*, p. 348

Squamanita umbonata (Sumstine) Bas, *comb. nov.*—FIGS. 1–4.

Vaginata umbonata Sumstine *in* Mycologia **6**: 35, pl. 117 fig. 1. 1914. — *Armillaria umbonata* (Sumstine) Murrill *in* N. Amer. Fl. **10**: 38. 1914.

Fruit-bodies solitary, gregarious or subcaespitose. Cap 35–60 mm wide, at first conical with slightly incurved margin, later on expanding and then with a sometimes very pronounced, acute, conical umbo, seldom becoming plano-convex to flat with slightly depressed centre, not hygrophanous, whitish, pale buff to ochraceous buff, fibrillose, the greater part covered with slightly darker ochraceous buff to pale ochraceous brown, coarsely fibrillose, appressed, often pointed, more or less concentrically arranged scales, which tend to darken to brown in older specimens; dry, somewhat shiny at margin, fleshy in centre, thin at margin. Gills moderately crowded, with 1–3 rounded to truncate small ones between each pair, white, rather thin, moderately broad, 3–5 mm wide, slightly ventricose, adnate, emarginately adnate or adnexed, sometimes slightly uncinate, often rather irregular, not or slightly intervenose; edge concolorous, often more or less incised. Stem 25–80 × 5–18 mm, equal or somewhat broadening at base and apex, whitish with buff-coloured floccose-fibrillose or slightly fribillose-scaly zones, arising from a cylindrical to clavate fusiform bulb which measures 30–70 × 24–40 mm (sometimes confluent at base with other bulbs); bulb greyish white with brownish to rusty spots, somewhat felted, sometimes slightly scaly (caused by superficial cracks in cortex), often the greater part covered with particles of soil; the transitional zone between stem and



Figs. 1–4. *Squamanita umbonata*. — 1. Fruit-bodies of Atkinson 20181 (× 1). — 2. Fruit-body of type after dried material (× 1). — 3. Spores of type (× 2500). — 4. Cystidia of type (× 500).

bulb with some irregular rings of tawny-ochraceous to dingy brown, fibrillose, appressed, or erect, obliquely upward-pointing scales or lacerate scales ("fimbriate volva" of Sumstine); sometimes with a slight floccose annular zone near apex (mentioned in Atkinson's description). Flesh white, rather firm. Smell rather strongly musty when crushed. Taste indistinct. Spore print wanting.

Spores (Fig. 3) 6.2–8.7 × 3.8–5.2 μ, ellipsoid to elongate ellipsoid, sometimes subreniform, with small apiculus, thin-walled, colourless, smooth, not reacting with Melzer's solution, not metachomatic in Cresyl Blue, not accumulating Congo Red. Basidia 4-spored, 27–32 × 9–10 μ, with clamp at base. Cystidia (Fig. 4) scattered on sides and edges of gills, (45–)55–88(–140) × 8.5–20 μ, slenderly fusiform to ventricose-fusiform, sometimes sublageniform, with obtuse to acute apex, thin-walled to moderately thick-walled, colourless, sometimes with some refractive bodies, especially in apex. Trama of gills regular, made up of hyphae with equal or inflated cells, from 3–6 μ wide just below subhymenium, to 30(–45) μ wide in the middle; subhymenium densely ramose, very narrow. Scales on cap consisting of (5–)10–25 (–35) μ wide, yellow-brown, radial hyphae, constricted at septa, with slightly thickened, coloured walls (pigment not distinctly encrusting, nor vacuolar). Cuticle as scales but hyphae slightly narrower, paler, and with thinner walls, scales and cuticle gradually passing into each other. Scales on base of stem of similar structure to scales on cap. Trama of stem consisting of longitudinal hyphae, their cells cylindrical to clavate, but always in chains; oleiferous hyphae present, scarce. Trama of bulb irregular, made up of thin-walled sometimes inflated elements, difficult to reinflate. Clamps abundant.

HABITAT.—Terrestrial in woods.

DISTRIBUTION.—North-eastern U.S.A.: Pennsylvania, New York, Massachusetts.

COLLECTIONS EXAMINED.—U.S.A.: Pennsylvania, Fayette Co., Ohiopyle, 12 Aug. 1908, *D. R. Sumstine* (type, 2 dried specim. & photograph, as *Amanitopsis umbonata*, CM); New York, Long Island, Port Jefferson, 26 Aug.–2 Sept. 1904, *G. F. Atkinson 20181* (no specim., but photograph & description, as *Armillaria* n. sp., CUP); Massachusetts, Hampshire Co., Mt. Toby forest, 25 Aug. 1963, *C. Bas 3808* (L, MASS).

In 1918 Atkinson studied the type of *Vaginata umbonata* and concluded that his Long Island fungus was identical and that the species belonged to the genus *Armillaria* (according to a letter of Atkinson to the Carnegie Museum, May 17, 1918). Unfortunately Atkinson's specimens seem to have been lost, but excellent photographs (copies of which were kindly presented by Prof. Dr. R. P. Korf to the Rijksherbarium at Leiden) and a detailed description are kept at Cornell University.

Thus far *S. umbonata* is the only species of *Squamanita* which has cystidia. In other respects this species is rather similar to *S. schreieri*, but the colours are much more faded.

When the present author studied the type, he was not aware of the occurrence of conidia in some species of *Squamanita* and did not specially look for them. In Bas 3808 he did not find any.

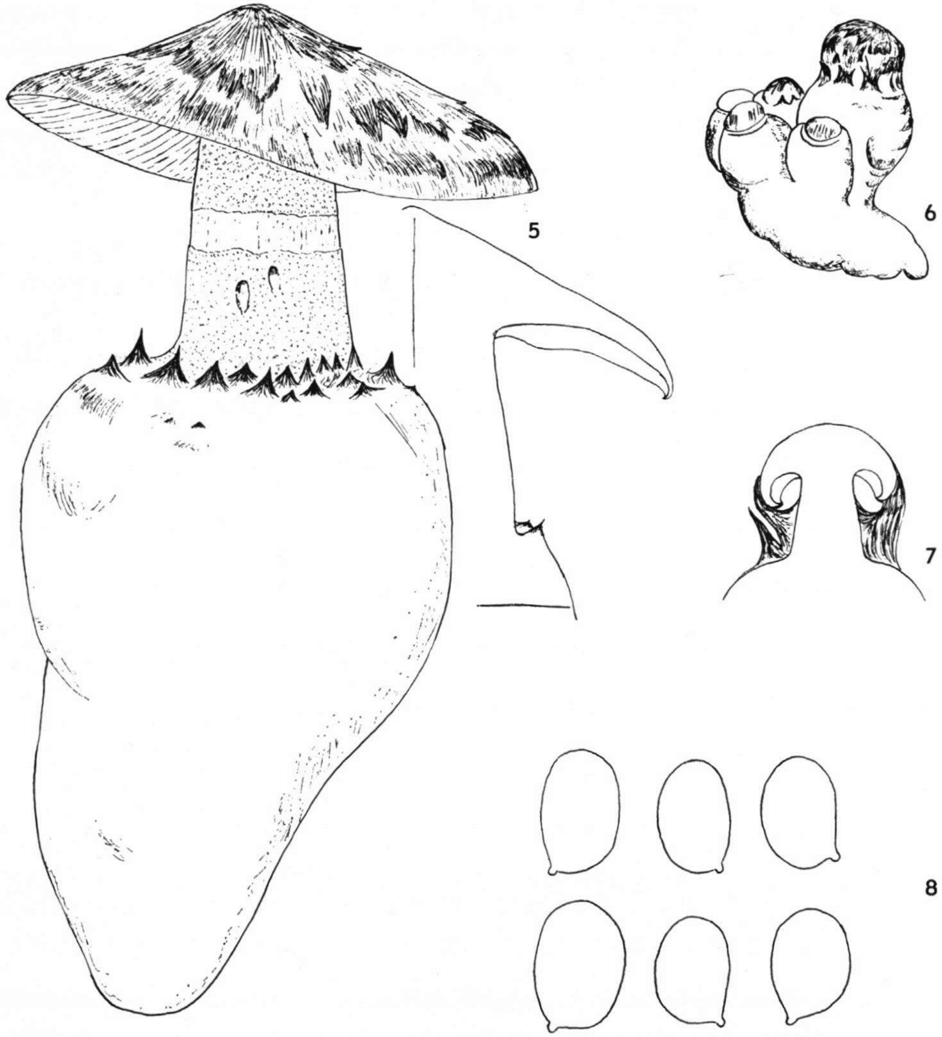
In connection with the interpretation of the part of the fruit-bodies below the scaly zone on the stem, it is significant that Sumstine as well as Atkinson described it as a bulb (a "bulbous root" and a "bulb" respectively).

SQUAMANITA SCHREIERI Imbach. — FIGS. 5–8.

Tricholoma schreieri Maire & Konrad *apud* Maire *in* Bull. Soc. Hist. nat. **36**: 27. 1945; Konrad *in* Schweiz. Z. Pilzk. **25**: 122. 1947; Konrad & Maubl., Agaricales **1**: 346. 1948.

Squamanita schreieri Imbach *in* Schweiz. Z. Pilzk. **20**: 130, 152. 1942 (no Latin descr.; "*Squamamanita*"). — *Squamanita schreieri* Imbach *in* Mitt. naturf. Ges. Luzern **16**: 83. 1946.

Coolia schreieri Huijsman *in* Meded. Nederl. mycol. Ver. **28**: 60. 1943 (nomen nudum).



Figs. 5–8. *Squamanita schreieri*. — 5. Fruit-bodies (× 1). — 6. Cluster of buds (× $^1/_3$). — 7. Section of bud (× 1). — 8. Spores (× 2500; from specimen leg. Bettschen). — Figs. 5–7 after Schreier.

DESCRIPTIONS AND ILLUSTRATIONS.—Schreier *in* Schweiz. Z. Pilzk. **16**: 97–100, pl. 2, 177–179. 1938 (as *Tricholoma* X); Schweiz. Pilztafeln **4**: fig. 1. 1945; Haller *in* Mitt. aargau. naturf. Ges. **24**: 144. 1953 (not seen); Bässler *in* Z. Pilzk. **25**: 113. 1959.

Fruit-bodies gregarious to subcaespitose. Cap 60–100 mm wide, hemispherical to convex at first, becoming plano-conical to flat with sometimes rather acute umbo, with acute margin at first slightly incurved, but soon expanding and often splitting, fleshy, not hygrophanous, whitish to yellow-ochraceous, fibrillose with mostly appressed, ochraceous brown to golden yellow or yellow-brown, fibrillose scales, dry, rather shiny; fibrillose cuticle adnate and confluent with scales. Gills crowded, narrow, 3—4 mm wide, thin, sometimes irregular, whitish, mostly subarcuate, attenuate at both ends, subdecurrent, sometimes adnate or slightly emarginate or nearly free; edge concolorous, often more or less crenulate; small gills abundant. Stem 25–50 × 20–30 mm, subcylindrical, arising from a firm whitish, often turnip-shaped bulb measuring up to 100 × 80 mm which is sometimes confluent with other bulbs; pale yellow, flocculose, at base of stem and on top of bulb with girdles of yellow to yellow-brown, fibrillose, pointed, appressed to erect scales, at apex with a whitish, later on brownish yellow fibrillose annular zone. Flesh white, rather solid, homogeneous. Smell nearly absent. Taste mild. Spore print white.

Spores (4–)5–7 × (3.5–)4–5 μ (6–8 × 5–6 μ according to Bässler, l.c.), broadly ellipsoid, thin-walled, with small apiculus, smooth, colourless, not reacting with Melzer's solution, not metachromatic in Cresyl Blue, not accumulating Congo Red. Basidia 4-spored, sometimes 2- or 3-spored, with clamp at base. Cystidia absent. Subhymenium narrow, ramose. Trama of gills subregular, composed of 4—12 μ wide hyphae, with some scattered oleiferous hyphae. Cuticle and scales on cuticle consisting of more or less parallel-radial, rather thin-walled golden yellow to brownish golden yellow, (5–)12–20 μ wide hyphae, in which pigment probably precipitated against inside of walls; just beneath the cuticle many oleiferous hyphae with distinctly intracellular pigment. Scales on top of bulb and base of stem of same structure as those on cap. Trama of stem made up of 5–15 μ wide, parallel-longitudinal hyphae. Trama of bulb consisting of 4–12(–25) μ wide parallel hyphae; cortex of bulb of interwoven 4–10 μ wide hyphae mixed with elongated ellipsoid to subglobose, up to 135 μ long and 80 μ wide inflated cells. Annular zone consisting of 3–15 μ wide, pale to golden yellow, thin-walled hyphae. Clamps abundant.

HABITAT.—Terrestrial in mixed, mostly alluvial woods on calcareous soil in north-western Switzerland and south-western Germany (Pfalz, near Neustad, Bässler, l.c.), often in the same habitat as *Amanita strobiliformis* (Vitt.) Gonn. & Rab. and *A. echinocephala* (Vitt.) Quél. An enumeration of localities was given by Imbach (1946: 83).

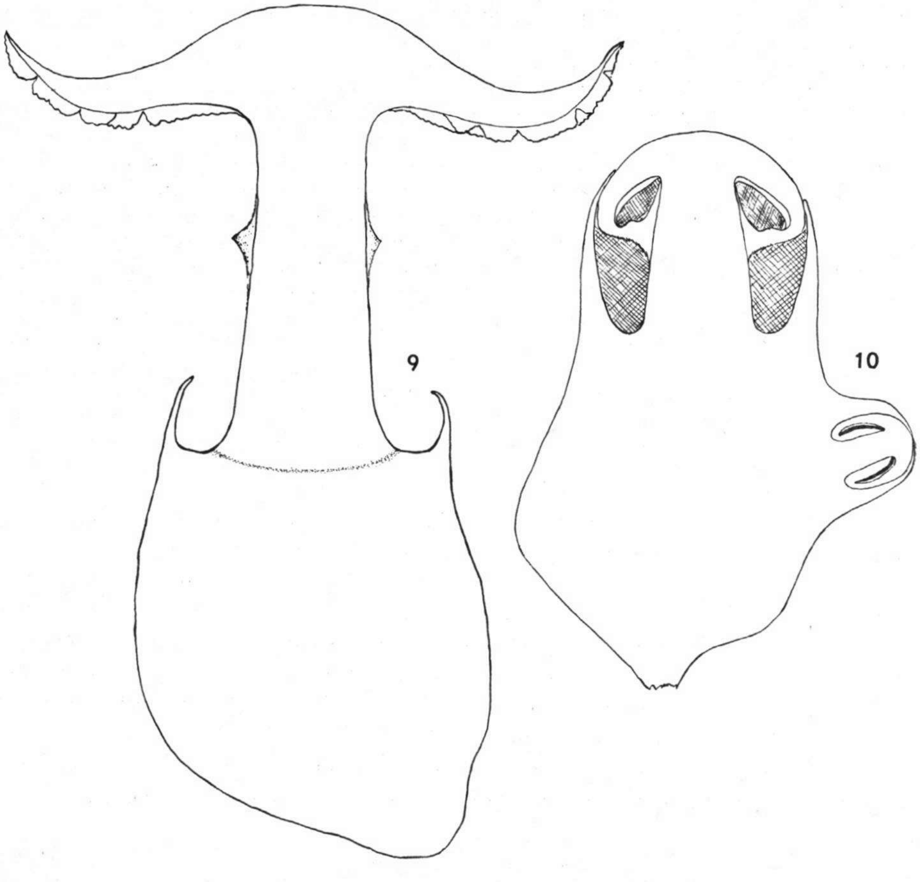
The description above is compiled from those published by Konrad & Maire, Schreier, and Imbach, completed with the author's observations on a fragment kindly sent to him by Mr. W. Bettschen, Biel. No conidia were found on this fragment.

Squamanita schreieri is undoubtly very rare, only a few localities are known in spite of the fact that the human population in its area is very mushroom-minded and this large and magnificent fungus is not likely to escape notice.

SQUAMANITA TROPICA Bas, *nomen provisorium*—FIGS. 9–10

The present species was collected by Mr. E. J. H. Corner in Malaya. Unfortunately the material got lost. However, from the drawings and the extensive descriptions available, it appears that it very probably belongs to the genus *Squamanita*.

Fruit-bodies gregarious or subcaespitose. Cap 80–110 mm wide, becoming plane and gibbous, margin incurved at first, revolute with age, dry or somewhat smeary at first, covered with broad, adpressed membranous to subfibrillose, tawny squamules derived from the breaking up of the veil which is continuous over the tawny disc, paler, yellowish white toward margin, there with adpressed tawny or yellow-tawny fibrils, rarely subsquamulose. Gills very crowded, shortly-decurrent or appearing free and distant owing to dilation of stem apex, rather irregular, white, narrow, 2–3 mm wide, tapering toward stem, breaking up transversely into short lengths; edge irregularly serrate-dentate, subundulate. Stem 60–70 × 16–23 mm, cylindrical, short, tawny-yellow, reticulately fibrillose to the narrow, villose-arachnoid tawny ring which is 20–30 mm from apex, tawny ochraceous and subfibrillose above ring, but extreme apex white and subscabrous; arising from a huge shortly-cylindrical or subclavate bulb, 50–60 × 45–55 mm, sometimes



Figs. 9–10. *Squamanita tropica.* — 9. Section of mature fruit-body (× $^{3}/_{4}$). — 10. Section of bulb with two primordia (× 1).

confluent with other bulbs, whitish, discolouring brownish, nearly smooth on outside, firm, sunk in humus, with a distant, thick, sheathing volva arising from margin of bulb, 5–10 mm from base of stem, forming a 10–15 mm deep cup; thin surface layer of bulb easily separable as a pellicle. Flesh white, thick in pileus, 12–18 mm over centre, 5–6 mm at half-way to margin, firm, fibrillose, somewhat spongy in bulb, and sharply distinct from fibrillose flesh of stem. Smell rather strong, of ethylacetate or pears, as in *Tricholoma caligatum* (Viv.) Ricken.

Spores 6–8 × 4–5 μ, subreniform or ellipsoid, colourless, smooth, with vacuolate contents, not colouring in JKJ. Basidia 26–32 × 8.5–11 μ, 2- and 4-spored, sterigmata 5 μ long. Cystidia absent.

HABITAT.—Terrestrial in humus in jungle.

COLLECTIONS EXAMINED.—Malaya, Johore, near Gunong Panti, 30 March 1930, *E. J. H. Corner* (as *Amanita* 6; material lost, only large pencil-drawings and long description, L).

The following observations were added to the description: "Remarkable for the very large cylindric sterile base, which is immersed in the humus. In some cases the bases of two or three individuals are confluent and in others two individuals appear to rise from the same sterile base, but each has its own volval cupula. Evidently the large base is first formed, surrounded by a thin separable pellicle of its own, then the fruit-body proper develops at the distal end of this structure, endogeneously with a gill-chamber and double veil. The outer veil is continuous with the tissue of the bulb and remains as a cupular volva at the base of the stem, while the second sheaths the stem and covers over the pileus: it is tawny yellow and forms the fibrillose-membranous ring and the fibrillose-membranous squamules over the pileus; these flat squamules as well as the even layer over the disc is fairly easily washed off by rain, so that the pileus becomes almost wholly white."

This species looks very much like a species of *Amanita*, but the mere fact that the narrow, subdecurrent gills have free edges during their development in the gill-chamber, makes it clear that it represents a different genus. And, although the structure of the trama of the gills, the cuticle and the scales on the cap and the occurrence of clamps have not been studied, it is very probable that this species belongs to the genus *Squamanita*. The sclerotial bulb particularly on which more than one fruit-body may develop and the type of gills remind one of that genus.

Squamanita tropica seems to be rather closely related to *S. schreieri* and *S. umbonata*, but is easy to distinguish by the presence of a volva on the top of the bulb and the absence of pointed scales at the base of the stem. This does not necessarily imply that this volva and these scales are homologous (see discussion on p. 353).

SQUAMANITA species?

A description of an unnamed agaric, which may be a species of *Squamanita*, was published by Sandor (1957: 50) from material collected from three localities near München. As the present author did not succeed in contacting Mr. R. Sandor, only an abstract of the description follows.

Fruit-bodies in clusters of 4–8. Cap 30–45 mm, convex to conico-convex, becoming expanded with or without umbo and margin sometimes turned upward, whitish with brownish red centre and with similar spots on limb, radially fibrillose, often with split margin. Gills subdistant, 4–7 mm wide, ventricose, emarginate, whitish with pale but distinct yellowish-pinkish tinge; edge concolorous, turning brownish when bruised, entire. Stem 25–50 × 5–10 mm, white with reddish to blackish red or blackish purple streaks and spots, minutely white felted to pruinose in places, arising from 12–17 mm wide bulbs which are connected by a common basal bulb; each stem at base surrounded by a volva-like, thick rim. Flesh whitish, not turning reddish, slightly hygrophanous, with farinaceous smell and taste, very slightly acrid. Spore print faintly but distinctly pinkish-yellowish.

Spores 4.8–5.6 × 4–4.6 μ, subglobose, faintly hexagonal when seen from above, non-amyloid. Basidia 4-spored, 28–34 × 7–8 μ, without carminophilous granules. Cystidia absent. Trama of gills regular, composed of 8–36 μ wide hyphae. Clamps present.

HABITAT.—Damp *Picea*-forest; October.

DISTRIBUTION.—Germany, Bavaria.

If the spores were not described as being faintly hexagonal when seen from above, there would be little doubt about Sandor's collections representing an unnamed species of *Squamanita*, as was already suggested by Schwöbel & Wandel (1958: 53). The colours, the lack of scales at the base of the stem, the size, the farinaceous smell, and the shape of the spores make it very improbable that Sandor's species is identical with *S. schreieri*, a possibility put forward by Benedix (1958: 53).

SQUAMANITA SCOTICA Bas, *nomen provisorium*—FIGS. 25–26

From the Royal Botanic Garden at Edinburgh a collection was received on loan under the name *S. odorata*, which appeared to represent an unnamed species. As the material is too poor to be designated type, this new species is only provisionally described here. There is no description of the fresh fungus available.

Cap about 9 mm, plano-convex, dark grey-brown with very faint lilaceous tinge (*Amanita porphyria* colour), subfibrillose, rather shiny (dried cap rather strongly rugulose), without evident scales. Gills (broken off) not very crowded, 23, probably adnate, dark brownish grey with violaceous tinge, intervenose. Stem about 20 mm long; the upper 8 mm about 1 mm thick, dark brownish grey with faint violaceous tinge and with loosely appressed, pale, fibrillose covering in places; the lower 12 mm (sclerotial part ?) about 2 mm thick, tawny ochraceous, longitudinally appressedly to innately fibrillose; the pale fibrils on the upper part suggesting a faint annular zone about 2.5 mm below apex; no scales, no volva. Spore print white (according to note on label; now pale cream).

Spores 5.4–6.5 × 5.4–6.3 μ, globose to subglobose, colourless, but sometimes somewhat dingy, slightly thick-walled, smooth, with small apiculus, amyloid, in Cresyl Blue a number of the spores with a metachromatic inner layer (which becomes detached from outer wall when contents contract), but many spores not metachromatic at all; spore-wall not accumulating Congo Red. Basidia 4-spored, few seen, 28–32 × 7–8 μ, with clamp at base; sterigmata remarkably long and slightly inflated in basal part. Edge of gills not studied. Pleurocystidia absent. Cuticle consisting of radial, faintly greyish-violaceous, 4–10 μ wide hyphae, surmounted by some scattered patches of more irregularly radial, darker hyphae of same width; grey-violet pigment membranal. Trama of stem made up of up to 15 μ wide longitudinal hyphae consisting of long cells; hyphae in cortex 3–8 μ wide; at surface loosely interwoven, 4–15 μ wide and greyish-violet by membranal or minutely encrusting pigment. Trama of bulb made up of 4–12 μ wide, longitudinal hyphae consisting of rather short cells; in cortex cells longer and hyphae narrower; at surface of bulb 4–10 μ wide, golden yellow encrusted, slightly irregular, longitudinal hyphae, absolutely without sphaerocysts. Clamps abundant. No conidia observed.

HABITAT.—In meadow land amongst short grass.

COLLECTIONS EXAMINED.—Scotland, Inverness-shire, Aviemore, Rothiemurchus, 16 Sept. 1957, *D. M. Henderson* 3655 (1 dried, broken tiny specimen; E).

Because of the amyloid spores, the species described above is an aberrant one in the present genus. However, the type of cuticle, probably with microscopical remnants of a fibrillose, coloured veil, the colours, the type of pigmentation, the relatively short stem arising from a broader cylindrical body (which may be broken off judging from the basal end of it), the small spores of which some are distinctly dingy, the presence of clamps, all make it probable that this species is a true *Squamanita*.

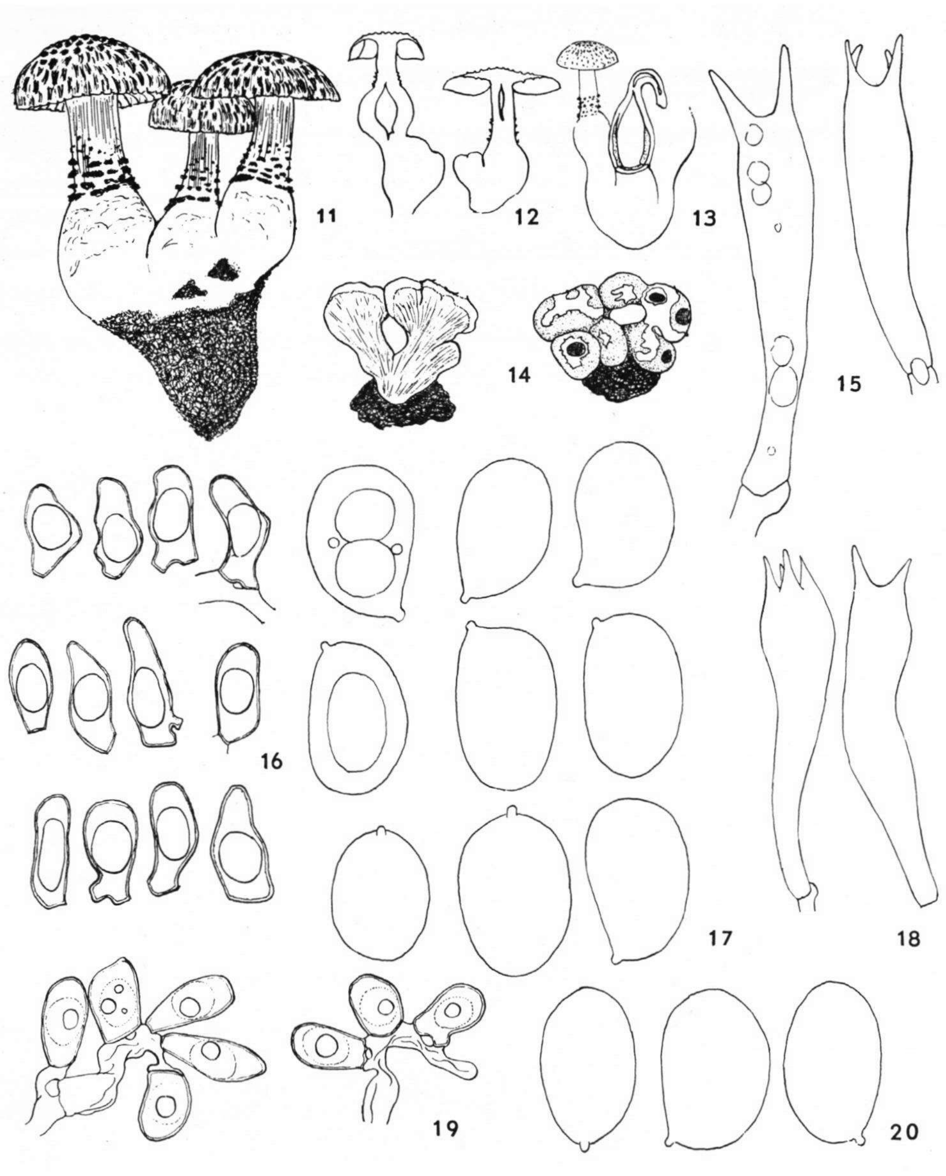
Squamanita odorata (Cool) Bas, *comb. nov.*—FIGS. 11–20

Lepiota odorata Cool *in* Meded. Nederl. mycol. Ver. **9**: 47, pl. 1, fig. 1. 1918. — *Coolia odorata* (Cool) Huijsman *in* Meded. Nederl. mycol. Ver. **28**: 54. 1943 (generic name not validly publ.). — *Tricholoma odoratum* (Cool) Konr. & Maubl., Agaricales **1**: 346. 1948. — *Squamanita odorata* (Cool) Imbach *in* Mitt. naturf. Ges. Luzern **15**: 83. 1946 (nomen provisorium); Moser, Blätter- u. Bauchpilze 66. 1953 (no full reference, no Latin descr.); 2. Aufl., 76. 1955 (ditto); Sing., Agaricales, 2nd Ed., 234. 1962 (ditto).

Coolia odorata (Cool) Huijsman forma *bispora* M. Lange *in* Friesia **4**: 309. 1953 (nom. nud., specific name not validly publ.).

DESCRIPTIONS & ILLUSTRATIONS.—Flora Batava **26**: pl. 2039a. 1924; Pearson *in* Trans. Brit. mycol. Soc. **35**: pl. 3 fig. 2 (exclusive of pl. 3 fig. 1 and descr. on p. 99); Stuntz & Isaacs *in* Mycologia **54**: 279, fig. 4–6, 39. 1962.

Mostly subcaespitose, sometimes forming clusters of more than 10 fruit-bodies. Cap 5–20(–40) mm wide, hemispherical at first, convex to plano-convex later on, sometimes with a broad low umbo, with margin slightly bent in or bent down, not entirely expanding, rather thin, not hygrophanous, dark greyish violaceous to dingy violaceous or lilaceous grey or grey-brown (e.g. Séguy 714), dry, fibrillose, covered with slightly darker scales, small, flat obtuse-angular felted patches in centre, but radially fibrillose, pointed scales, sometimes with recurving tips on limb, making cap minutely squarrose, especially at margin; the latter denticulate-fimbriate when young, easily splitting with age; scales and cuticle adnate. Gills somewhat crowded to rather distant, with 1–3 small gills between each pair, moderately broad, 2.5–7 mm wide, adnate, emarginate, or uncinate, rather thick, sometimes branching, slightly paler than cap, violaceous lilac-grey (e.g. between Séguy 180 and 232); edge concolorous, entire. Stem 10–35 × 3–10 mm, cylindrical or slightly widening below, concolorous with gills, minutely loosely longitudinally fibrillose, slightly shining, at base set with 2–4 incomplete rings of more or less erect floccose-fibrillose, dark violaceous grey-brown warts; stem arising from a 15–30 × 10–25 mm large, rather soft, ochraceous, ochraceous buff to rusty ochraceous, subglobose to ellipsoid, sometimes marginate bulb often fused with other bulbs or with several bulbs seated on a common basal one; outside of bulb felted to subglabrous, sometimes with a slight and narrow, membranous, ochraceous limb on upper part. Flesh pale dingy violaceous to whitish in cap and stem, ochraceous buff in bulb. Smell strong, heavy, sweetish aromatic, reminding the present author of the smell of *Hebeloma*



Figs. 11–20. *Squamanita odorata.* — 11. Fruit-bodies of lectotype (× 1). — 12. Sections of fruit-bodies (× 1). — 13. Abortive fruit-body with conidial layer (dotted area) in wall of bulb (× 1). — 14. Cluster of bulbs producing conidia just below peeling cortex; dark discs are probably primordia (× 1). — 15. Basidia (× 1250). — 16. Conidia (× 1250). — 17. Spores (× 2500). — 18. Basidia of type of *S. odorata* forma *bispora* (× 1250). — 19. Conidiophores (× 1250). — 20. Spores of type of *S. odorata* forma *bispora* (× 2500).

sacchariolens, but sweeter. Taste not distinctive. Spore print white (?; see discussion on p. 351).

Spores 6.5–8.5(–9.3) × 4.2–6.2 μ, ellipsoid, ovoid, obovoid, or subreniform, thin-walled, colourless to slightly dingy, smooth, with small apiculus, not reacting with Melzer's solution, not metachromatic in Cresyl Blue, not accumulating Congo Red. Basidia 27–42 × 6–8.5 μ, 4-spored but a small number 2- and 3-spored, with clamp at base. Cystidia absent. Subhymenium very narrow, about 10 μ wide, ramose. Trama of gills subregular, made up of slightly wavy, 3–20(–30) μ wide, longitudinal hyphae, the broader ones in the centre and constricted at the septa. Cuticle and scales on cuticle consisting of more or less radial, 5–16 μ wide, violaceous-grey to brownish-grey hyphae, the broader ones constricted at the septa; hyphae of scales darker than those of cuticle; cells mostly between 30 and 60 μ long; pigment probably membranal, but some hyphae minutely granular at surface; dark grey oleiferous hyphae rather abundant. Trama of stem composed of 4–14 μ wide, parallel longitudinal, nearly colourless hyphae intermixed with scattered violaceous grey oleiferous hyphae. Scales at base of stem of same structure as those on cap. Cortex of bulb made up of interwoven, brownish yellow encrusted, 2–8(–20) μ wide hyphae with slightly thickened walls, not gelatinized at surface. Trama of bulb consisting of 3–10 μ wide parallel to slightly interwoven, nearly colourless hyphae.

Conidia (Fig. 16) found in Bas 4000 in the wall of the hollow bulb of an abortive or damaged fruit-body (attached to a cluster of three normal ones), forming a layer (looking cartilagineous in dried state) between inner and outer layer of wall and in another collection (Netherlands, Amersfoort, Sept. 1916, leg. A. Joman) on top of some sclerotia, forming a thick layer just below cortex, 9–13 × 4.5–6 μ, irregularly clavate, cylindrical, ellipsoid or broadly fusiform, with clamps when young, later more or less bifid at base, colourless, with moderately thickened wall; conidiophores very thin-walled, colourless, easily collapsing, bearing clamps; older conidia-bearing branches non-septate, sickle-shaped (Fig. 19); development of conidia basifugal.

HABITAT.—Terrestrial in gardens (only in wooded areas), parks, forest plantations and woods; apparently in wooded areas where original structure of soil has been disturbed; in The Netherlands on sandy and loamy soil.

DISTRIBUTION.—Known from nearly 20 localities in The Netherlands, mostly in the central part, from one in Denmark (M. Lange, 1953: 307) and from one in the western U.S.A. (Stuntz & Isaacs, 1962: 279).

SPECIMENS EXAMINED.—NETHERLANDS: Gelderland: Wilp, 2 Oct. 1955, *W. J. Reuvecamp jr.* (L); 19 Sept. 1954, *W. J. Reuvecamp jr.* (L); Wageningen, 18 Oct. 1963, *C. Bas 4000* (L); Utrecht: Amersfoort, Sept. 1916 (3 collections), 23 Sept. 1916, *A. Joman* (L); Huis ter Heide, "Bosch en Duin", 5 Oct. 1916, *A. W. Beckering* (LECTOTYPE!, cluster of specimens in liquid, depicted in Flora Batava **26**: pl. 2039b upper fig., *in* Meded. Ned. mycol. Ver. **9**: fig. 1, pl. 1 fig. 2, and *in* Levende Nat. **22**: 424 fig. 3; L); Huis ter Heide, Sept. 1917, 2 Sept. 1917, Oct. 1917, *J. A. R. van Stolk* (L), Sept. 1920, *H. van Stolk* (L); Bilthoven, Oct. 1933, *B. E. Bouwman* (L). Noord-Holland: Laren, Oct. 1942, *A. J. Sevenhuijsen* (L). — DENMARK: North Seeland, Tokkekøb, 18 Sept. & 9 Oct. 1948, *M. Lange* (C). — U.S.A.: Washington, north of Olympia, Oct. 1951, *Stuntz 6400* (WTU, L).

RECORDS IN DUTCH LITERATURE.—Overijssel: Delden, 1942, *A. C. S. Schweers* (*in* Meded. Nederl. mycol. Ver. **28**: 55. 1943). Gelderland: Wapenvelde, 6 Oct. 1920, *van der Meulen* (*in* Levende Nat. **25**: 294. 1921). Utrecht: Zeist, 1917, *C. Brakman* (*in* Meded. Nederl. mycol. Ver. **9**: 48. 1918); near Loosdrecht, 1938, *J. Daams* (ditto, **28**: 55. 1943); Baarn, 10 Oct. 1937, *anonymus* (*in* Fungus **9**: 28. 1937). Noord-Brabant: Dorst, Oct. 1955, *P. B. Jansen* (*in* Coolia **4**: 19. 1957).

In the original description the spores are said to be pinkish, but Cool merely observed them under the microscope. It seems that the only spore print (a thin one) was obtained by A. C. S. Schweers, which one was white (Huijsman, 1943: 55). But under high power a number of the spores are distinctly dingy and it is to be expected that a thick spore print will show some colour. However, the sporulation seems to be rather poor.

M. Lange's (1953: 309) forma *bispora* has no taxonomical value. The present author found 2-, 3-, and 4-spored basidia in the type-material of that form, as well as in other collections of *S. odorata*. Clamps were found to be present too.

The distribution of *S. odorata* is remarkable. The species has been known now for nearly 50 years and still its area in Europe seems to be almost restricted to the central part of The Netherlands. The only correct European record from outside this area, is that from Denmark. The recent discovery of *S. odorata* in the western U.S.A. by Stuntz & Isaacs (1962: 279) makes it probable that its area of distribution is a very disjunct one. However, its sudden appearance in several places in The Netherlands in 1915–1917 and its ecology (probable preference for disturbed forest-soil) might indicate that it is imported into Europe. It is remarkable that *S. paradoxa* seems to have the same type of distribution pattern. It will be very interesting to know more about the ecology of both species.

The development of *S. odorata* has been studied by Reijnders (1952: 23) and will be discussed on p. 352.

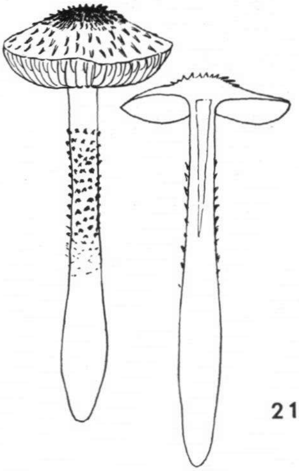
The discovery of chlamydospores on some of the sclerotial bulbs raises the question of what the function of the bulbs can be. Do they produce first chlamydospores and then fruit-bodies or do they produce only chlamydospores when the fruit-bodies fail to develop, or are some of the bulbs specialized in producing chlamydospores ? It is possible that the bulbs have a longer life than the fruit-bodies. It is even possible, though in view of the soft consistency rather improbable, that they are perennial, and that the process of producing fruit-bodies and/or chlamydospores is repeated.

Squamanita pearsonii Bas, *spec. nov.*—FIGS. 21–24

MISAPPLICATION.—*Tricholoma odoratum* (Cool) Konrad & Maubl. *sensu* Pearson *in* Trans. Brit. mycol. Soc. **35**: 99, pl. 3 fig. 1. 1952.

Pileus 25 mm latus, convexus, dein applanatus, griseo-lilaceus vel violaceo-lilaceus, squamulis obscure purpureis fibrillosis ornatus. Lamellae subconfertae, adnatae vel emarginatae, albidae. Stipes 55 × 5 mm, flocculoso-fibrillosus, apice violaceo-lilaceus, infra pallide lilaceus vel sordide ochraceus verrucisque erectis obscure purpureis ornatus. Bulbus elongatus, ochraceus. Sporae 7–9(–10) × 4.5–5(–6) μ, ellipsoideae vel elongato-ellipsoideae, interdum subovatae, hyalinae, pseudo-amyloideae. Cystidia nulla. Pilei cuticula squamulaeque hyphis radiatis 3–25 μ latis violaceo-griseolis compositae. Trama lamellarum regulare. Fibulae creberrimae. — TYPUS: R. W. G. Dennis s. n., 24 Sept. 1950, Scotland, Rothiemurchus Forest (K).

Cap 25 mm wide, convex then nearly flat, greyish lilac to violaceous lilac, dry, fibrillose, sometimes slightly shiny, with dark purplish, fibrillose, rather narrow, pointed scales, appressed and scattered at margin, erect and crowded on disc.



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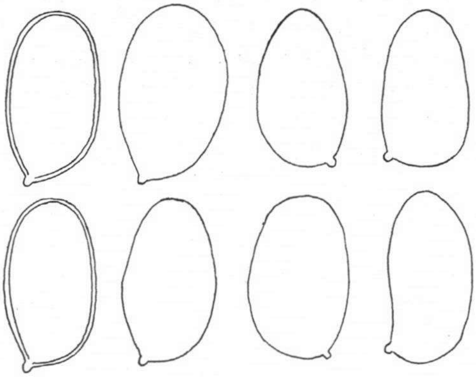

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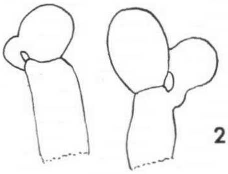

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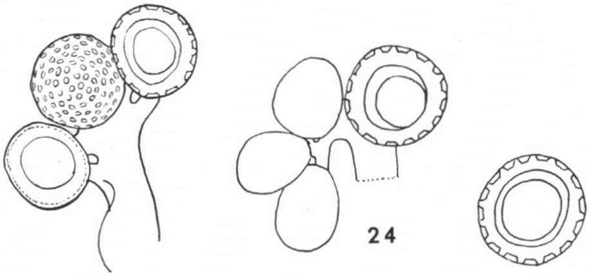

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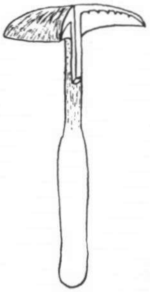

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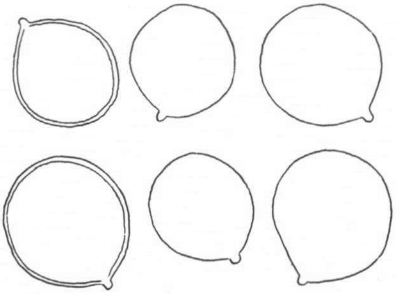


26

Figs. 21–24. *Squamanita pearsonii.* — 21. Fruit-bodies (× 1; after Pearson). — 22. Spores (× 2500). — 23. Young conidiophores (× 1250). — 24. Older conidiophores and chlamydospores (× 1250).

Figs. 25–26. *Squamanita scotica.* — 25. Fruit-body, reconstructed from dried broken specimen (× 2). — 26. Spores (× 2500).

Gills rather distant, ventricose, adnate-emarginate, moderately broad, whitish, intervenose, with 1–3 attenuate small gills between each pair; edge concolorous, entire. Stem about 30 × 5 mm, slightly tapering upward, probably becoming more or less hollow, from violaceous lilac at apex to dingy yellow below, flocculose-fibrillose, lower two thirds set with dark purple erect to slightly recurved fibrillose small scales; lower part gradually passing into a slender fusiform, about 20 × 8 mm large bulb, ochraceous yellow, subfibrillose under a pale very thin pruinose covering (conidia!). Flesh violaceous in cap, paler in stem and yellow in bulb. Taste and smell unknown. Spore print wanting.

Spores 7.2–8.9(–10.1) × 4.3–5.1(–6.0) μ, ellipsoid to elongate, sometimes elongate-subovoid, mostly colourless, but some distinctly dingy, thick-walled (wall about 0.8 μ thick), with granular contents and with very small apiculus, without germ pore or callus, smooth, distinctly pseudo-amyloid (double wall equally colouring), not metachromatic in Cresyl Blue [but contents blue with 2(–3) reddish bodies; nuclei?], strongly colouring in Congo Red. Basidia 4-spored, sometimes 3- or 2-spored, 27–32 × 7.3–9.7 μ, with clamp at base; sterigmata up to 5.5 μ long. Cystidia absent. Edge of gills fertile. Trama of gills regular, consisting of 4–25(–40) μ wide hyphae, the broader ones constricted at the septa; subhymenium narrow, 10–15 μ wide, ramose. Cuticle made up of loosely interwoven to subradial, 3–25 μ wide, pale greyish, thin-walled hyphae. Scales on cap consisting of parallel, radial, rather dark brownish grey, slightly thick-walled, 3–20 μ wide hyphae and some scattered dark brown-grey oleiferous hyphae. Scales on stem of same structure as those on cap; hyphae 8–16 μ wide. Covering of bulb consisting of 3–12 μ wide more or less parallel, longitudinal, brownish yellow hyphae and densely branching conidiophores and conidia. Trama of bulb consisting of longitudinal, parallel to slightly interwoven, 3–10 μ wide hyphae and some brownish yellow oleiferous hyphae. Trama of stem consisting of longitudinal, parallel 3–30 μ wide, very pale hyphae and some yellowish grey oleiferous hyphae. Pigments: (lilaceous-)brownish grey pigment membranal (or very minutely encrusting ?) but distinctly encrusting in some of the narrowest hyphae of scales on stem and intracellular in oleiferous hyphae; brownish yellow pigment difficult to localize, probably membranal, but intracellular in oleiferous hyphae. Clamps abundant.

Conidia (Fig. 24), chlamydospores, 9.5–12.3 × 8.5–10.4 μ, at first colourless and obovoid, becoming brownish yellow and globose, very thick-walled; wall not reacting with Melzer's solution, consisting of at least 3 layers, when mature the outer one hyaline colourless, embedding the truncate-conical brownish yellow warts on the middle layer; in Cresyl Blue outer layer not colouring, middle layer becoming lilac pink to blue, inner layer lilac-red. Conidiophores colourless, thin-walled, densely branching, with clamps, the older conidia-bearing branches non-septate, sickle-shaped.

HABITAT.—Type found under *Pinus silvestris* amongst moss.

DISTRIBUTION.—Scotland.

COLLECTION EXAMINED.—SCOTLAND, Inverness-shire, Aviemore, Rothiemurchus Forest, 24 Sept. 1950, *R. W. G. Dennis* (type: 2 dried, broken but nearly complete specimens, K).

Undoubtedly *S. pearsonii* differs widely from *S. odorata*. The spores are thick-walled and distinctly pseudo-amyloid. Heating of a small part of a gill in ammoniacal Congo Red renders the spores much more coloured than the underlying tissue; this is not the case in *S. odorata*. The gills are whitish. Moreover the conidia are globose and ornamented in *S. pearsonii* and irregularly clavate to fusiform and smooth in *S. odorata*.

As the type is the only collection known, it is difficult to say whether the much more slender habit of the type-specimen, especially of the bulb, is a distinctive character too.

The pseudo-amyloid spores and the scaly cap of *S. pearsonii* remind one of the genus *Lepiota*. However, the adnate gills and the remarkable chlamydospores on the bulb make it clear that this is a true *Squamanita*.

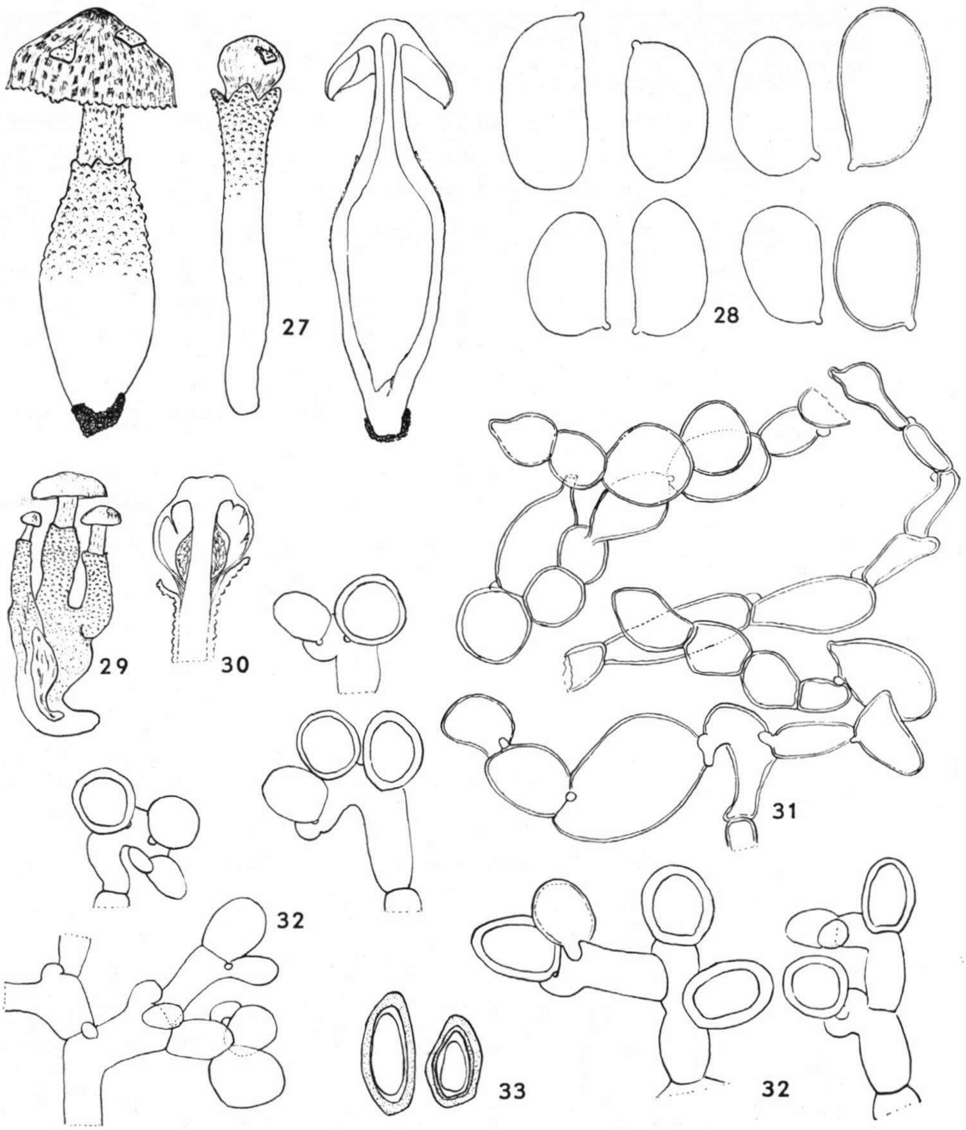
Squamanita paradoxa (A. H. Sm. & Singer) Bas, *comb. nov.*—FIGS. 27–33

Cystoderma paradoxum A. H. Sm. & Singer *in* Mycologia **40**: 454, fig. 1. 1948.

DESCRIPTIONS AND ILLUSTRATIONS.—Herink *in* Česká Mykol. **8**: 60. 1954; Horak *in* Z. Pilzk. **28**: 16, fig. 2. 1962; *in* Mitt. schweiz. Anst. forstl. Versuchsw. **39**: 73, pl. 3 fig. 17. 1963.

Gregarious to subcaespitose. Cap 8–35 mm wide, convex to plano-convex, often with a broad, low umbo, but sometimes flat or even slightly depressed in centre, margin slightly incurved at first, becoming straight and somewhat lacerate later on, thin, not hygrophanous, only slightly translucent-striate at margin when extremely wet, pallid lilac to dark violaceous drab or lilaceous grey, appressedly fibrillose, at margin sometimes appressedly fibrillose-scaly, dry, superficial fibrils becoming blackish with age; young buttons entirely covered with a brownish ochraceous ("Sudan brown" according to Smith & Singer), granular-warty, membranous veil, leaving patches on young caps but mostly soon completely disappearing. Gills 10–24, with 0–3 rounded to attenuate small ones between each pair, subdistant to distant, thick, broad, arcuate-adnate, subdecurrent, broadly adnate or adnexed, sometimes anastomosing, intervenose, lilaceous grey to brownish vinaceous (slightly paler than cap); edge concolorous, entire. Stem 8–25 × 1–6 mm, subcylindrical, pale lilac to pale violaceous, fibrillose-subsquamulose, arising from a stem-like to ventricose fusiform, 20–60 × 4–18 mm large, ochraceous brown to tawny ochraceous brown, granular-warty, solid to hollow sclerotial body often confluent with other such sclerotia or inserted on a common basal body; sometimes lower parts of sclerotium whitish felted. Flesh in stem and cap greyish violaceous, greyish lilac or pale brownish drab, in sclerotium pale with ochraceous brown outline. Smell not distinctive according to Smith & Singer; intensively perfume-like when young, fetid with age according to Horak; obnoxious as in *Lactarius porninsis* according to Herink. Taste mild. Spore print white (Horak).

Spores (7.7–)8.1–10.8 × 4.5–6.1 μ, elongate-ellipsoid, colourless to distinctly dingy, with moderately thickened hyaline wall and granular contents, binucleate, with small apiculus, non-amyloid to weakly but distinctly pseudo-amyloid; wall probably double, slightly accumulating Congo Red, distinctly metachromatic in Cresyl Blue. Basidia 4-spored, 34–43 × 7.5–10 μ, with clamps at base, non-carminophilous; sterigmata up to 6.5 μ long, Cystidia absent. Edge of gills fertile. Trama of gills regular, composed of about 5 μ wide hyphae just beneath subhymenium to chains of up to 35 μ wide cells in the middle; subhymenium ramose, very narrow, about 10 μ wide. Cuticle made up of 4–18 μ wide, more or less radial (at surface sometimes irregular arranged), pale brownish grey hyphae, constricted at septa, probably with membranal pigment, gradually passing into denser trama below, with some grey-brown oleiferous hyphae; very rarely cells of most superficial hyphae so short that they are nearly isodiametric. Brownish ochraceous veil composed of thin-walled and colourless to slightly thick-walled and yellow brown encrusted, globose, ellipsoid, ovoid, or citriform, up to 55 × 35 μ large cells in chains forming



Figs. 27–33. *Squamanita paradoxa.* — 27. Fruit-bodies (× 1). — 28. Spores (× 2500). — 29. Cluster of fruit-bodies (× 1; after dried material). — 30. Section of bud (× 5). — 31. Chains of cells on limb of volva (× 550). — 32. Conidiophores (× 850). — 33. Mature chlamydospores (× 850). All figures from Horak 61/152.

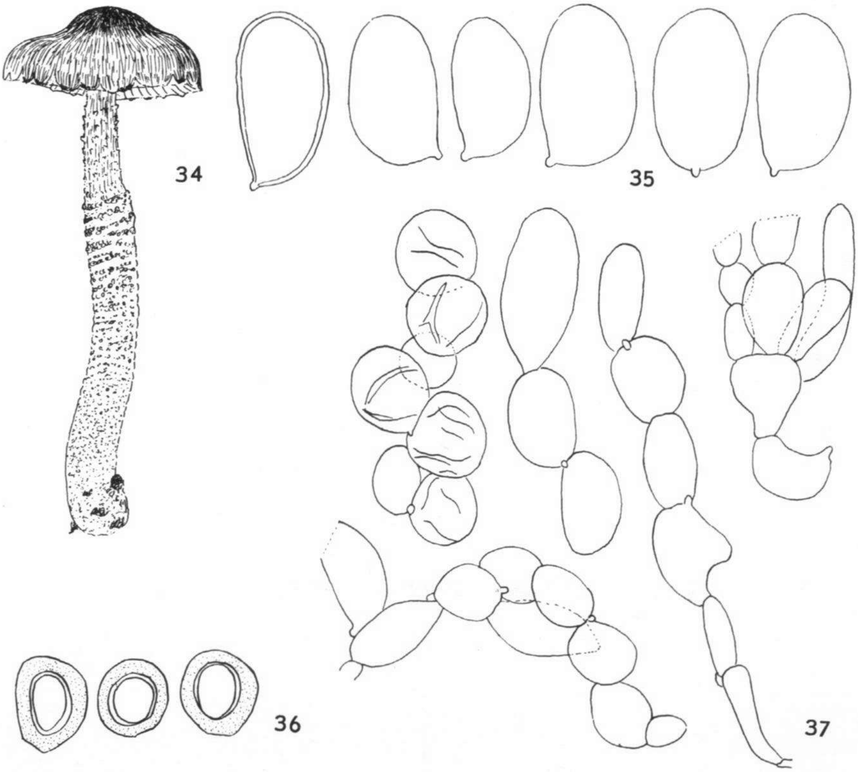
the warts and more or less parallel, colourless to pale yellow-brown hyphae forming the layer on which the warts are situated. Yellow-brown-pigment turning brownish red in KOH. Tissue of warts on sclerotial part often intermixed with numerous chlamydospores (very few in paratype). Covering of stem consisting of 6–12 μ wide, loosely interwoven pale hyphae; flocks formed by free ends. Trama of stem: 4–22 μ wide, pale greyish, longitudinal hyphae. Trama of stem-like part of sclerotial body: 2.5–10 μ wide, longitudinal, nearly colourless hyphae and many coiling-interweaving hyphae of same width. Clamps abundant.

Conidia (Fig. 33) 11–16(–19) × 7.5–12.5 μ, very thick-walled, colourless to pale brownish yellow, ovoid, ellipsoid, subglobose, broadly fusiform or fusiform; conidial wall composed of at least 2 layers, fixing Congo Red rather strongly, inner layer (sometimes also outer layer) strongly metachromatic in Cresyl Blue. Conidiophores colourless, 4–6 μ wide, septate, thin-walled, branching hyphae with clamps; conidia-bearing branches non-septate sickle-shaped.

HABITAT.—Terrestrial among mosses in woods or near scattered trees.

DISTRIBUTION.—U.S.A. (Oregon), Czechoslovakia, Switzerland.

COLLECTIONS EXAMINED.—U.S.A., Oregon, Mt. Hood National Forest, 27 Oct.



Figs. 34–37. *Squamanita paradoxa.* — 34. Fruit-body of type (× 1; after Smith & Sing.). — 35. Spores (× 2500). — 36. Chlamydospores found on stem (× 850). — 37. Chains of cells on limb of volva (× 550). — Figs. 35–37 from paratype Smith 28341.

1947, *A. H. Smith 28341* (paratype, MICH). — CZECHOSLOVAKIA, Bohemia, Kluky near Hradec Královê, 2 Oct. 1949, *Zd. Schaeffer* (herb. J. A. Herink 651/49; fragments in L). — SWITZERLAND, Graubünden, Dischmatal, 27 Sept. 1961, *E. Horak 61/152* (Herb. Horak).

The above description is compiled mainly from the descriptions of Smith & Singer (1948: 454) and Horak (1962: 16, 1963: 73) and supplemented with the present author's observations on the dried material of the collections mentioned above.

Smith & Singer reported the odour of the American material as being indistinct, while Horak as well as Herink (1954: 60) mentioned a strong smell. The spores of Smith 28341 are slightly but distinctly pseudo-amyloid and those of the two European collections not or perhaps very faintly so. Moreover the inflated cells of the outer veil are less strongly pigmented and thinner in the American material than in the European. However, these slight discrepancies seems not to warrant the description of the European form as a distinct taxon.

The conidia are very abundant on the surface of the stem-like sclerotium in Herink's as well as in Horak's material. In Smith 28341 conidiophores have not been observed, but as several loose condidia occur among the cells of the covering on the sclerotial body, apparently conidia are produced in the American form too.

There is some doubt about the colour of the spores. Horak's spore print of the present species is extremely thin; too thin indeed to be sure that the spores are really white. In Smith 28341 there are accumulations of spores on the gill, which are macroscopically visible as rather dark brown (!) stripes. Under high magnification these spores are distinctly hyaline dingy. This colour is not due to the fact that one is looking through many spore-walls at once, owing to the accumulation of the spores. Individual dingy spores are distinguishable from more scattered colourless spores elsewhere on the gills. It is as if the accumulations of spores become coloured by diffusion of a pigment from the inner parts of the gill. The same phenomenon was observed to a lesser degree in *S. odorata*, *S. pearsonii*, and *S. scotica*.

In none of the published descriptions of the present species are an annulus or other remnants of a velum partiale mentioned. However, in a very young bud (Fig. 30) in Horak's collection, the space between the edges of the gills and the stem is stuffed with a very loose, whitish fibrillose tissue, consisting of 4–10 μ wide colourless, thin-walled, rather short-celled hyphae, more or less constricted at septa and with clamps. Apparently this tissue is so little coherent that it is found on the elongated stem only as a slight fibrillose coating.

DISCUSSION

The genus *Squamanita* as treated in the present paper shows a great deal of variation in certain important characters. The spores for instance may be thin- or thick-walled, non-amyloid, amyloid, or pseudo-amyloid, orthochromatic or metachromatic in Cresyl Blye, strongly colouring in ammoniacal Congo Red or not.

Apparently complications arise only in species which have thick-walled spores.

The pale to yellow-brown species and *S. odorata* of the violet-grey group have thin-walled spores, which are non-amyloid, orthochromatic in Cresyl Blue, and do not accumulate Congo Red. However, the other three species of the violet-grey group have more or less thick-walled spores and those are pseudo-amyloid and accumulate Congo Red in two of the species, and are amyloid and do not accumulate Congo Red in the third. In one of the species characterized by pseudo-amyloid spores, the latter are, in addition, distinctly metachromatic in Cresyl Blue.

The combination of species with amyloid, non-amyloid and pseudo-amyloid spores in one genus is rare but does occur, e.g. in *Cystoderma* (Singer 1962: 485). Moreover, a number of other characters (veils, chlamydospores, bulb, pigmentation) makes a close relationship of the species concerned very probable.

The interpretation of veils and velar remnants offers a real problem in *Squamanita*. In *S. paradoxa* (Fig. 27) and *S. tropica* (Fig. 9) a more or less membranal volva seems to represent the universal veil. In *S. tropica* (Fig. 9), *S. schreieri* (Fig. 5), and perhaps *S. paradoxa* (Fig. 27) there seem to be more or less developed remnants of a partial veil. And last but not least in *S. odorata* (Fig. 11), *S. pearsonii* (Fig. 21), *S. schreieri* (Fig. 5) and *S. umbonata* (Fig. 1) the base of the stem bears a number of pointed scales, which find their equals on the cap.

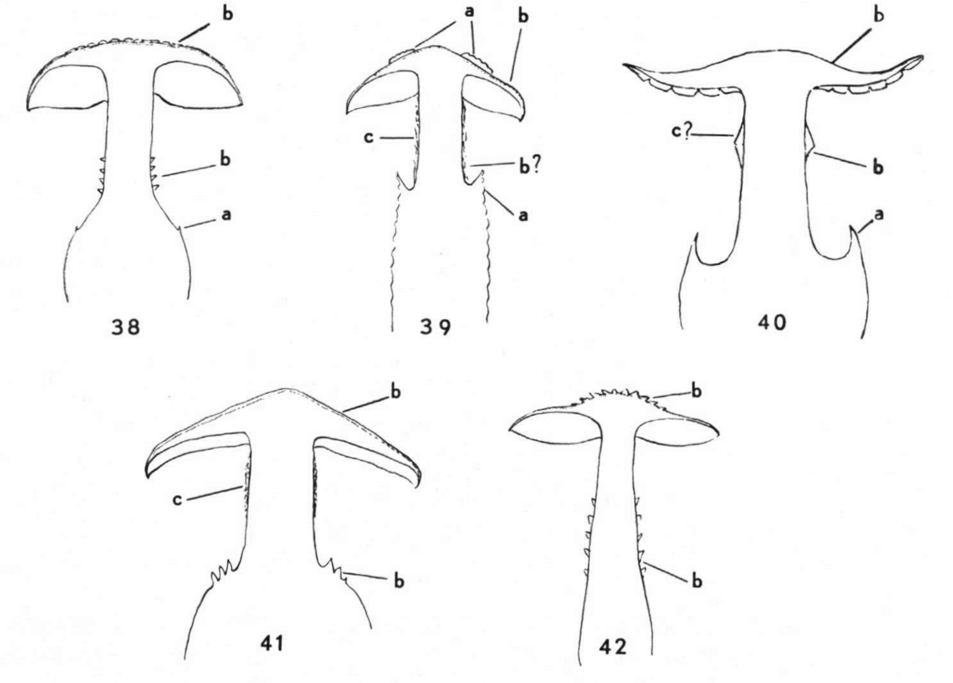
Reijnders (1952: 23) studied the development of *S. odorata* and found that the hymenium in that species develops entirely endogeneously on account of the fact that in the primordium the margin of the cap is confluent with the base of the stem. A partial veil seems to be lacking. The peripheral layer of the very young cap is differentiated from the trama of the cap, as its hyphae run parallel and the cells are shorter and broader than those of the trama. From this peripheral layer, called the universal veil by Reijnders, the scales on the cap and on the base of the stem (Fig. 38b) in adult specimens are derived.

It is interesting that Reijnders found that the cortical layer of the sclerotium-like bulb covers the very young primordium. This layer consists of hyphae which are sometimes thick-walled, becomes gelatinous in places, and disappears very early according to Reijnders. From his own observations the present author may add that in some adult fruit-bodies of *S. odorata*, there is a very faint limb (Fig. 38a) on the top of the bulb, just below the scaly zone on the base of the stem. It is remarkable that Reijnders did not call this layer a veil. Perhaps he considered the bulb not a part of the fruit-body. Still it is difficult to see the difference between the situation in *Squamanita* and that in *Amanita* and *Volvariella*, where the fruit-body also develops inside a bulb and where the universal veil is continuous with the bulb.

Consideration of the facts revealed by Reijnders about the development of *S. odorata* renders the velar structure of *S. paradoxa* less paradoxical than they seem to be at first sight. It is very probable that the brownish ochraceous warty veil (Fig. 39a), which covers the young buds and continues over the surface of the bulb in that species, is homologous with the early disappearing cortical layer in *S. odorata* (Fig. 38a). The layer, which in *S. odorata* is called universal veil by Reijnders, is less developed in *S. paradoxa* where the cap and the stem are merely fibrillose-subsquamulose. However, in a section of a dried bud (Fig. 30) it was found that the lower part of the fibrillose covering of the stem (Fig. 39b) is probably derived from the outer layer of the margin of the cap.

In the same section the space between the edges of the gills and the stem is filled with loose, whitish hyphae. There seems therefore to be a slight partial veil in *S. paradoxa*, which forms the upper part of the fibrillose covering of the stem (Fig. 39c). Consequently *S. paradoxa* would have three veils, although two of them are only slightly developed.

In *S. tropica* there is a distinct volval limb around the base of the stem (Fig. 40a). As there are no scales at the base of the stem as in *S. odorata* and *S. schreieri*, one is tempted to consider this volval limb of *S. tropica* as being homologous with the scales on the base of the stem of the other species. But from Corner's observation (see p. 340) that the outer veil forming the cupular volva is continuous with the tissue of the bulb, it is more plausible that this limb is homologous with the ochraceous-brown veil of *S. paradoxa* and the rudimentary cortical layer in *S. odorata*. The more so as Corner described a second veil which is tawny yellow, sheaths the stem, covers the cap, and forms the ring and the flat squamules on the cap (Fig. 40b). It is



Figs. 38–42. Schematical fruit-bodies of species of *Squamanita*. — 38. *S. odorata*. — 39. *S. paradoxa*. — 40. *S. tropica*. — 41. *S. schreieri*. — 42. *S. pearsonii*. — Letters *a*–c referring to remnants of veils. a, outer universal veil, b, inner universal veil, c, partial veil.

apparently the ring, or at least a part of it, of *S. tropica* which is homologous with the scales on the base of the stem in *S. odorata* and *S. schreieri*. From Corner's drawing one gets the impression that a partial veil is also present and participates in the formation of the ring. Probably the reticulate fibrillose covering of the stem between volva and ring is a remnant of the second outer veil, which has been torn apart by the relatively strong elongation of the basal part of the stem in this species.

In *S. schreieri* there is evidence again of a true partial veil (Fig. 41c). The scales on the base of the stem are formed by the inner universal veil (Fig. 41b). The outer universal veil (the rudimentary cortical layer in *S. odorata*; the volva in *S. paradoxa* and *S. tropica*) seems to be lacking but may be found perhaps in very young primordia.

In *S. umbonata* the situation seems to be the same as in *S. schreieri*. In the few fruit-bodies known of *S. pearsonii* only the remnants of the inner universal veil are evident (Fig. 42b).

To summarize it may be said that in the genus *Squamanita* probably three veils are potentially present, although seldom all are present in one species. First, there is the outer universal veil, which is continuous with the cortex of the bulb and consequently covers the young primordium and the bulb. This veil is very obvious in *S. paradoxa* and *S. tropica*, but only visible in very young stages of *S. odorata*. As *S. odorata* is the only species of which the development has been studied, it is well possible that such a rudimentary outer universal veil is present in some of the other species too. In the author's opinion this veil is the one that is comparable to the universal veil of such genera as *Amanita* and *Volvariella*.

The second veil is here provisionally called the inner universal veil. It covers the primordial cap, gills and stem. It is not sharply different from the trama of the cap and is attached to that part of the primordium which is going to form the base of the stem. Later on, its remnants form the fibrillose to scaly covering of the cap and of the base of the stem: more rarely it seems to participate in the formation of an annulus together with the partial veil (*S. tropica*). This inner universal veil is apparently present in all species studied but very evidently so in *S. odorata*, *S. pearsonii*, *S. tropica*, *S. umbonata*, and *S. schreieri*. It seems to be one of the important features of *Squamanita*.

The third veil is the partial veil of which evidence is found in *S. umbonata*, *S. schreieri*, *S. tropica*, and *S. paradoxa*. However, it is never very strongly developed. In *S. paradoxa* it seems to fill the space between the edges of the gills and the stem.

It hardly needs to be stressed that many of the facts mentioned above have to be checked on further collections, as only scanty material was available of most of the species treated in this paper.

As the production of chlamydospores on or in the fruit-bodies of Agaricales is rather rare, it is remarkable that three of the seven species of *Squamanita* described in this paper, viz. *S. odorata*, *S. pearsonii*, and *S. paradoxa*, appear to produce terminal chlamydospores (aleuriospores) in profusion on or just below the cortex of the bulb.

Moreover, the chlamydospores of those three species are so different that they can be distinguished at once (Figs. 16, 24, 33): yet they are all formed in the same peculiar way, probably not described before, viz. by the proliferation of clamps, which is clearly illustrated in the Figs. 23 and 32.

One may look upon this way of producing conidia as a rather extraordinary one. However, from literature it appears that proliferation of clamps is perhaps a common way of multiplication of asci and basidia. In this connection the opinion of Greis (1938) is very interesting. That author considered the production of many asci in a small area by means of proliferation to be the main function of the clamp of the Ascomycetes. His figures show how, in this manner, clusters of asci are formed in *Pyronema* and *Sordaria*. In the Basidiomycetes the clamp would be in the process of losing its function. But still in a number of cases, e.g. *Hypholoma* and *Corticium* according to Greis, proliferation of clamps at the base of basidia would occur.

Rogers (1936) described how, by means of proliferation of clamps at the base of basidia in *Sebacina prolifera* Rogers, unilateral cymose clusters of basidia are formed. Heinemann (1963: 453) considered the group of *Hygrophorus psittacinus* and related species to be of subgeneric rank, to be named *Hygrophorus* subgenus *Gliophorus* (Herink) Heinemann, on account of the bifid basidia and the therefore reticulate structure of the subhymenium. His fig. 40c especially shows that very probably this structure is due to the formation of basidia by proliferation of clamps. By including some species with a dry cap and stem in this subgenus *Gliophorus*, Heinemann even made the structure of the base of the basidia and the subhymenium the key-character of it.

The foregoing are only examples of proliferation of clamps at the base of reproductive cells. However, Routien (1948) described the formation of complex branching systems of hyphae in cultures of *Polyporus cinnabarinus* Fr. by proliferation of clamps at the septa of hyphae. With these examples in mind it will be clear that the way of formation of conidia in *Squamanita* is less peculiar than one would think at first sight.

The fact that the conidia in *Squamanita* are formed on the bulbs, raises the question whether these bulbs have a longer life than the fruit-bodies. It is even possible that the production of conidia on the bulbs is more or less independant of the formation of basidiocarps. As far as is known at present, conidia and basidiocarps occur simultaneously in *S. pearsonii* and *S. paradoxa*. However, in *S. odorata* bulbs are found on which conidia are born at a time when the primordia are still very small (Fig. 14). If it should prove that the growth of basidiocarps on such bulbs is suppressed in favour of the formation of conidia, these bulbs would be comparable to the clavarioid conidiocarps which Singer (1952: 73) described for *Armillariella ditopa* Sing. from South America.

It is a problem what to call the tubers on which the basidiocarps in *Squamanita* develop. Singer (1962: 25) tentatively named them carpophoroids, which he defined as sterile bodies and gasteroid carpophores that have no visible function, formed the same way as carpophores. In other words, carpophoroids are sterile bodies replacing carpophores or aberrant carpophores which have adopted a gastroid shape.

The tubers of *Squamanita* do not fit into these two categories of carpophoroids. They are formed in advance, and not instead, of the basidiocarps. Moreover they develop at a different level from the basidiocarps with regard to the surface of the substrate. The same applies to the tubers of the American *Tricholoma sclerotoideum* described by Morse (1943: 573) and mentioned by Singer (1962: 20) as bodies that perhaps may be considered carpophoroids. In that case the carpophores arise from cheese-like, up to 8 × 12 cm large tubers, which very probably are formed shortly before, and in the same rainy period as, the carpophores. These tubers have no differentiated cortex.

The tubers of *Squamanita* have been called sclerotia by some authors. This seems the right thing to do if one follows Josserand (1952: 99), who defined a sclerotium as a condensation of mycelium of variable size and from which fruit-bodies arise. However, the present author thinks that Snell & Dick's definition (1957: 139) of a sclerotium is more to the point. It runs: "A sclerotium is a resting body of variable size, composed of a hardened mass of hyphae . . ., usually with a darkened rind, from which fruit-bodies, stromata, conidiophores or mycelium may develop." This definition considerably restricts the meaning of the term sclerotium, making it more precise by stressing the relatively long duration of life, the firm consistency, and the usually present cortex. In this way the definition comes closer to that of the classical sclerotium, which is a durable mycelial formation enabling species not only to endure unfavourable periods but also to produce fruit-bodies at the desired moments or to resume growth with great power after improved environmental conditions.

Taken in this sense the term sclerotium is not applicable to the tubers found in the species of *Squamanita* or in *Tricholoma sclerotoideum.* The term "protocarpic tubers" is proposed herewith for these short-lived, relatively soft and fleshy tubers without a true rind and which are able to produce carpophores.

Relationships.—The name *Squamanita* is not a very felicitous one for the present genus. Although some of its species, e.g. *S. tropica,* at first sight resemble certain species of *Amanita* rather closely, there is a very large gap between these two genera. Not only is the bilateral structure of the trama of the gills lacking in *Squamanita,* but also the development and attachment of the gills is completely different, the trama of the stem lacks the typical terminal inflated elements of the stem of *Amanita* and the structure of the cuticle is different.

The structure and attachment of the gills and the kind of basidia in *Squamanita* make it probable that this genus belongs to the Tricholomataceae. In this connection it is significant that Konrad & Maublanc (1948: 345) treated the genus *Squamanita* under its synonym *Coolia* as a section of the genus *Tricholoma!* However, there is hardly any doubt now that *Squamanita* deserves generic rank. Especially the complicated velar structures and the sclerotium on which fruit-bodies as well as typical chlamydospores may be formed are important features. It may be stressed here, that the species of the genus *Tricholoma*, as recently treated by Singer (1962: 246), which most strongly resemble the species of *Squamanita* by the presence of a distinct veil and a scaly cap, such as *T. caligatum* (Viv.) Rick. and *T. focale* (Fr.) Rick., have clampless hyphae (checked in two collections of both species). Reijnders (1952: 33) studied the development of *T. focale* and found the veil of that species to be a reinforced velum partiale, which means that the development of *T. focale* is much simpler than that of *Squamanita odorata* (see p. 352).

The genus *Catathelasma* Lovej. (= *Biannularia* G. Beck) is one of the genera with the most complicated velar structures within the Tricholomataceae. According to Reijnders (1963: 57) *C. imperiale* (Fr. apud Lund) Sing. is bivelangiocarp, which means that there is a velum universale and a velum partiale. The trama of the young gills is divergent but becomes more regular with age. The spores are large, elongate and amyloid. Clamps are present. There are some special points of resemblance to *Squamanita*. Kühner & Romagnesi (1953: 143) mentioned that the brown fibrils of the cuticle continue on the underside of the inner veil, this reminds one very much of the "inner velum universale" of *Squamanita* described above (see p. 354). In the section of a bud depicted by Konrad & Maublanc (1926: pl. 280) it may be observed that the base of the stem is a more or less fusiform bulb and that the inner veil as well as the outer veil are attached to it very closely together and just above its broadest part. On the other hand, the development of *C. imperiale* appears to be widely different from that of *S. odorata*, as the margin of the primordial cap is strongly involute and the gill-room is stuffed with lipsanenchym (Reijnders 1963: pl. 16 fig. 3).

A genus that certainly has to be compared with *Squamanita* is *Floccularia* Pouzar alias *Armillaria* (Fr. ex Fr.) Staude sensu Sing. Its best known representative is *F. luteovirens* (A. & S. ex Fr.) Pouzar. This species has colourless, thin-walled, amyloid spores, a distinct annulus, and a fibrillose-scaly cap and lower part of the stem. Some authors place it in the genus *Amanita* on account of the bilateral trama of the gills. The present author studied a collection of this species kindly sent on loan by Dr. A. H. Smith, Ann Arbor, (Smith 47434, U.S.A., Washington, Mt. Rainier, 1954). In a young specimen, of which the cap had just opened, he found the trama of the gills to be very regular in the central part and only very slightly diverging in a thin layer about one tenth of the width of the gills under the subhymenium (deviation not more than 10°). This is very unlike the structure of the gill in *Amanita*. Moreover, the stem of *F. luteovirens* consists of regular, 4–10 μ wide, longitudinal hyphae. Consequently the genus *Floccularia* is better placed in the Tricholomataceae.

The scales on the cap of *F. luteovirens* consist of broad, irregularly arranged to radial hyphae, constricted at the septa, similar to those on the cap of *Squamanita*, and just as in that genus the scales are not sharply distinct from the cuticle[1] and the

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[1] The present author did not find the cuticle of thin subparallel hyphae mentioned by Singer (1948: 120).

trama underneath. Clamps are abundant. However, a sclerotial bulb is lacking and the only species of *Squamanita* with amyloid spores (*S. scotica*) does not resemble *F. luteovirens* very much. Yet, *Floccularia* is probably more closely related to *Squamanita* than *Catathelasma*. In this connection the fact that the margin of the cap seems to be only slightly incurved in *Floccularia* may be of importance.

Some features of *Squamanita* are reminiscent of the Agaricaceae *sensu stricto*, especially the pseudo-amyloid spores of two species, viz. *S. pearsonii* and *S. paradoxa*. What is more, the last named species bears such a great resemblance to certain species of *Cystoderma*, that it was originally described as belonging to that genus, mainly on account of the chains of spherocysts forming the outer layer of the "outer" universal veil. In addition to this, the fact that *Cystoderma*, like *Squamanita*, is one of the few genera in which species occur with non-amyloid, amyloid, and pseudo-amyloid spores (Singer 1963: 485) and the fact that the yellow-brown pigment in the veil of *S. paradoxa* turns reddish in KOH as in some species of *Cystoderma*, lead one to conclude that there is a close relationship between *Cystoderma* and *Squamanita*. However, in the author's opinion this speaks more for placing *Cystoderma* in the Tricholomataceae, than for placing *Squamanita* in the Agaricaceae. Against the latter arrangement militate the adnate gills, the continuation of the trama of the stem in the trama of the cap, the homomorphous edge of the gills, and the hardly differentiated cuticle. None of these characters on its own is decisive, but together they give a strong indication. On the other hand, the spores of *Squamanita* are probably binucleate (*S. pearsonii*, *S. paradoxa*). This would be a character in favour of placing it in the Agaricaceae (Kühner 1945: 620).

Summarizing, it may be said that the genus *Squamanita* seems to represent one of the more intricately constructed genera of the Tricholomataceae, but that some of its characters suggest relations with the Agaricaceae.

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